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Physiological response of early and late maturity oilseed rape cultivars to drought under two climate conditions

Respuesta fisiológica de cultivares tempranos y tardíos de colza a la sequía en dos condiciones climáticas

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Abstract. Two experiments were performed in 2011-2012 to investigate the response of three oilseed rape cultivars to drought stress, grown under two climate conditions in Iran (cold and hot climates). The experiments were conducted using a randomized complete-block design arranged in split-plot with three replicates. The irrigation treatments (FI: full irrigation; WIF: withholding irrigation at flowering stage, and WIS: withholding irrigation at the silique formation stage until physiological maturity) were allocated to main plots, whereas subplots consisted of the oilseed rape cultivars: early maturating (GKH2005), relatively late maturing (Opera) and late maturing (Okapi). Drought caused a significant reduction in seed number, 1000-seed weight, seed and oil yield, harvest index, relative water content (RWC) and leaf stomatal conductance. Oilseed rape cultivars responded to irrigation treatments in different ways. The maximum seed number per silique in the main stem was observed in Okapi cultivar under WIS, whereas GKH2005 cultivar produced the minimum seed number per silique in the main stem in WIF conditions. There were no significant differences among oilseed rape cultivars in terms of seed yield when grown under full irrigation condition; however, under drought stress conditions, the maximum and minimum seed yields were obtained from GKH2005 and Okapi cultivars, respectively. In general, results suggest that stomatal conductance, RWC and silique number per secondary branches were the most important traits contributing to drought tolerance.

Keywords: Drought stress; Oilseed rape cultivars; Relative water content; Seed yield; Stomatal conductance.

Resumen. Los experimentos se realizaron usando un diseño de bloques completos aleatorizado dispuestos en parcela dividida con tres repeticiones. Los tratamientos de riego (FI: riego completo; WIF: retención de riego en la etapa de floración y SIO: riego por retención en la etapa de formación de silicua hasta la madurez fisiológica) se asignaron a las parcelas principales, mientras que las subparcelas consistieron en tres cultivares de colza: uno de maduración temprana (GKH2005), otro relativamente tardío (Opera), y finalmente otro de maduración tardía (Okapi). La sequía causó una reducción significativa en el número de semillas, peso de 1000 semillas, el rendimiento de semillas y el aceite, el índice de cosecha, contenido relativo de agua (RWC) y la conductancia estomática. Los cultivares de colza respondieron a los tratamientos de riego de diferentes maneras. Se observó un número máximo de semillas por silicua en el tallo principal en el cultivar Okapi bajo WIS, mientras que el cultivar GKH2005 produjo el menor número de semillas por silicua en el tallo principal en condiciones WIF. No hubo diferencias significativas entre los cultivares de colza en términos de rendimiento de semilla cuando se cultivaron bajo condiciones de irrigación completa; sin embargo, bajo condiciones de estrés por sequía, el rendimiento máximo y mínimo de semillas se obtuvieron en los cultivares GKH2005 y Okapi, respectivamente.

Palabras clave: Estrés por sequía; Cultivares de colza; Contenido relativo de agua; Rendimiento de semilla; Conductancia estomática.

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INTRODUCTION

Drought is the most serious stress for global agriculture, approximately affecting 40% of the world's land area (Zhang et al., 2014). Furthermore, climate change is likely to lead to changes in global temperature and precipitations patterns in some parts of the world, which will have a dramatic impact on crop growth and productivity (Trenberth *et al.,* 2014). Thus, there is an urgent need to develop varieties that can maintain optimum yield levels under drought conditions.

Water is one of the major factors affecting plant growth, development and yield, especially in arid and semi-arid regions, where plants are often exposed to periods of water shortage (drought stress). Iran is a vast country with different types of *climates*, where approximately 85% of the land is located in arid, semi-arid or hyper arid regions. It has been reported that annual rainfall, number of rainy-days and monthly rainfall have significantly decreased in the last few decades, in arid and semi-arid areas of Iran (Modarres & da Silva, 2007).

Among the oilseed crops, *Brassica* species are one of the most affected by drought, as these crops are mainly grown in arid and semiarid areas. Oilseed rape growth and seed production have greatly decreased by drought stress. This yield reduction can be reduced by combining water storage and irrigation, crop management and plant breeding approaches (Zhang et al., 2014). Plants respond to drought stress through a number of biochemical, physiological and developmental morphology changes (Morison & Baker, 2007; Shirani Rad & Zandi, 2012; Jabbari et al., 2013). Adaptation to drought is definitely one of the most complex biological processes, which include numerous alterations such as reduced growth, up or down-regulation of specific genes, transient increases in ABA levels, build-up of compatible solutes and protective enzymes, enhanced levels of antioxidants and inhibition of energy-consuming pathways (Salekdeh *et al.*, 2009). Drought tolerance is a complex trait, thus assessment of the degree of drought tolerance of different genotypes is critical. Since plants' physiological responses to drought stress may vary at different developmental stages, it has been considered that different indicators should be used to recognize the phenotype in drought tolerance studies (Tuberosa, 2012). Moreover, recent studies have indicated that the responses of different varieties to drought stress were diverse (Jabbari et al., 2013; Shekari et al., 2015; Jabbari et al., 2016). Those varieties with higher drought stress-tolerance showed higher water use efficiency, lower reduction in dry matter accumulation and grain yield, and greater quality stability.

Several techniques and parameters such as leaf water potential, leaf osmotic potential, RWC, SPAD value and stomatal conductance (SC) are widely used to screen drought tolerant plants including oilseed rape (Fanaei et al., 2009; Ghasemyan & Shirani Rad, 2012; Shekari et al., 2015; Jabbari et al., 2016). In this context, Shekari et al. (2015) reported that high RWC in oilseed rape leaves was maintained in Cobra (*Brassica napus* L. cv. Cobra) genotype by stomata closure. The studies on drought stress tolerance in *Brassica* species have revealed that genotypic variation plays a key role in plants water status, as a measure of tolerance to be positively correlated with yield (Fanaei et al., 2009; Habibi, 2014; Jabbari et al., 2016). Jabbari et al. (2016) reported that five cultivars of *Brassica napus* L. showed different responses to irrigation treatments for SC, SPAD value, root length and diameter, morphologic characteristics, yield and yield components. Higher seed yield under drought stress conditions was due to higher rooting depth and root diameter in tolerant oilseed rape cultivars (Jabbari et al., 2016).

Oilseed rape having different and early maturity cultivars, higher seed oil percentage than other oilseeds, capacity for using autumn and winter rainfall, high water use efficiency, and relative tolerance to drought (Albarak, 2006) is an appropriate crop for cultivation in arid and semi-arid regions of Iran, compared to other crops.

The primary objective of this research was to study the effect of drought stress on seed yield and physiological traits of different oilseed rape cultivars, grown in different regions of Iran. Specifically, the main aims of our study were (1) to determine selected cultivars which might be drought-stress tolerant, and (2) to investigate the relationship between seed yield, and physiological and agronomical traits on early, relatively late, and late maturing oilseed rape cultivars.

MATERIALS AND METHODS

Study site and general methodology. The experiments were conducted during the 2011-2012 growing seasons at the research center farm of Yazd, Iran (31° 55′ N, 54° 16′ E and 1230 masl) and at the Shahriyar research station, Shahriyar, Iran (35° 39′ N, 51° 03′ E and 1024 masl). The Yazd region is characterized by having a hot climate (BWh by Köppen-Geiger climate classification system), with an average annual rainfall of only 60 mm. The average annual temperature is 20.0 °C in Yazd. The Shahriyar region is characterized by having cold climates (BSk by the Köppen-Geiger climate classification system) with relatively warm summers and cold winters. The average annual temperature is 17.8 °C, and the average annual rainfall is 220 mm. Daily meteorological data on precipitation and air temperature were obtained from the nearest weather station and are displayed in Fig. 1. Before planting at both regions, several soil samples were taken at depths of 0-30 cm, composite samples were collected, air-dried, crushed, and tested for physical and chemical properties (Table 1).

Land preparation, establishing the treatments and planting. Oilseed rape was planted following wheat in Yazd and Shahriyar. The field was prepared by shallow plowing, followed by disking in September and October. Weeds were controlled by applying trifluralin (2.5 liters/ha) and then in-

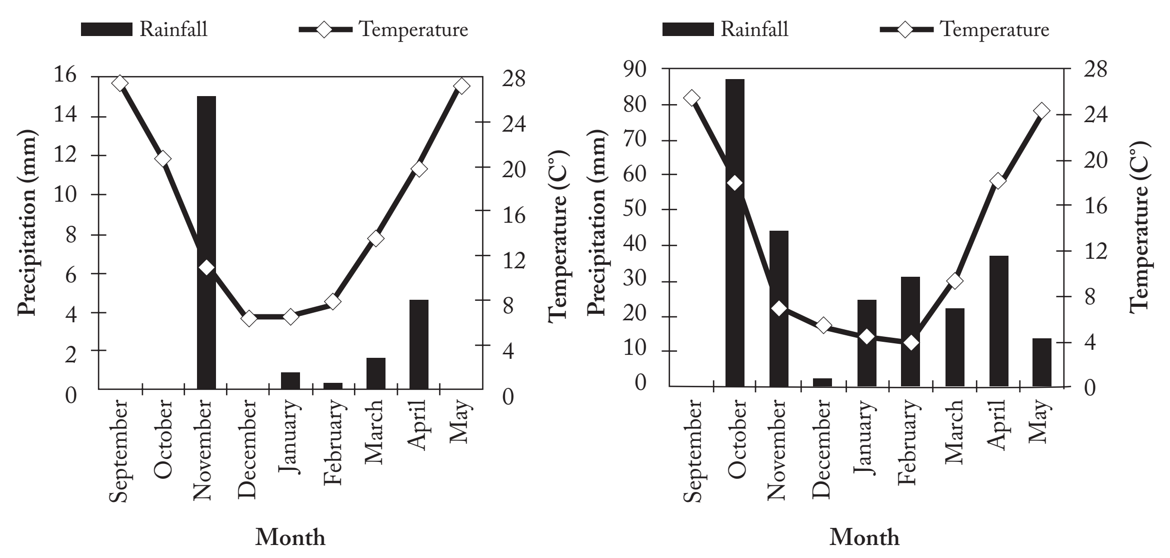

Fig. 1. Monthly temperature and precipitation during the growing season in 2011-2012 at Shahriyar (right) and Yazd (left) regions. Note the change in scale for rainfall.

Fig. 1. Temperatura y precipitación mensuales durante la estación de crecimiento en 2011-2012 en las regiones Sahriyar (derecha) y Yazd (izquierda). Notar el cambio de escala para lluvia entre los paneles.

Table 1. Soil physical and chemical properties at the experimental site (Yazd as hot and Shahriyar as cold climate) for 2011-2012.

Tabla 1. Propiedades físicas y químicas del suelo en el sitio experimental (Yazd con un clima cálido y Shahriyar con un clima frío) durante 2011-2012.

Location	Depth of sampling	EC (ds/m)	pH	Total Nitrogen (%)	Available Phosphorus (ppm)	Available Potassium (ppm)	Sand	Silt	Clay	Soil texture
								(%)		
Yazd	0-30	3.88	7.8	0.014	5.02	107.9	64.2	10.8	25	Sandy clay loam
Shahriyar	0-30	1.18	7.2	0.11	12.50	275.0	45	34	21	Loam

corporating it into the soil using a disk. Each experimental unit was 5 m long, and consisted of 6 rows spaced 0.3 m apart. There were 2 m gaps between the blocks, and a 1 m alley was established between each plot to prevent lateral water movement and other interferences. The experiment was conducted using a randomized complete-block design with a split-plot arrangement of treatments and three replicates. The main plot treatment was irrigation, which was defined with respect to withholding irrigation [FI: full irrigation (control), WIF: withholding irrigation after flowering stage, and WIS: withholding irrigation after silique formation stage]. The subplots consisted of three oilseed rape cultivars (GKH2005 as an early maturing, Opera as a relatively late maturing, and Okapi as a late maturing cultivar) (Table 2).

Chemical N fertilizer was divided into three equal amounts and applied at three stages: sowing, stem elongation and initiation of flowering. Potassium and phosphorus fertilizers were applied at sowing time. Oilseed rape cultivars were sown by hand at depths of 3 cm on 23 October at both regions.

Table 2. Name and origin of oilseed rape cultivars tested in this experiment.

Tabla 2. Nombre y origen de los cultivares de colza ensayados en este experimento en dos lugares, Irán.

Number	Cultivar names	Origin	Growth type
1	GKH2005	Hungary	Winter (early maturing)
2	Opera	Sweden	Winter (relatively late maturing)
3	Okapi	France	Winter (late maturing)

To ensure good emergence, the experimental plots were overseeded and then thinned (to 5 cm spacing) to achieve the recommended plant density of 670000 plants/ha at the two-leaf stage. Immediately after sowing, the soil was irrigated. Irrigation scheduling was determined according to daily changes of soil water content (ΔSW) at the depth of root development. A deficit approach was used to estimate irrigation requirements: soil water content at field capacity (FC) was defined as no drought stress. Available water was determined by the difference between the water content at field capacity and permanent wilting point (PWP) and measured by weighting of soil sampling method. Under full irrigation treatment and also before the initiation of the drought stress treatments (WIF and WIS treatments), irrigation was applied similarly in all plots when 40% of the available water had been consumed at the depth of root development. The frequencies of per irrigation treatment in each region are shown in Table 3. Also, the changing trend of soil moisture content under each irrigation treatment in Yazd and Shahriyar regions is shown in Figures 2 and 3, separately. *Brevicoryne brassicae* was controlled by applying Metasystox (1.5 liters/ha) and *Epicometis hirta* was removed by hand.

Plant measurements. After the onset of irrigation treatments, RWC of leaves was calculated (Pask et al., 2012). To measure RWC, three leaves from each plot were weighed (fresh weight, FW) immediately after being harvested from the plants. The same tissues were then placed in a vial of distilled water for 24 h at 5 °C (in darkness). Thereafter, their turgid weights (TW) were measured. The samples were then dried in an oven at 70 °C for 48 h to obtain their dry weights (DW). Relative water contents were calculated by the following equation:

$$\text{RWC}\ (\%) = (\text{FW} - \text{DW}) / (\text{TW} - \text{DW}) \times 100 \qquad (1)$$

In addition, the stomatal conductance was measured with a porometer device (Delta-T AP_4, Delta-T Devices, Cambridge, UK) after the beginning of the irrigation treatments at 8-day-intervals. Relative water content and stomatal conductance were measured in Yazd region.

Seven plants were harvested from each plot to determine morphological traits (including plant height, silique number per main stem and silique number per secondary branch) and

Table 3. Frequency and amounts of water in each irrigation treatments at two locations (Yazd as hot and Shahriyar as cold climate).
Tabla 3. Frecuencia de riego en cada uno de los tratamientos de riego en dos lugares (Yazd desierto cálido y Shahriyar clima semi-árido frío).

Treatments Locations	Irrigation frequency		
	Full irrigation	WIF treatment	WIS treatment
Yazd	12	8	10
Shahriyar	9	5	7
Treatments **Locations**	**Amounts of water (m^3 / ha)**		
	Full irrigation	WIF treatment	WIS treatment
Yazd	6600	4400	5500
Shahriyar	4950	2750	3850

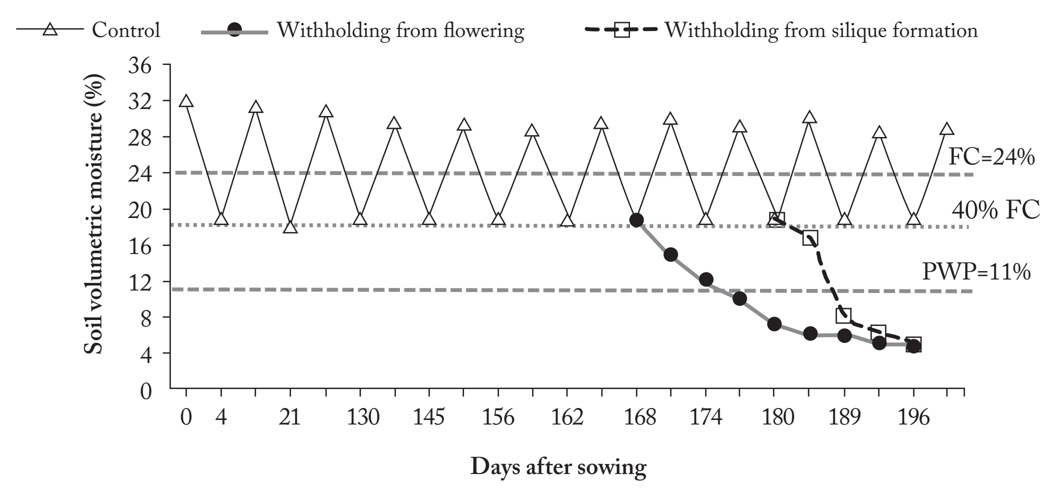

Fig. 2. Changing trend of soil moisture content under each irrigation treatment in Yazd region (hot desert climates).
Fig. 2. Cambio de tendencia del contenido de humedad del suelo bajo cada tratamiento de riego en la región de Yazd (clima cálido del desierto).

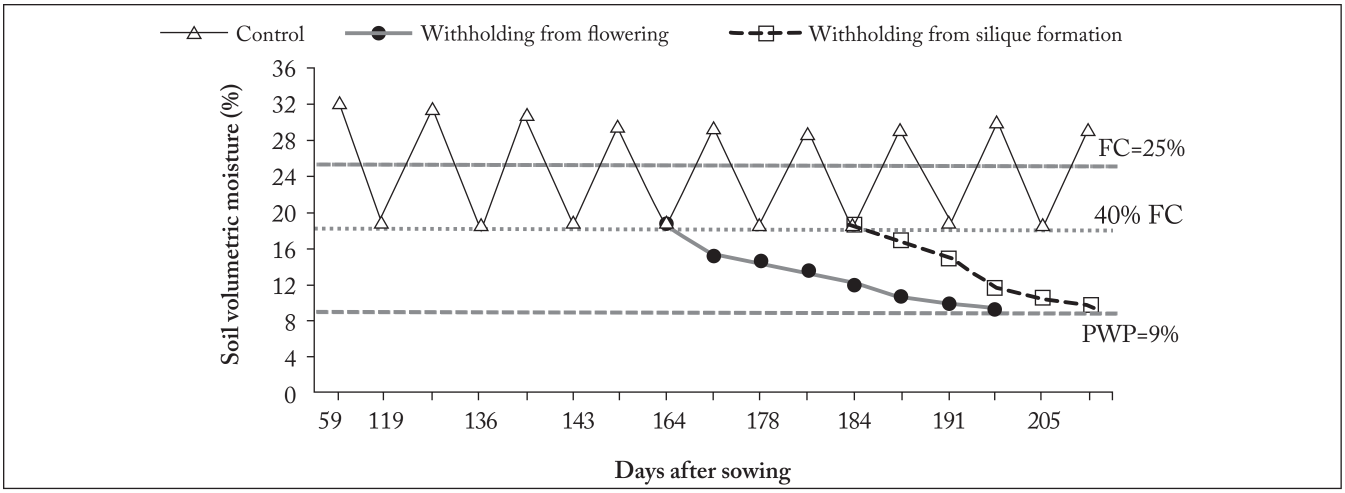

Fig. 3. Changing trend of soil moisture content under each irrigation treatment in Shahriyar region (cold semi-arid climates).
Fig. 3. Cambio de tendencia del contenido de humedad del suelo bajo cada tratamiento de riego en la región Shahriyar (clima frío semiárido).

yield components (including silique number per plant, seed number per silique and 1000-seed-weight). At the physiological maturity stage, 4.8 m^2 of each plot were hand-harvested to measure dry matter and seed yield. Harvest index (HI) was determined as the ratio of seed yield to above ground biomass. The oil percentage of the seeds was determined using a nuclear magnetic resonance device (NMR, Mq20). Also, oil yield was estimated by multiplying seed oil percentage by seed yield.

Statistical analysis of data. All data were subjected to analysis of variance (ANOVA) using SAS software (SAS Institute, 2002). The Bartlett test showed homogeneity in the variance of all traits in both regions. Probabilities of significance ($P \leq 0.01$ or 0.05) were used to test the significance among the main treatment effects and interactions. When an *F*-test indicated statistical significance, the protected least significant difference (FLSD) was used to separate the means of the main effects, and the significant interaction effects were separated by slicing method.

RESULTS

Agronomic traits. The maximum growth duration (GD) was found in the full irrigation treatment (206 days) and drought stress treatments (WIF and WIS treatments) reduced GD by 2.9 and 5.6%, respectively, compared to control (Table 5). The results indicated that GD decreased due to drought stress in all of the three oilseed rape cultivars; however, this reduction was not the same in all cultivars (Table 6). The maximum GD was observed in Okapi cultivar grown under full irrigation. The GKH2005 cultivar, an early maturing cultivar, showed the minimum GD under different ir-

Table 4. Mean comparison of morphological and agronomical traits of the studied oilseed rape cultivars at two locations (Yazd and Shahriyar).
Tabla 4. Comparación de medias de las características morfológicas y agronómicas de cultivares de colza estudiados en dos lugares (Yazd y Shahriyar).

Locations	**GD**†**(days)**	**PH (cm)**	**SNM**	**SNB**	**SLM (cm)**	**SLB (cm)**
	ns††	**	**	**	**	*
Yazd	200.6	122.7	38	79	7.6	6.1
Shahriyar	200.4	129.3	65	162	6.8	6.5
Locations	**SNSM**	**SNSB**	**SW (g)**	**SY (kg/ha)**	**HI (%)**	**OY (kg/ha)**
	**	**	**	**	*	**
Yazd	26	19	2.9	1829	23.0	795
Shahriyar	24	21	3.7	2110	24.6	927

†GD= Growth duration, PH = Plant height, SNM = Silique number on main stem, SNB = Silique number on secondary branch, SLM = Silique length on main stem, SLB = Silique length on secondary branch, SNSM = Seed number in silique per main stem, SNSB = Seed number in secondary branch, SW = 1000 seed weight, SY = Seed yield, HI = Harvest Index, OY = Oil yield.
††(ns) No significant differences, (** & *): significant difference at 1% and 5% level, respectively.

Table 5. Effect of irrigation and cultivar treatments on some morphological and agronomical traits of oilseed rape.
Tabla 5. Efecto del tratamiento de riego y cultivares en algunos rasgos morfológicos y agronómicos de los cultivares de colza.

Treatment	**GD[†](days)**	**PH (cm)**	**SNM**	**SNB**	**SLM (cm)**	**SLB (cm)**	**SNSM**
	**[††]	**	**	**	ns	**	**
Irrigation							
Full irrigation	206.3 a[†††]	129.9 a	61.8 a	155.6 a	7.53 a	6.93 a	27.3 a
WIF treatment	200.3 b	120.3 b	40.7 c	93.3 c	6.95 a	5.93 b	20.2 c
WIS treatment	194.7 c	127.7 a	52.6 b	113.4 b	7.07 a	5.96 b	25.1 b
LSD	**0.815**	**3.201**	**3.300**	**7.075**	**0.631**	**0.406**	**1.23**

Treatment	**SNSB**	**SW (g)**	**SY (kg/ha)**	**HI (%)**	**OY (kg/ha)**
	**	**	*	**	**
Irrigation					
Full irrigation	25.04 a	3.70 a	2620 a	24.9 a	1157 a
WIF treatment	17.08 b	3.19 b	1309 c	22.3 b	562 c
WIS treatment	22.13 a	3.01 b	1980 b	24.1 a	864 b
LSD	**3.086**	**0.216**	**172**	**1.44**	**110**

Treatment	**GD[†](days)**	**PH (cm)**	**SNM**	**SNB**	**SLM (cm)**	**SLB (cm)**	**SNSM**
	**	**	**	**	ns	*	**
Cultivars							
GKH 2005	197.5 c	125.3 b	54.6 a	156.7 a	7.37 a	6.59 a	25.3 a
Opera	201.2 b	123.5 b	52.4 a	97.6 c	7.23 ab	6.25 ab	22.7 b
Okapi	202.7 a	129.1 a	48.1 b	108.2 b	6.94 b	5.98 b	24.6 a
LSD	**0.719**	**2.44**	**3.4**	**7.7**	**0.36**	**0.46**	**1.33**

Treatment	SNSB	SW (g)	SY (kg/ha)	HI (%)	OY (kg/ha)
Cultivars	**	Ns	**	**	**
GKH 2005	22.10 a	3.34 ns	2208 a	25.1 a	954 a
Opera	20.00 b	3.39 ns	1895 b	24.1 a	819 b
Okapi	22.16 a	3.17 ns	1805 b	22.2 b	809 b
LSD	**1.21**	**0.26**	**136**	**1.3**	**72**

[†] GD= Growth duration, PH = Plant height, SNM = Silique number on main stem, SNB = Silique number on secondary branch, SLM = Silique length on main stem, SLB = Silique length on secondary branch, SNSM = Seed number in silique per main stem, SNSB = Seed number in secondary branch, SW = 1000 seed weight, SY = Seed yield, HI = Harvest Index, OY = Oil yield.

[††] (ns) No significant differences, (** & *): significant difference at 1% and 5% level, respectively.

[†††] Mean values of the same category followed by different letters are significant at P≤0.05 level.

rigation treatments (Table 6). In other words, although GD decreased in all cultivars exposed to drought stress, this reduction was more pronounced in GKH2005 than in Okapi or Opera cultivars.

Means comparison of plant height (PH) indicated that average PH in cold climate on Shahriyar was much higher than that observed on hot climate for Yazd (Table 4). There was no significant difference between full irrigation and WIS treatments in terms of PH (Table 5). Assessment of PH revealed that the highest and shortest plants were determined on Okapi, a late maturing cultivar, grown under full irrigation, and GKH2005, an early maturing cultivar, grown under drought stress, respectively (Table 6).

The maximum silique number on main (SNM) and secondary branches (SNB) was related to cold climate in Shahriyar (Table 4). The SNM and SNB were 38 and 79 in hot climate in Yazd, and 65 and 162 in cold climate in Shahriyar, respectively (Table 4). In addition, WIF and WIS treatments decreased total silique number by 38 and 24% compared with the full irrigation treatment, respectively (Table 5). Results indicated that the GKH2005 cultivar produced the maximum main branch's silique number under full irrigation and drought

Table 6. Means comparison of morphological and agronomical traits of the studied oilseed rape cultivars under different irrigation treatments (by slicing).

Tabla 6. Comparación de medias de las características morfológicas y agronómicas de las variedades de colza estudiadas bajo diferentes tratamientos de riego (por corte).

	GD[†](days)			**PH (cm)**		
Irrigation / **Cultivar**	**Full irrigation**	**WIF treatment**	**WIS treatment**	**Full irrigation**	**WIF treatment**	**WIS treatment**
GKH 2005	202.8 b[††]	197.0 b	192.6 b	125.9 b	118.8ab	131.3 a
Opera	208.1 a	201.6 a	193.6 b	131.2ab	118.1 b	121.1 b
Okapi	208.1 a	202.3 a	197.8 a	132.8 a	123.8 a	130.8 a
LSD	**0.51**	**1.59**	**1.62**	**5.48**	**5.22**	**3.64**

	SNB			**SNM**		
Irrigation / **Cultivar**	**Full irrigation**	**WIF treatment**	**WIS treatment**	**Full irrigation**	**WIF treatment**	**WIS treatment**
GKH 2005	61.5 b	48.2 a	54.1 a	175.2 a	139.6 a	155.1 a
Opera	68.6 a	38.5 b	50.2 a	136.1 c	66.4 b	90.1 b
Okapi	55.4 c	35.4 b	53.5 a	155.6 b	73.8 b	95.1 b
LSD	**5.3**	**6.7**	**6.2**	**13.7**	**17.7**	**6.7**

	SNSM			**SY (kg/ha)**		
Irrigation / **Cultivar**	**Full irrigation**	**WIF treatment**	**WIS treatment**	**Full irrigation**	**WIF treatment**	**WIS treatment**
GKH 2005	27.4 a	23.5 a	24.9 b	2729 ns	1591 a	2305 a
Opera	25.9 b	18.2 b	23.9 b	2686 ns	1176 b	1824 b
Okapi	28.7 a	18.8 b	26.4 a	2445 ns	1161 b	1811 b
LSD	**1.7**	**3.4**	**1.3**	**384**	**179**	**183**

[†] GD = Growth duration, PH = Plant height, SNM = Silique number on main stem, SNB = Silique number on secondary branch, SNSM = Seed number in silique per main stem, SY = Seed yield.

[††] Mean values of the same category followed by different letters are significant at $P \leq 0.05$ level.

stress conditions (Table 6). Moreover, although there was a negligible difference between oilseed rape cultivars in terms of SNM, GKH2005 cultivar produced significantly and noticeably higher SNB than Okapi and Opera (Table 5 and 6).

Silique length on main stem (SLM) decreased from 7.6 cm under hot climate in Yazd to 6.8 cm in cold climate in Shahriyar (Table 4). By contrast, silique length on secondary branch (SLB) in Shahriyar was 1.6 cm higher than that in Yazd (Table 4). The longest (6.59 cm) and shortest (5.98 cm) silique on secondary branches were observed on GKH2005 and Okapi cultivars, respectively (Table 5). The Opera cultivar showed intermediate values in terms of silique length (Table 5).

Maximum seed number in silique per main stem (SNSM) and secondary branches (SNSB) was related to Yazd regions. According to the results, SNSM and SNSB decreased from 26 and 24 in Yazd region to 22 and 19 in Shahriyar region, respectively. In both experiments, a significant and direct correlation between the SLM and SNSM was observed in Yazd (0.64**), and Shahriyar regions (0.60**) ($P<0.001$).

Under full irrigation and WIS treatments, the maximum SNSM was observed on Okapi cultivar, whereas the GKH2005 cultivar produced the least SNSM when irrigation was terminated at the flowering stage (Table 6). Although SNSM was significantly affected by irrigation treatments, SNSB was not affected by irrigation treatments (Table 5). It seems that an inverse relationship between silique number and seed number was responsible for these results. A significant and negative correlation was observed between the SNSM and SNM in Yazd (-0.58*) and Shahriyar (-0.54**) ($P<0.001$), and between SNSB and SNB (-0.69** and -0.58**, in Yazd and Shahriyar, respectively; $P<0.001$).

The maximum 1000-seed weight (3.70 g) was achieved at the full irrigation treatment (Table5). WIF and WIS treatments decreased SW by 13.8 and 18.6%, respectively, when compared with the control treatment (Table 5).

The average seed yield (SY) and harvest index (HI) in Shahriyar region were significantly higher than those in Yazd region (Table 4). There was no significant difference among

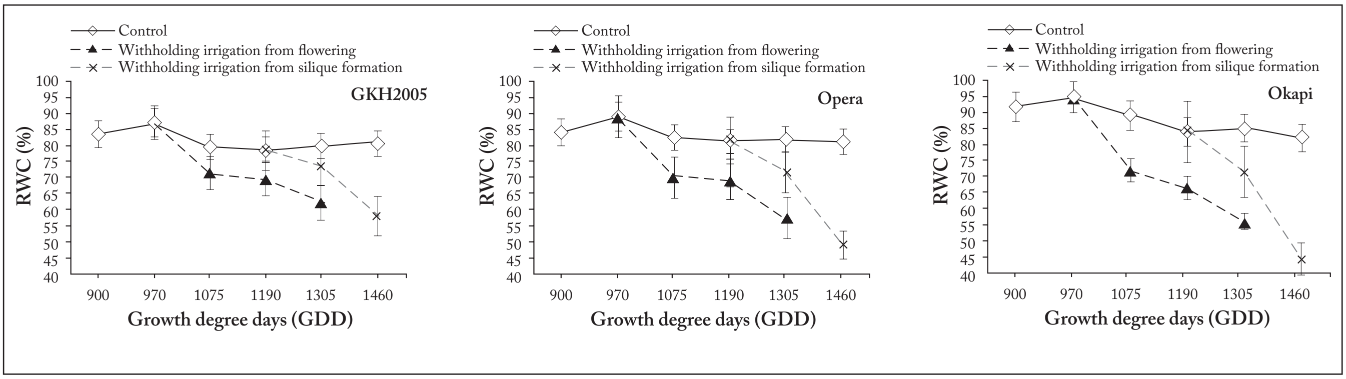

Fig. 4. Effect of irrigation treatments on relative water content (RWC) of three oilseed rape cultivars. Vertical bars indicate standard error (n=9).
Fig. 4. Efecto de los tratamientos de riego en el contenido relativo de agua (RWC) de tres cultivares de colza. Las barras verticales indican error estándar (n=9).

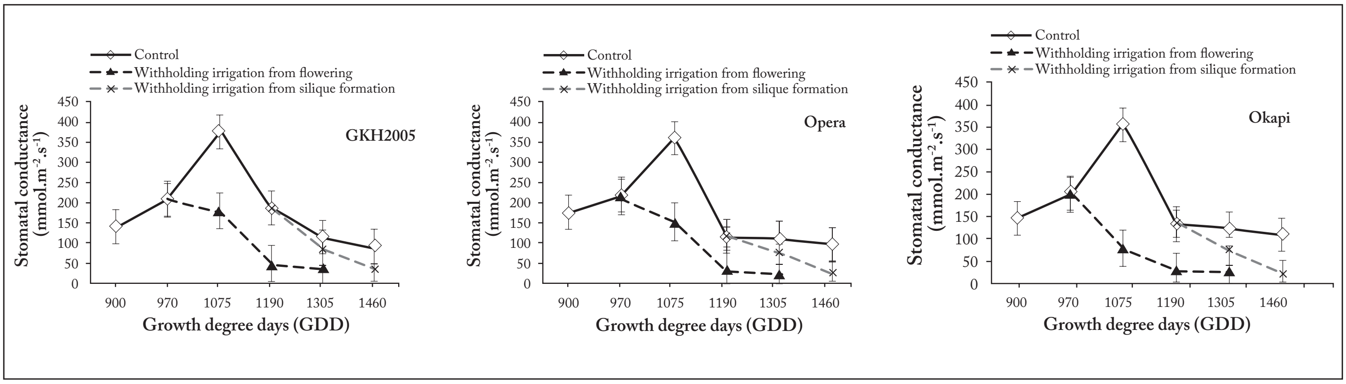

Fig. 5. Effect of irrigation treatments on stomatal conductance (SC) of three oilseed rape cultivars. Vertical bars indicate standard error (n=9).
Fig. 5. Efecto de los tratamientos de riego en la conductancia estomática (SC) de tres cultivares de colza. Las barras verticales indican el error estándar (n=9).

oilseed rape cultivars grown under full irrigation conditions in terms of SY. However, at the end of the irrigation treatments, the maximum and minimum SY were obtained on the GKH2005 and Okapi cultivars, respectively (Table 6). Among the irrigation treatments, the lower HI was observed in the WIF (22%) treatment (Table 6). A significant and direct correlation between the seed yield and yield components was observed as follows: SY and SNM 0.78** and 0.80**, in Yazd and Shahriyar, respectively; SY and SNB 0.79** and 0.90**, in Yazd and Shahriyar, respectively; SY and SLM 0.66** in Yazd; SY and SLB 0.80** in Yazd; SY and SNSM 0.74** and 0.43* in Yazd and Shahriyar, respectively; SY and SNSB 0.88** and 0.51** in Yazd and Shahriyar, respectively; SY and SW 0.72** in Yazd). In addition, in both experiments it was observed a positive correlation between the SY and HI (0.76** and 0.72**, in Yazd and Shahriyar, respectively; $P<0.001$).

The maximum oil yield (OY) was observed in the full irrigation treatment, and drought stress significantly reduced OY (Table 5). In addition, there was no significant difference between drought stress treatments related to oil yield (Table 5). A significant and positive correlation occurred between OY and SY in both experiments (0.99** and 0.97**, in Yazd and Shahriyar, respectively; $P<0.001$). The maximum OY (954 kg/ha) was related to the GKH2005 cultivar, an early maturing cultivar which also produced the maximum SY (Table 5).

Water relations. Drought stress treatments significantly decreased relative water content (RWC) in all the cultivars compared with the full irrigation treatment (Fig. 4); however, this reduction was different among the cultivars. The highest and lowest RWC were observed when drought stress was imposed on Okapi and GKH2005 cultivars, respectively. The maximum RWC reduction (36%) was observed on the Okapi cultivar after 160 days from emergence, when irrigation was withheld from the flowering stage (WIF treatment). By contrast, the minimum reduction (11%) occurred in the GKH2005 cultivar (Fig. 4). Furthermore, the maximum and minimum RWCs were observed in the GKH2005 and Okapi cultivars, respectively, when irrigation was withheld from the silique formation stage (WIS treatment) (Fig. 4). Positive correlations occurred between RWC and SY (0.85**), as well as RWC and SNB (0.87**) ($P<0.001$).

Changes of stomatal conductance (SC) on the three oilseed rape cultivars grown under different irrigation treatments are shown in Fig. 5. The maximum SC was shown on the GKH2005 cultivar grown under full irrigation condition (375 mmol/m^2/s at 168 day after emergence). Although drought stress noticeably decreased SC in all cultivars, different cultivars responded to drought stress in different ways (Fig. 5). Under drought stress conditions, the maximum SC was observed on the GKH2005 cultivar (Fig. 5). Direct correlations occurred between SC and RWC (0.94**), as well as SC and SY (0.87**) ($P<0.001$).

DISCUSSION

In this study, we evaluated the response of early and late maturity oilseed rape cultivars to drought stress under two different climate conditions (cold or hot climates). For most of the traits evaluated in this study (including PH, SNM, SNB, SLB, SNSB, SW, SY, HI and OY), cold climate in Shahriyar had higher mean values than hot climate in Yazd (Table 4). This may be due to more favorable growth conditions, especially during April and May, months which coincide with flowering and silique formation stages in Shahriyar compared with Yazd region (Fig. 1). Moreover, the soil of Yazd region was much poorer than that in Shahriyar (Table 1), and this factor might have influenced in addition to rainfall and temperature.

In contrast, SLM and SNSM were significantly higher in Yazd than Shahriyar (Table 4). Longer silique on main stem in hot climate of Yazd may be due to a lower number of SNM, which causes more assimilate transfer to each sink. On the other hand, smaller silique on secondary branches (SLB) in Yazd region compared with Shahriyar (Table 4) may be due to water shortage in the soil because of lower rainfall, and subsequently more competition for assimilates among the siliques located on secondary branches. In addition, shorter siliques formed on the main stem in the Shahriyar region could be a major reason for a lower SNSM (Table 4).

Also, the results revealed that WIS treatment (irrigation until the silique formation stage) could reduce GD more than WIF treatment (irrigation until the flowering stage) (Table 5). This might be due to this fact that silique formation stage is closer to physiological maturity stage. Generally, reduction in GD in response to drought stress is known as a phenological mechanism by which plants hasten to complete their life cycles before the onset of a severe drought. The role of phenological mechanisms in escaping from drought has been investigated by Berger et al. (2006). In addition, the results indicate that early maturing oilseed rape cultivars are more capable to escape from drought than late maturing cultivars.

Drought stress, especially the WIS treatment, had no significant effect on PH compared with full irrigation (Table 5). This is due to reduced vegetative growth from silique formation stage, as the plants allocate increasingly greater proportions of assimilates to reproductive organs such as flowers and siliques. Generally, late maturing cultivars are taller than early maturing cultivars as stem elongation would continue until flowering stage; however, genetic potential of the cultivars should be taken into account. Reduction in PH on account of drought stress has been previously reported by Jabbari et al. (2013).

The reduction in silique number under drought stress conditions is mainly due to a decline in pollination and flower abortion which are possibly a consequence of a reduced photosynthetic supply. It has been reported that the reduction in silique number under stressful conditions is related to flower and silique abortion rather than a reduction in flower production (Faraji et al., 2009). Moreover, the results showed that drought stress, especially after the flowering stage, has a greater effect on secondary branch's silique number in comparison to those on the main stem. The reason can be attributed to flowering order in the main stem and secondary branches. Main stem flowering was less affected by withholding irrigation at the flowering stage. This was because at this stage, there was still some available water stored at deep layers of the soil that plants could absorb. Although there was a negligible difference between oilseed rape cultivars in terms of SNM, GKH2005 cultivar produced the maximum SNM compared with Okapi and Opera (Table 5 and 6). Since SNM play a key role in determining seed yield, the benefit of early maturing cultivars is considerable, especially under drought stress conditions (Table 6).

In oilseed rape, siliques are photosynthetically active organs so that their photosynthesis strongly affect seed yield by affecting seed weight (Ma et al., 2001). In this study, differences between the cultivars in terms of silique length come from differences in genetic background. The difference in silique length has been previously reported by Hoseinzadeh et al. (2010) who compared Opera, Okapi and Zarfam cultivars. In this study, drought stress (WIF and WIS treatments) significantly decreased silique length in the primary branch but not in the main stem (Table 5). In oilseed rape, most of the siliques on the main stem form in the middle of the flowering stage, so there will be still some available moisture after withholding irrigation at this stage. This will help siliques to grow and reach their potential length. By contrast, siliques on secondary branches form a bit later, which coincidences with soil water shortage; therefore, siliques' growth would be limited.

In late maturing cultivars (i.e., Okapi), drought stress (especially in the WIF treatment) reduces the leaf activity period by accelerating leaf senescence and reducing net photosynthetic rate. This in turn leads to increasing pollen sterility, seed abortion and finally reduced seed number on siliques. On the contrary, in early maturing cultivars (i.e., GKH2005), the plants generally exhibit a degree of phenological plasticity, and escape from drought periods through completing their life cycle before drought stress becomes severe. The results obtained in this study are in agreement with those reported by Bitarafan & Shirani Rad (2012).

Our results showed that the effect of the WIS treatment on SW was more pronounced than that of the WIF treatment (Table 5). Withholding irrigation from the flowering stage (WIF treatment) decreased SW through reducing net photosynthetic rate and photosynthates production. However, reduction in sink size (seed size) due to the WIS treatment was more likely due to increased leaf senescence, reduced leaf area duration and disruption in assimilate transfer into the seeds. The current results mirror those reported by Bitarafan & Shirani Rad (2012) who studied seed weight changes in response to withholding irrigation in oilseed rape.

Among the oilseed rape cultivars, the GKH2005 cultivar resulted in lower yield loss under drought stress conditions through rapid completion of its life cycle, escaping from drought thus allocating its photosynthates to sinks (i.e., siliques and seeds) (Tables 5 and 6). Early maturing cultivars are able to escape from drought periods by completing their life cycle before the harshest conditions set in. Furthermore, higher SY of GKH2005 was due to maximum SNB in compared to others, especially under drought stress conditions. In this study, among yield components in both regions, SNB had the highest correlation with seed yield which indicates the importance of this trait on seed yield of oilseed rape.

The least HI (14.5%) was related to the WIF treatment (Table 5). By contrast, the WIS treatment did not affect photosynthate allocation to the seed, and subsequently HI (Table 5). According to the results it can be concluded that the negative effect of withholding irrigation from the flowering stage was more pronounced on SY rather than on dry matter accumulation, which resulted in a severe HI reduction. It should be kept in mind that on indeterminate plants (like oilseed rape), (1) there is a competition between vegetative and reproductive organs for the assimilates produced, and (2) drought stress whether during the flowering or silique formation stage would affect photosynthate allocation between vegetative and reproductive organs (Sinaki et al., 2007). Considering the differences among oilseed rape cultivars, it seems that those cultivars that have a greater ability to allocate more photosynthates to economic parts (siliques and seeds in oilseed rape) will be able to produce more consistent yields and HI under drought stress conditions.

Oil yield reflects not only the seed but also the production quantity. Thus, in this paper, the oil yield was considered instead of the seed oil content. In this study, although drought stress had no significant effects on seed oil percentage (data not shown), OY was considerably affected by drought stress (Table 5). It means that the seed oil percentage is mainly controlled by genetic factors, whereas OY is a function of the genotype, seed yield and slightly on the seed oil percentage. Results revealed that in both regions, a significant and positive correlation occurred between OY and SY. Therefore, the maximum OY was related to the GKH2005 cultivar, an early maturing cultivar which also produced the maximum SY (Table 5).

RWC is one of the physiological features affecting plant growth so that higher amounts of it are necessary for continuation of growth, especially under drought stress conditions. RWC correlates with stomatal conductance: stomatal conductance decreases with a reduction in RWC, reflecting the reduction on the CO_2 supply and photosynthetic rate (Mailer et al., 2002). In this study, irrespective of the timing of withholding irrigation, RWC decreased smoothly in the GKH2005 cultivar, whereas RWC dropped dramatically in the Opera and Okapi cultivars, under drought stress (Fig. 4). For instance, the WIS treatment (192 days after emergence) decreased RWC in the GKH2005 cultivars from 81% (under full irrigation treatment) to 58% (Fig. 4). This reduction in RWC was from 81 to 49% in Opera, and 81 to 45% in Okapi cultivars (Fig. 4). In other words, GKH2005 was more successful in conserving leaf water content in comparison to other cultivars. It has been reported that higher RWC in drought tolerant cultivars might be due to some biochemical and physiological mechanisms such as osmolyte biosynthesis and stomatal closure during drought periods (Jiang & Huang, 2001). The current results confirm those found by Gunasekera et al. (2004) in oilseed rape.

Stomatal conductance (SC), as a plant physiological trait, is controlled by evapotranspiration and subsequently dry matter production depends on SC (Mujdeci et al., 2011). In this study, the reduction in SC in the GKH2005 cultivar was found to be less than that in the Opera and Okapi cultivars (Fig. 5). For example, in comparison with the full irrigation treatment, SC decreased by 56, 77 and 78% in the GKH2005, Opera and Okapi cultivars, respectively, due to withholding irrigation from the flowering stage (Fig. 5). Similar results have been found when irrigation was terminated from the silique formation stage (Fig. 5). Reduction in SC in oilseed rape plants grown under drought stress conditions has been reported by Wang et al. (2005). These authors stated that reductions in SC are a primary response to drought stress, and it is derived from abscisic acid accumulation in leaves. Chavez et al. (2002) reported that stomatal closure is a drought avoidance mechanism by which plants attempt to conserve moisture. Stomatal opening is controlled by the turgor of guard cells, which is presumably controlled by the local water relations. Thereafter, reductions in RWC should cause reductions in SC and transpiration. In the current study, the GKH2005 cultivar not only showed the maximum RWC but also the maximum SC.

In general and according to the results, although drought stress could affect oilseed rape growth and production, the maximum effect was related to withholding irrigation from the flowering stage. From the results, higher RWC and SC play a crucial role in increasing drought stress tolerance in oilseed rape. In addition, the results revealed that silique number, especially on branches, is the most important yield component affecting final seed yields in oilseed rape grown under drought stress conditions. The GKH2005 as an early maturing cultivar, showed a higher RWC and SC in comparison with the other cultivars, and therefore was less affected by drought stress. Moreover, the GKH2005 cultivar produced the maximum silique number on the main stem and branches, seed number in the siliques, and seed and oil yield under different drought stress conditions. The results demonstrated that seed yield in cold climate (Shahriyar) was much higher than that in hot climate (Yazd), which might have been because more rainfall was recorded in the Shahriyar region. Finally, the GKH2005 cultivar could produce more seed yield as a result of being an early maturing cultivar, a drought escaping mechanism.

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