

**RESPONSE OF SOME PHYSIOLOGICAL
PARAMETERS OF SUNFLOWER (*HELIANTHUS
ANNUUS* L.) TO VARIATION IN THE LIGHT
ENVIRONMENT**

*Majid Jami Al-Ahmadi, Samaneh Laleh,
Seyed Vahid Eslami, Zahra Sharifi*

Department of Agronomy and Plant Breeding
University of Birjand in Birjand, Iran.

Key words: defoliation, dry matter allocation, plant density, R:FR ratio, stem elongation.

Abstract

Light is considered as an important source of energy for all types of plants, and any change in its quality or quantity such as R:FR ratio affects plant growth through physiological, morphological, and biochemical processes. To examine the impact of changes in light quality on sunflower canopy, a factorial experiment with three replications was conducted at the Research Farm of Faculty of Agriculture, University of Birjand, in spring and summer 2014. The treatments included planting density (5 and 10 plants per square meter), leaf arrangement (no defoliation, and defoliating 50% of leaves of each plant when heads became visible), and the colors of optical filters wrapped around the shoot (blue cellophane with R:FR = 1.84 passing blue spectrum with the wavelength 480.62 nm, white cellophane as a control treatment for the blue one with R:FR = 2.40 which transmit the whole spectrum contained in the sunlight, and a control where no filter was used). The use of blue filters resulted in greater stem elongation, reduced stem diameter, and reduced amounts of plant dry matter allocated to each sunflower head as well as the achene number per capitulum. Blue filters had no significant impact on 100-grain weight. During the growing period, reduction in the dry matter allocated to stem was smaller when blue filters were used, especially for the defoliation treatments, compared to where no filter or white filters were used. Defoliation in combination with using blue filters at a density of 5 plants m⁻² increased specific leaf area (SLA) due to larger leaf areas. It seems any variation in R:FR, plant density, and/or leaf density can influence sunflower yield through affecting photo-morphological processes.

Introduction

As an important environmental factor, light not only acts as a source of energy but also regulates morphological processes in plants (ALABYEV et al. 2002). Quality of light affects growth, flowering, and morphology of plants (KUBOTA et al. 2000). Quality and quantity of light are altered through plant canopy. Quantity of light drops in shades while quality of light changes through increase in quantity of infrared light (700–800 nm) and reduction in blue (400–500 nm), and red light (600–700 nm) (SARALA et al. 2007). Green leaves absorb red light and reflect infrared. Therefore, closed and dense canopies have lower red to far red ratio (R:FR) and reflect larger quantities of infrared light (KASPERBAUER 1987, KASPERBAUER and KARLEN 1994, MALIAKAL et al. 1999). Allocation of dry matter to different parts of a plant under farming conditions is associated with the R:FR ratio received during the growing period (KASPERBAUER 1987).

Red light-intercepting films have been designed to decrease R:FR (WILSON and RAJAPAKSE 2001). There are instances where light quality variations were employed to develop desirable changes in plant products in the market. For example, FR increased chlorophyll content and leaf length as two important factors for marketable *Allium wakegi* (YAMAZAKI et al. 2000). Lowered R:FR (0.01, 0.43, and 0.65) has been reported to improve growth and flowering in *Eustoma grandiflorum*, while evidence suggested that increased R:FR delayed its growth and flowering (YAMADA et al. 2008). Plants that receive lower R:FR often have longer leaves with smaller width, longer stems, and smaller roots. Stem elongation is the first observed response to reduced R:FR even when light cannot directly touch the stem (KASPERBAUER and KARLEN 1994). Such responses may negatively affect crop productivity as reduction in R:FR may limit available resources for growth of harvestable organs of sunflower (LIBENSON et al. 2002).

A large body of research has focused on responses of photoreceptors and phytochromes to FR and R (ZHOU and SINGH 2002). Reduced R:FR ratios received through phytochromes at the base of grassy plants shoot (LIBENSON et al. 2002) are known to affect stem elongation in response to crowding and vegetation shading, and this is believed to be a form of adaptive phenotypic plasticity. Stem elongation allows a plant to develop its leaves above those of the adjacent plants to receive more light.

Using phytochrome family of photoreceptors, plants are able to sense changes in light quality (MALIAKAL et al. 1999). Irradiating the plant with blue light will cause canopy to grow toward the light. This phenomenon, referred to as phototropism, is one of the most well-known responses in

plants (VOLKOV et al. 2004). A phototropic response is composed of four processes: receiving light signal, signal transduction, transforming the signal into physiological response, and creating a directional growth response (VOLKOV et al. 2004). Irradiation of soybean with blue light plays an effective role in positive phototropism. In addition, researchers have pointed out that K^+ and Ca^{2+} channel blockers, like tetraethyl ammonium chloride and $ZnCl_2$, can block propagation of action potentials induced by blue light and may inhibit phototropism in soybean (VOLKOV et al. 2005).

Leaf epinasty is controlled by cell elongation on the abaxial epidermis triggered by blue light irradiation of the axial side of the leaf. It is observed that blue light, under red light conditions, created a larger leaf area in lettuce (FUKUDA et al., 2008). The rate of O_2 evolution by wheat seedlings with blue light, compared to red light, was over 50% (optimal temperature) and 60% (after exerting $45^\circ C$) (ALYABYEV et al. 2002). A study on incomplete mutants produced in response to specific spectral wavelength indicated that blue and far-red lights are effective in blocking ethylene impacts (VANDENBUSSCHE and VAN DER STRAETEN 2004). The phytohormone abscisic acid, cytoplasmic concentration of the secondary messenger Ca^{2+} , as well as blue and red lights modulate sensitivity of stomatal guard cells to internal CO_2 (LÜTTGE 2007).

Reduced leaf area is a common response to fungal and arthropod attack, hails, herbivory, etc. A number of studies tried to explain the effects of defoliation on plants (MORIONDO et al. 2003). Defoliation studies have provided a better understanding of physiological processes involved in vegetative and reproduction growth in several crops (CRUZ-CASTILLO et al. 2010). For sunflower (*Helianthus annuus* L.) there has been a large emphasis on the link between the reduction in leaf number and final amount of plant production (MORIONDO et al. 2003, ALIMOHAMMADI and AZIZOV 2011). In this regard, the aim of this work was to analyze sunflower responses to artificial manipulation of R:FR ratio, blue light, plant density, and defoliation for better understanding of some plants physiological processes, such as source-sink relationships, dry matter allocation, and compensation manner.

Materials and Methods

The experiment was carried out in Research Farm of Faculty of Agriculture, University of Birjand, Iran, during spring and summer 2014. The farm is located 8 km far from Birjand, adjacent to Birjand-Kerman Road ($32^\circ 56'N$, $59^\circ 13'E$, 1480 m elevation). Based on Emberger's classification,

the region is a hot arid region. The soil contained 20% clay, 19.4% silt, 60.6% sand, with an electrical conductivity (EC) of 3.85 dS m^{-1} and a pH of 7.97. The preceding crop in the experimental field was sugar beet. The common farming operations were used to prepare the seed bed. The same amount of fertilizer was applied to all plots based on soil tests before planting, including 30 kg ha^{-1} phosphorus (P), 75 kg ha^{-1} potassium (K), and 138 kg ha^{-1} N. One third of the nitrogen fertilizer plus all P and K fertilizers were applied before the planting and the remainder of N fertilizer was added to the soil at 6-8 leaves stage along with irrigation. Weeds were removed by hand hoeing over the entire growing season. No indication of disease and insect damages were observed from germination to final harvest. Irrigation method was the same for all treatments (7-days irrigation intervals).

The study conducted using a factorial experiment based on randomized complete block design with three replications. Each plot consisted of 7 planting rows. The treatments included planting density (5 and 10 pl m^{-2}), leaf arrangement (no defoliation, and defoliating 50% of leaves of plants (every other leaf) at flowering stage), and the colors of optical filters wrapped around the stem (blue cellophane with R:FR = 1.84 passing blue spectrum with the wavelength 480.62 nm, white cellophane as a control treatment for the blue one with R:FR = 2.40 which passed the whole spectrum contained in the sunlight, and a control where no filter was used with R:FR = 2.40). The plant rows were spaced at 50 cm with a space of 40 cm (for 5 pl m^{-2}) and 20 cm (for 10 pl m^{-2}) between two adjacent plants. To plant the crop, 3 to 5-cm deep holes were dug at the pre-specified spacing. Three sunflower (Euroflor cultivar) seeds were sown at each hole on 29 April and emerged plants were thinned to one plant at 2-4-leaf stage. Euroflor is an oily single cross hybrid, French origin, with intermediate maturity and lodging resistance (YOUSEFPOOR and YADAVI 2014). At the beginning of the flowering stage (20 June) and after exerting leaf density treatment, cellophane filters were wrapped around the stems, leaving a 2-cm space to let the air flow. The wrappings were maintained until stem elongation was completed.

Samples were taken at three stages: head-visible stage (HV, 26 June), pollination (PO, 14 July), and physiological maturity (PM, 20 August). At each stage, three plants were randomly selected from the second, fourth, and sixth rows of each plot by leaving 50 cm at either side (to allow for marginal effect). Before each sampling, the radiation flux density was measured at the top and bottom of canopy using Sun scan (AccuPAR LP-80, DECAGON devices, Made in USA) at 11:00 to 13:00 (Table 1). Furthermore, number and area of leaves, stem length and diameter, as well as

Table 1
Radiation intensity [$\mu\text{mo m}^{-2} \text{s}^{-1}$] at above and bottom of the sunflower canopy, measured at different growth stages. Plants were sown at two different plant density (5 and 10 pl m^{-2}) and all measurements were carried out between 11:00 and 13:00

Specification	Measuring place	
	above the canopy	bottom of the canopy
Growth stages		10 pl m^{-2} 5 pl m^{-2}
Head visible (26 June)	1420	300 540.33
Pollination (14 July)	1332	490.66 798.5
Physiological maturity (20 August)	1066.5	451 566.25

the dry weight of leaves, stem, and inflorescence were measured, separately. At the third sampling, achene number per capitulum and weight of 100-grain were also measured. Leaf area meter (WD₃-R₃ model, Delta-T Devices, UK) was used to measure leaf area. The stem length was measured using ruler, stem diameter was determined with caliper, and achenes were counted by seed counter (Contador Model, Pfeuffer GmbH, Germany). To measure dry weight, plant parts were first placed in an oven set at 72°C for 48 hours. SLA, leaf weight ratio (LWR) and capitulum weight ratio (CWR) were obtained using Equations (1), (2), and (3), respectively.

$$\text{SLA} [\text{cm}^2 \text{g}^{-1}] = \text{LA}/\text{LDW} \quad (1)$$

$$\text{LWR} [\text{g g}^{-1}] = \text{LDW}/\text{TDW} \quad (2)$$

$$\text{CWR} [\text{g g}^{-1}] = \text{TCW}/\text{TDW} \quad (3)$$

Where, LA and LDW are leaf area and leaf dry weight, respectively; TDW and TCW indicate total and capitulum dry weights, respectively.

The data were normalized and analyzed by Genstat (V.9) and the means were compared using FLSD.

Results and Discussion

In the present study, the first growth response of sunflower to increase in density from 5 to 10 pl m^{-2} , was an increase in the length and reduction in the diameter of stem; however with the progress of growing stages, the difference between the two levels of density reduced (Table 2). Increased plant densities decreases light penetration inside the canopy and increases the level of competition between individual plants for water and nutrients and meantime, plants react to increase in crowding with different mechanisms including morphological changes such as changes in stem length and specific leaf area (SLA) (LAMBERS et al. 2008). There was

a negative correlation between the length and diameter of the stem (-0.80, -0.32 and -0.29 in the stages of emerging inflorescence, pollination and physiological maturity, $df = 35$). With increase in plant density and decrease in light penetration into the canopy, the competition for absorbing light will increase and the plants, especially those sensitive to shade, will increase their height in order to receive more light as a mechanism for shade avoidance (ROSHDI et al. 2009, XIAO et al. 2006, SMITH 1982, MILLER and FICK 1978). This will mainly be accomplished to the cost of reduction in the stem diameter (BABAEI-AGHDAM et al. 2009). It is known that phytochrome B has a significant role in forming this response, even though two phytochromes D and E are also involved in inducing the mentioned reaction (FRANKLIN and WHITELAM 2004).

Increasing plant density per area did not have a considerable effect on the number of leaves in the plant, even though a minor reduction was observed with the progress of growing season. Nevertheless, this density increase primarily caused an increase in the leaf area in the stages of florescence emergence and pollination, which could be a response to reduction to the radiation availability at these stages. On the other hand, as growth continued, as a result of density increase, the leaves number and area reduced at the physiological maturity, indicating the leaves abscission in high density after the pollination (Table 2). This may be a result of increase in competition and shading in the density of 10 pl m^{-2} which exerts a high pressure on available sources. Leaf area reduction in plants as a result of density increase has previously been reported in sunflower (BANGE et al. 1997) and corn (SANGOI et al. 2002). Basically, plants growth and development in response to competition for light is much more effective than any other factor in controlling leaf area expansion (BALDISSERA et al. 2014).

Despite increasing leaf area and decreasing leaf dry weight at high density, no significant difference was observed in LWR between the two plant densities (Table 2). This indicates that plants allocated the same rate of produced assimilates to the leaves at high and low densities. These factors together caused an increase in SLA at higher densities in all three growth stages in spite of allocating the same amount (and a lower amount) of dry matter to the leaves. This indicates that plants struggle to enhance their leaf area through decreasing the leaves thickness, which is a response to increased competition for incident radiation, leading to more light absorption in each unit of weight assigned for leaf production. However, in the next growing stages, the difference of SLA between the two densities became lower (Table 2), which might be owing to the indirect effect of defoliation treatment (Table 2) and increase in light penetrating through canopy (Table 1).

Table 2
Average growth parameters for sunflower at 5 and 10 pl m⁻², measured in three stages during crop cycle

Sampling stage§	HV		PO			PM			
	5	10	LSD	5	10	LSD	5	10	LSD
Plant density [pl m ⁻²]	57.16±4.91*	76.25±3.5	7.064	84.13±0.28	92.83±0.28	5.46	94.02±2.08	102.52±2.66	5.57
Shoot length [cm]	0.97±0.18	0.69±0.14	0.152	1.12±0.03	0.99±0.05	0.08	1.40±0.05	1.16±0.06	0.15
Shoot diameter [cm]	17.33±1.58	18.33±0.44	2.483	10.91±0.29	10.55±0.24	0.913	10.61±0.41	9.25±0.37	0.98
Leaf number [no pl ⁻¹]	955.06±116.12	1148.35±72.06	71.698	479.05±31.0	632.19±10.8	102.90	506.35±24.1	407.04±27.8	65.95
Leaf dry weight [g pl ⁻¹]	11.71±2.52	10.18±2.80	0.559	11.48±0.8	8.77±0.33	1.29	10.41±0.86	7.62±0.14	1.55
Shoot dry weight [g pl ⁻¹]	19.68±2.96	15.51±2.80	1.548	20.20±0.79	15.65±1.35	3.08	28.36±2.41	20.20±1.20	3.78
Capitulum dry weight [g]	4.39±2.97	3.71±2.83	0.249	17.89±0.76	13.77±1.57	2.88	47.47±1.11	39.48±3.17	5.87
SLA [cm ² g ⁻¹]	81.51±29.77	112.77 ±46.93	78.572	43.39±6.34	71.11±3.05	9.91	48.62±7.58	53.42±13.46	20.263
LWR [g g ⁻¹]	0.327±0.02	0.346±0.03	0.072	0.231±0.007	0.229±0.01	0.0219	0.120±0.014	0.113±0.010	0.0169
CWR [g g ⁻¹]	0.122±0.05	0.126±0.05	0.0202	0.36±0.010	0.36±0.016	0.0577	0.55±0.004	0.58±0.016	0.042
Grains per Capitulum	-	-	-	-	-	-	459.86	374.38	49.87
Grain weight [g 100 achene ⁻¹]	-	-	-	-	-	-	5.03	3.65	0.84

* Means ±standard error

§ Three sampling stages refer to head-visible stage (HV), pollination (PO), and physiological maturity (PM)

SLA increase as a result of increase in plant density has also been observed in other plants such as potatoes (VOS 1995) and tomatoes (HEUVELINK et al. 1999), the reason of which has ascribed to the reduction in the average of the light received by leaf area in high densities (LEE and HEUVELINK 2003). Generally speaking, high densities cause a response similar with the situation being plants in the shade; the plants growing in shade, have more tendency to expand their leaf area, and their leaves are rather thin and thus they have high SLA and low leaf mass density (LAMBERS et al. 2008). Reduction in sunflower leaf dry weight in response to increased densities is caused by photosynthates deviation to acquire resources such as radiation, water and nutrients, as a result of intensification of interplant competition (POURSAKHY and KHAJEPOUR 2014).

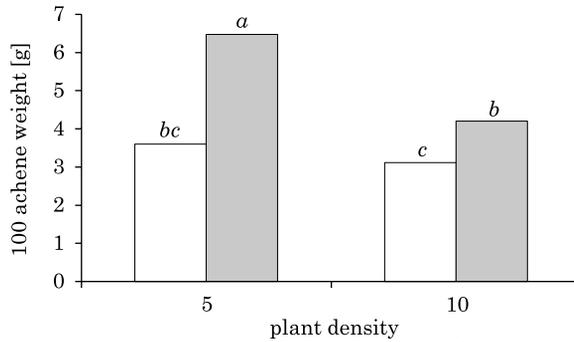


Fig. 1. A comparison of 100-grain weight [g] for 5 and 10 pl m⁻² during physiological maturity stage under two situations: no defoliation (shaded bars) and defoliation (white bars). Bars with at least one common letter indicate no significant difference according to LSD_{5%}

In addition to the leaf weight, the dry weight of the stem and capitulum of sunflower or, in other words, the dry weight of the whole plant, also decreased in response to density increase (Table 2). The stem dry weight in the density of 10 pl m⁻² were 21.2, 22.5 and 28.7 percent lower than the values gained in the density of 5 pl m⁻² in the stages of head visible, pollination and physiological maturity, respectively (Table 2). POURSAKHY and KHAJEPOUR (2014) observed that increase in the density of sunflower plants caused reductions in stem dry weight of individual plants. Similarly, at the physiological maturity, high plant density (10 pl m⁻²) caused small capitulum with less weight which was most likely due to a lower achene number (18.5%) and lower 100-achene weight (27.4%) compared to the density of 5 pl m⁻² (Table 2 and Figure 1). achene weight reductions at high densities indicates a drop in production capability of individual plants (source limitation) and reduction of the whole photosynthates partitioned for seed filling (BARROS et al. 2004). The interesting point is that the capitulum weight ratio (CWR) did not show significant differences between the

two densities at any growth stages (Table 2). Basically, thinner leaves with higher SLA produced at high densities have a shorter life span (LAMBERS et al. 2008), which in turn limits the source activity of plants. Negative effect of increased density on weight reduction of achene in sunflower has also previously been reported (GHOLINEZHAD et al. 2009, HOLT and ZENTNER 1985). IBRAHIM (2012) found that low density of sunflower is effective in height reduction and increase in achene weight, leaf area, diameter of capitulum, oil percentage, unsaturated fatty acids percentage (oleic and linoleic) and the length of maturation period. He stated the reason of such changes was the greater usage of assimilates for competition at high densities compared to lower densities. BARROS et al. (2004) reported that two densities of 3.5 and 4.6 pl m⁻² of sunflower produced the same number of achenes per m⁻², with a lower achene weight at higher density. They attributed this lower achene weight at higher density to less produced dry matter in that density, which reduced remobilization of assimilates during achene filling period. This condition will finally lead to a reduction in radiation use efficiency (RUE) as a result of increase in plant density (MORRISON and STEWART 1995).

Using blue filter caused more reductions in R/FR (7.10%) in comparison with white filter (4.7%) and the control (0.075%). Physiological and morphological responses of sunflower to the quality of radiation were the same in both stages of pollination and physiological maturity. White filter did not induce a significant difference in stem length compared to the control in the two mentioned stages, whereas blue filter caused a significant increase in stem length compared to the control (Table 3). On the other hand, control plants had the highest stem diameter and using white and blue filters caused 5 and 16.5 % decrease in stem diameter compared to the control, respectively, while this reduction was only significant in blue filter treatment (Table 3). This has also been observed in soybean plants in which the decrease of red to far-red ratio reduced stem diameter (YANG et al. 2014). It seems that a reduction in R/FR ratio during the plant growth is one of the most substantial factors causing elongation in plant height and at the same time reduction in stem diameter. In the plant canopy, the quality of radiation transmitted through the leaves or reflected is changed. This is because the plants absorb red light and transmit or reflect far-red radiation. This causes a reduction in R/FR under shaded environments (TAIZ and ZEIGER 2006). As blue filter absorbs and reflects a part of incident visible light spectrum, it can induce the effects of increased far-red radiation (or reduction in R/FR ratio) in the plant. Increase in the internodes length and stem elongation as a result of reduced R/FR ratio have been reported in *Sinapis alba*, *Chenopodium album* and *Datura ferox* (BOOTH et al. 2003).

Table 3

Average growth parameters for sunflower: impacts of optical filters at pollination and physiological maturity stages

Treatments	Shoot length [cm]	Shoot diameter [cm]	Leaf no.	Leaf area [cm ² pl ⁻¹]	LDW [g pl ⁻¹]	SDW [g pl ⁻¹]	CDW [g pl ⁻¹]	LWR [g g ⁻¹]	CWR [g g ⁻¹]	GPC	
Pollination											
Light filters	blue	98.958	0.915	12.7	688.5167	12.287	24.298	11.033	0.258	0.231	–
	white	85.375	1.096	10.3	526.770	9.1	15.460	17.083	0.218	0.410	–
	control	81.125	1.163	9.2	451.587	9.008	14.024	19.396	0.212	0.457	–
	LSD	6.69	0.13	1.16	126.03	1.58	3.78	3.53	0.0279	0.073	–
Physiological maturity											
light filters	blue	105.62	1.02	11.791	569.7	10.93	30.15	33.25	0.144	0.449	327.5
	white	95.125	1.32	9.25	414.98	8.29	22.39	46.74	0.100	0.641	450.12
	control	94.083	1.5	8.75	385.4	7.82	20.29	50.44	0.106	0.610	473.75
	LSD	6.82	0.24	1.49	80.78	1.90	4.63	7.1	0.021	0.054	81.96

LDW – leaf dry weight; SDW – shoot dry weight; CDW – capitulum dry weight; LWR – leaf weight ratio; CWR – capitulum weight ratio; GPC – grains per capitulum

BALOCH et al. (2009) stated that phytochromes and photoreceptors families are responsible for perceiving the R/FR ratio throughout canopy and decrease in this ratio can lead to stimulating the elongation of internodes and consequently increasing the stem height. They believed that the effects of far-red radiation on stem growth can be considered as a part of shade avoidance response. Similarly, the high amounts of intercepted far-red radiation stimulates the plants, through decreasing P_{fr}/P_{total} , to allocate more assimilates to the stem in order to reach a greater height (TAIZ and ZEIGER 2006) (Figure 2). It is thought that phytochrome B is involved

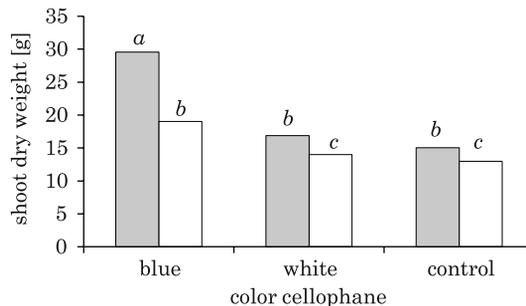


Fig. 2. A comparison of shoot dry weight [g] at pollination stage for three treatments (blue filter, white filter, and the control treatment) under two situations: no defoliation (shaded bars) and defoliation (white bars). Bars with at least one common letter indicate no significant difference according to $LSD_{5\%}$

in intensifying the response of stem elongation to a reduction in R/FR ratio (XIONG et al. 2002). It has also been observed that R/FR reduction can increase the content of gibberellic acid (GA_1) and auxin (IAA) phytohormones in internodes and leaves of sunflower, which in turn reduces the level of ethylene in internodes, (KUREPIN and WALTON 2007, KUREPIN et al. 2007) through influencing DNA (PRICE and JOHNSTON 1996). Increase in stem length, plant fresh and dry weight and leaf area as affected by far-red radiation has also been observed in watermelon (HEATHER et al. 1997).

Reducing R/FR using blue filter caused more increase in SLA at maturity compared with white filter and the control (Table 4). Similarly, the blue filter increased LWR, leaf number and area, and leaf and stem dry weights during plant growth, whereas it significantly reduced the capitulum weight ratio (CWR) (Table 3 and Table 4, Figure 3). Similar results have been reported in different plants, for example, OYAERT et al. (1999) reported that using blue filter increased leaf number per plant, plant dry and fresh weight, and LWR in chrysanthemums. Increased stem dry and fresh weights under high levels of far-red radiation has also been reported

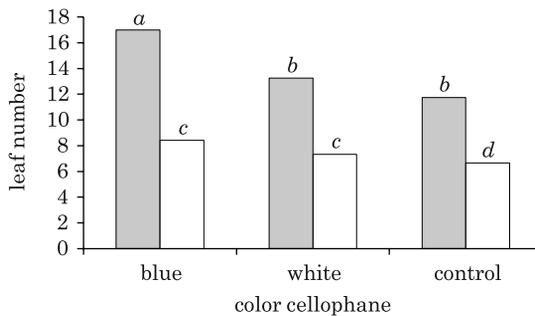


Fig. 3. A comparison of leaf number in pollination stage for three treatments (blue filter, white filter, and the control treatment) under two situations: no defoliation (shaded bars) and defoliation (white bars). Bars with at least one common letter indicate no significant difference according to $LSD_{5\%}$

in lettuce (KRIZEK and ORMROD 1980). The variation rate in different traits caused by blue filter and the control treatment at the pollination stage was different as compared with the physiological maturity stage. For example, using blue filter caused more increase in some traits in the pollination stage compared to the physiological maturity, including number of leaves (38%, 34%), leaf area (52.4%, 47.8%), stem dry weight (73.2%, 48.5%) and stem length (22%, 12.2%). On the other hand, rate of increase in some other traits resulting from using blue filter was lower in the pollination stage compared to physiological maturity including leaf dry weight (36.4%, 39.7%) and then LWR (21.6% and 35.8%). In contrast, there was

a sharp decline in capitulum diameter at pollination (49.4%) and stem diameter at physiological maturity (32%) as a result of using blue filter (Table 3). It seems that greater increase in the characteristics such as leaf number, leaf area, stem dry weight and stem length resulting from blue filter (compared to the control) at pollination stage is owing to the greater importance of shade avoidance responses at this stage, which leads to more assimilate allocation to stem elongation and leaf area expansion in this critical phase of plant growth. Given that blue filter creates a lower level of R/FR ratio, it induces the sensing of being under high density or shade conditions by plants, and the morpho-physiological responses that arise in these conditions are similar to the responses resulted by cultivating plants at high density to some extent. LAMBERS et al. (2008) stated that the plants growing in shade invest a large portion of their assimilate and other resources in leaf area; these plants have a high leaf area ratio, rather thin leaves with a low mass density. Elongating stems is another strategy employed by plants growing under shade conditions. It has been stated that low R/FR ratios caused stem elongation in *Vigna sinensis*, and it seems that preventing stem elongation by light is related to decrease in responsibility of tissues to Gibberlines (OLSZEWSKI et al. 2002).

Table 4

Average values for some physiological traits measured at pollination (PO) and physiological maturity (PM) stages, as influenced by optical filter, plant density, and leaf density treatments

Light filters		Blue				White				Control			
Plant density [pl m ⁻²]		5		10		5		10		5		10	
Leaf density		<i>D</i> *	<i>C</i>	<i>D</i>	<i>C</i>								
Total dry weight [g]	PO	44.34	63.28	34.28	48.57	41.75	53.23	32.00	39.60	39.34	55.58	35.30	39.50
	PM	62.20	104.05	56.50	74.62	71.46	103.14	57.89	77.23	67.62	109.05	57.86	79.74
Shoot dry weight [g]	PO	22.26	33.93	15.82	25.18	15.13	19.29	12.87	14.55	13.3	17.3	12.65	12.85
	PM	26.58	45.08	21.57	27.37	21.87	32.08	13.2	22.45	16.23	28.32	15.9	20.74
Leaf dry weight [g]	PO	11.43	16.67	8.83	12.22	8.18	11.63	6.8	9.78	7.82	13.18	7.17	7.87
	PM	8.4	16.68	6.62	12.05	8.02	11.83	5.3	8.02	7.25	10.3	5.48	8.25
Capitulum dry weight [g]	PO	10.65	12.683	9.633	11.166	18.433	22.3	12.33	15.27	18.22	25.1	15.48	18.78
	PM	27.22	42.28	28.31	35.2	41.58	59.23	39.39	46.76	44.13	70.43	36.48	50.75
Leaf area [cm ² pl ⁻¹]	PO	468.58	758.45	569.35	957.68	346.32	537.08	431.68	792.00	306.52	457.37	450.78	591.68
	PM	561.05	724.47	390.28	603.03	367.63	508.55	310.87	472.90	370.23	506.18	258.52	406.68
SLA [cm ² g ⁻¹]	PO	43.27	46.08	64.42	77.45	45.35	46.08	63.17	81.71	39.50	40.11	62.91	75.22
	PM	73.86	44.09	79.95	51.03	48.19	42.37	72.62	61.99	55.84	49.80	60.71	51.20
LWR [g g ⁻¹]	PO	0.26	0.26	0.25	0.26	0.20	0.22	0.21	0.25	0.20	0.23	0.19	0.22
	PM	0.13	0.16	0.12	0.16	0.11	0.12	0.09	0.10	0.09	0.11	0.09	0.10
CWR [g g ⁻¹]	PO	0.25	0.20	0.28	0.24	0.44	0.42	0.40	0.39	0.46	0.45	0.20	0.18
	PM	0.43	0.40	0.50	0.46	0.58	0.57	0.68	0.61	0.65	0.65	0.43	0.39

* *D* – defoliation; *C* – no defoliation (control)

The reduction in R/FR through using blue filter also caused a reduction in capitulum weight, achenes per capitulum and CWR (Table 3), while it had no significant effect on achene weight (data not shown). This effect is similar to the response where sunflower is cultivated at high densities which lead to a reduction in the achenes per capitulum and achene weight (Table 2). Competition between adjacent plants at high densities usually causes a drop in produced biomass and also assigning more resources for vegetative growth and, as a result, a reduction in achenes per capitulum (GARDNER et al. 1985). It seems that reducing R/FR ratio using blue filter in this study, through simulating crowding and competition between plants, has forced them to allocate more dry matter to vegetative organs such as stem and leaves (LIBENSON et al. 2002) and to remobilize assimilates from reproductive organs to promote vegetative growth (TAIZ and ZEIGER 2006). Obviously, this will lead to reduced reproductive growth and subsequently less achene set in sunflower plants. In this case, achene yield and achenes number per plant will decrease, with no effect on achene weight. Under these conditions, the competition that occurs between vegetative and reproductive structures is harmful for seed setting and seed filling (LIBENSON et al. 2002). It has been proved that in response to R/FR reduction, the level of soluble metabolites and structural carbohydrates (cell-wall carbohydrates) increase and sucrose concentration reduces in sunflower stem, which expectedly are in the favor of carbon unloading from stem phloem (MAZZELLA et al. 2008).

Defoliation, beside its direct effects on reducing leaf number, area and dry weight per plant, caused a significant reduction in stem and capitulum dry weights at pollination and physiological maturity, and also decreased SLA, achenes per capitulum and achene weight at pollination stage, while did not have a significant impact on the stem length and diameter (Table 5). It is acceptable that a damage such as removing leaves can affect a number of plant physiological processes, like sink and source balance, hormone production and changes in radiation absorption in different layers of canopy. In both stages of pollination and physiological maturity, defoliation treatment was accompanied with a compensative response to increase single leaf area per plant; in the way that in the stage of pollination, the average area of single leaf in defoliated plants and in the control treatment were 57.4 and 48.7 cm², respectively, which reduced to 52.3 and 42.4 cm² at physiological maturity. This indicates that the defoliated plants increased the single leaf area in order to compensate the manipulated reduction in their leaf area (Table 5). By increasing radiation entry into the canopy and increase in R/FR, defoliation caused SLA reduction at the pollination stage. Forming thick leaves with low SLA appears to be

a kind of avoiding from high radiation damage which have been previously observed in different plants such as tobacco (BALLARE et al. 1994) and *Plantago lanceolata* (VAN HINSBERG and VAN TIELEREN 1997), that is the result of forming thick ladder tissue consisting of two cell layers in the growing leaves (TERASHIMA et al. 2006, YANO and TERASHIMA 2001).

Table 5
Average growth parameters for sunflower: impacts of leaf density at pollination and physiological maturity stages

Sampling stage	Pollination			Physiological maturity		
	defoliation	control	LSD 5%	defoliation	control	LSD 5%
Leaf density						
Shoot length [cm]	88.36	88.611	5.249	96.611	100	5.352
Shoot diameter [cm]	1.044	1.072	0.103	1.186	1.377	0.193
Leaf number [no pl ⁻¹]	7.472	14	0.95	7.194	12.66	1.21
Leaf area [cm ² pl ⁻¹]	428.872	682.377	102.90	376.43	536.9	65.95
Leaf dry weight [g pl ⁻¹]	8.488	11.775	1.29	6.844	11.188	1.55
Shoot dry weight [g pl ⁻¹]	15.336	20.518	3.08	19.22	29.34	3.78
Capitulum dry weight [g]	14.125	17.550	2.15	36.18	50.77	5.87
SLA [cm ² g ⁻¹]	52.201	62.307	7.39	65.194	50.080	20.263
Grains per capitulum	–	–	–	378.47	455.77	49.87
Grain weight [g 100 achene ⁻¹]	–	–	–	3.35	5.33	0.84

In the maturity stage, more leaves shed in control plants and the SLA severely increased in defoliated plants. All of these factors together caused a reduced difference between control and defoliated plants at the maturity stage (Table 5). This indicates that sunflower is able to compensate the damage caused by defoliation in certain growing stages through increase in leaf area or delay in its senescence and that the effect of defoliation on crop yield mostly depends on the growing stage (in which defoliation has occurred), the rate of defoliation and genotype (POLAT et al. 2011, SCHNEITER and JOHNSON 1994, SCHNEITER et al. 1987, MORIONDO et al. 2003). When the reproductive phase begins, the vegetative phase does not stop completely and as the demand for the carbohydrates in reproductive organs increases, the plant will be able to meet the sinks demands by maintaining its remaining leaves (SEVERINO et al. 2010). Although it has been stated that leaf removal will enhance photosynthesis and growing of remained leaves (ALKIO et al. 2003), it seems that resources deviation from reproductive growth toward compensatory mechanisms has caused the plant not to have a chance to recover its yield (number and weight of achenes) – Table 5. Defoliation caused a 37% reduction in leaf area at

the pollination stage, while the capitulum dry weight and total biomass decreased 19.5 and 23.4%, respectively, indicating the high compensation ability of sunflower at this growth stage.

In the physiological maturity, cutting half of the leaves caused a 30% decrease in leaf area, while the achenes per capitulum dry weight, achene weight and total biomass (capitulum + leaf + stem) decreased 16.9, 28.7, 37 and 31.8 percent, respectively, indicating the greater sensitivity of achene weight to defoliation treatment than achene number (Table 5). Decrease in capitulum diameter (POLAT et al. 2011) and achene number per capitulum (NEZAMI et al. 2008) have been reported as two important components in determining sunflower achene yield under defoliation conditions; which is due to the influence of leaf removal in reducing source to sink ratio (ALKIO et al. 2003). Eventually, decrease in photosynthesizing area as well as loss of stored carbohydrates in shedding structures and increase in energy consumption for compensatory processes as the result of defoliation will cause severe reduction of biomass and achene (both number and weight) production. This may indicate that sunflower yield production is a source-limited process. It has been reported that reduction in source-sink ratio through shading over soybean plants (increased density) or defoliation can reduce the size of cotyledon cells, leading to lower seed weights (LINDSTRÖM et al. 2006).

While defoliation in 5 pl m⁻² density caused 44.3% decrease in 100-achenes weight, this came down to 25.9% in 10 pl m⁻² density, indicating more impact of increasing density on the control plants (Figure 1). Lower reduction of achene weight as the result of defoliation at high density might be correlated to the compensatory role of greater density for the enhanced radiation penetration into the canopy due to defoliation. A similar reaction was seen in leaf dry weight under the influence of density and defoliation at the pollination stage (Figure 4). Due to the loss of some sources of

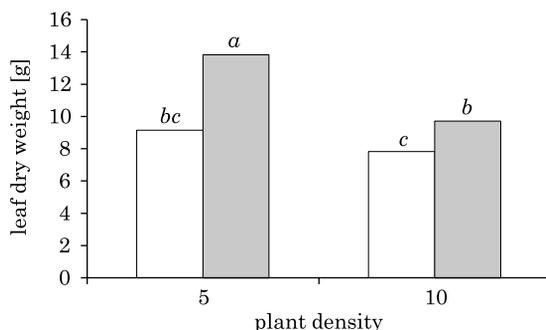


Fig. 4. A comparison of leaf dry weight (gr) for 5 and 10 pl m⁻² during pollination stage under two situations: no defoliation (shaded bars) and defoliation (white bars). Bars with at least one common letter indicate no significant difference according to LSD_{5%}

assimilates (IBRAHIM 2012), defoliation caused a decrease in achene weight and leaf dry weight in both densities. However, by increasing the radiation penetration into canopy, the difference of the achene and leaf weight at high density (10 pl m^{-2}) to low density (5 pl m^{-2}) was reduced. One of the possible reasons for this decreased difference between two densities can be an increase in the proportion of sunlit leaves and better radiation distribution through canopy under defoliation treatment. Using blue filter in both groups of control and defoliated plants, which simulates the shade and high density conditions, resulted in a greater dry stem weight, whereas defoliation accompanied with blue filter, white filter and control (without filter) caused 35.5, 17.2 and 13.9 percent reduction in stem dry weight compared to non-defoliated plants, respectively (Figure 2). The highest number of leaves were also observed in plants covered with blue filter (Figure 3). In both the total above-ground dry weight and number of leaves, the greatest difference between control and defoliated plants was observed where the blue filter was used. As the blue filter decreases R/FR in canopy and, on the other hand, defoliation increases radiation penetration into the canopy and therefore the R/FR ratio, it seems that defoliation has mitigated the effects of used blue filter on the leaves number and stem dry weight of sunflower.

Even though defoliation and a reduction in plant density caused more light penetration through canopy, blue filter covering on the stems caused the plants not to be able to completely perceive this increase in radiation level in canopy and then as a result, plants showed a response similar to the condition of low R/FR ratio in canopy. Using blue filter combined with defoliation and density of 5 pl m^{-2} led to considerable increase in stem dry weight at the pollination and physiological maturity compared with white filter and control (Table 4). Previous findings indicate that increase in R/FR ratio causes reduction in stem dry weight in chrysanthemum (*Den-dranthema × grandiflorum* (Ramat.) Kitamura) and bell pepper (*Capsicum annuum* L.) (LI et al. 2000). On the other hand, the cumulative effect of decrease in R/FR ratio on promoting dry matter allocation to the stems has been previously reported (HURD 1974, KASPERBAUER 1987).

Decrease in R/FR ratio is effective in accelerating leaves senescence, and perceiving an increase in R radiation by phytochromes in sunflower delays this phenomenon (BALLARE and CASAL 2000). At the end of the growth (stage 3), the leaf area in the defoliated plants at 5 pl m^{-2} in all optical filter treatments, unlike the non-defoliated plants, still was increasing, while at high density, leaf area showed a decreasing trend (Table 4). It seems that leaf removal, especially in combination with blue filter and low density, has slowed the aging process of leaves by activating the mecha-

nisms of compensating for source shortage. By removing the leaves, it appears that radiation is distributed more uniformly inside the canopy and the lower leaves that received little radiation, especially at high density, compensate for detached leaves. In high density, as well, a much less decline in leaf area was occurred in the defoliated filtered plants than intact ones (Table 4).

In comparison with control (intact) plants, defoliation in both densities and in all applied filters caused a reduction in LWR or, in other words, dry matter allocation to the leaves in both pollination and physiological maturity stages. As a compensatory mechanism for this leaf area removal and reduction in partitioning, SLA increased at the maturity stage in all filters in the density of 5 pl m⁻² that can be a response to increase in the intensity of the radiation intercepted by remained leaves (Table 4). While the number of leaves in defoliation treatment decreased to half, the amount of decrease in leaf area in different treatments ranged between 22 to 40%, and SLA in all treatments in the stage of physiological maturity increased from 12 to 67% as compared to its previous stage, which indicates a severe reduction in leaf thickness to compensate the leaf area reduction at the physiological maturity stage (Table 4). Two mechanisms have been proposed for increasing leaf area: changing the allocation of assimilates during leaf growth through decreasing dry matter allocated to the stem, or increasing the SLA and more leaf area accompanied with the same biomass invested in leaves (MORIONDO et al. 2003).

In all levels of density and defoliation, using blue filter caused a severe increase in leaf area as compared to white filter and control (without filter) in similar levels of density and defoliation. In the physiological maturity, using blue filter accompanied with defoliation in both densities led to a higher SLA as compared to its corresponding treatments in white filter and control (Table 4). As previous studies showed the effect of a reduction in R/FR ratio on increasing the leaf area (HEATHER et al. 1997), it is expected that using blue filter with reducing R/FR ratio exerts more influence on increasing leaf area than its dry weight.

Increased density effectively decreased SLA in all three filters (blue, white and control) and the amount of SLA reduction in non-defoliated plants at the physiological maturity stage compared to the previous stage was higher in 10 pl m⁻² than 5 pl m⁻². Using blue filter in each density, with or without defoliation, increased leaf dry weight compared with using white filter and control at similar levels of density and defoliation (Table 4). According to BRITZ and SAGER (1990) when plants are growing under reduced levels of blue light, transport of photosynthates outside the leaves is reduced, thus their leaves dry weight would be increased. As blue filter

Table 6

Correlation coefficients between measured traits in three sampling stages ($n = 36$)

Shoot length	Shoot diameter	Leaf number	Leaf area	Leaf dry weight	Shoot dry weight	Capitulum dry weight	SLA	LWR	CWR	Achene per Capitulum	100 Achenes weight	
Heading visible stage												
1	1											
2	-0.817 ^{ns}	1										
3	0.005 ^{ns}	0.343 ^{ns}	1									
4	0.799 ^{ns}	-0.719 ^{ns}	-0.509 ^{ns}	1								
5	-0.431 ^{ns}	0.839 [*]	0.213 ^{ns}	-0.244 ^{ns}	1							
6	-0.595 ^{ns}	0.858 [*]	0.094 ^{ns}	-0.317 ^{ns}	-0.947 ^{**}	1						
7	-0.047 ^{ns}	0.334 ^{ns}	0.307 ^{ns}	0.383 ^{ns}	0.743 ^{ns}	0.753 ^{ns}	1					
8	0.629 ^{ns}	-0.940 ^{**}	0.374 ^{ns}	0.614 ^{ns}	-0.880 [*]	-0.824 [*]	-0.374 ^{ns}	1				
9	-0.213 ^{ns}	0.451 ^{ns}	0.616 ^{ns}	-0.576 ^{ns}	0.241 ^{ns}	0.028 ^{ns}	-0.390 ^{ns}	-0.550 ^{ns}	1			
10	0.143 ^{ns}	0.061 ^{ns}	-0.442 ^{ns}	0.582 ^{ns}	0.515 ^{ns}	0.558 ^{ns}	0.952 ^{**}	-0.103 ^{ns}	0.624 ^{ns}	1		
Pollination stage												
1	1											
2	-0.324 [*]	1										
3	0.295 [*]	-0.219 ^{ns}	1									
4	0.557 ^{**}	-0.294 [*]	0.766 ^{**}	1								
5	0.139 ^{ns}	-0.213 ^{ns}	0.675 ^{**}	0.380 [*]	1							
6	0.387 ^{**}	-0.199 ^{ns}	0.681 ^{**}	0.502 ^{**}	0.746 ^{**}	1						
7	-0.609 ^{**}	0.386 [*]	-0.015 ^{ns}	-0.313 [*]	0.069 ^{ns}	-0.262 ^{ns}	1					
8	0.385 [*]	-0.183 ^{ns}	0.249 ^{ns}	0.669 ^{**}	-0.383 [*]	-0.121 ^{ns}	-0.314 [*]	1				
9	0.370 [*]	-0.416 ^{**}	0.310 [*]	0.345 [*]	0.595 ^{**}	0.262 ^{ns}	-0.477 ^{**}	-0.103 ^{ns}	1			
10	-0.657 ^{**}	0.365 [*]	-0.434 ^{**}	-0.504 ^{**}	-0.490 ^{**}	-0.746 ^{**}	0.787 ^{**}	-0.078 ^{ns}	-0.612 ^{**}	1		
Physiological maturity stage												
1	1											
2	-0.294 [*]	1										
3	0.169 ^{ns}	-0.018 ^{ns}	1									
4	0.313 [*]	-0.067 ^{ns}	0.604 ^{**}	1								
5	-0.058 ^{ns}	0.025 ^{ns}	0.831 ^{**}	0.621 ^{**}	1							
6	0.204 ^{ns}	-0.093 ^{ns}	0.755 ^{**}	0.713 ^{**}	0.692 ^{**}	1						
7	-0.351 [*]	0.682 ^{**}	0.332 [*]	0.007 ^{ns}	0.261 ^{ns}	0.145 ^{ns}	1					
8	0.431 ^{**}	-0.085 ^{ns}	-0.402 ^{**}	0.174 ^{ns}	-0.590 ^{**}	-0.139 ^{ns}	-0.265 ^{ns}	1				
9	-0.011 ^{ns}	-0.310 [*]	0.493 ^{**}	0.382 [*]	0.745 ^{**}	0.305 [*]	-0.321 [*]	-0.602 ^{**}	1			
10	-0.391 ^{**}	0.493 ^{**}	-0.452 ^{**}	-0.626 ^{**}	-0.493 ^{**}	-0.676 ^{**}	0.557 ^{**}	0.050 ^{ns}	-0.645 ^{**}	1		
11	-0.091 ^{ns}	0.581 ^{**}	0.019 ^{ns}	0.081 ^{ns}	-0.079 ^{ns}	0.064 ^{ns}	0.545 ^{**}	0.145 ^{ns}	-0.462 ^{**}	0.400 ^{**}	1	
12	0.156 ^{ns}	0.311 [*]	0.543 ^{**}	0.346 [*]	0.424 ^{**}	0.644 ^{**}	0.429 ^{**}	-0.091 ^{ns}	-0.039 ^{ns}	-0.168 ^{ns}	0.418 ^{**}	1

** and * means correlation is significant at the 0.01 and 0.05 probability level, respectively;
^{ns} means correlation is not significant

reflects blue light, using this filter may face plants with the blue light deficiency. Simultaneously, as growth proceed, leaf dry weight and LWR decreased and leaf area and stem dry weight increased under blue filter+ leaf removal +low density, as compared to the previous stage (Table 4). Therefore, as low density and leaf removal causes more radiation penetration and increase in R/FR ratio through canopy, which in turn is effective in increasing SLA (MORIONDO et al. 2003), the reduction in leaf thickness and increase in leaf area (SLA increase) after limiting the source (leaf defoliation) in the above-mentioned treatment combination is an effort for compensating the decrease in radiation interception during the growth season and preventing from a sharp drop in growth of reproductive organs.

In all filters and plant densities, defoliation reduced capitulum dry weight as compared to the control. In each stage, using blue filter in all levels of density and defoliation caused severe reduction in capitulum dry weight in comparison with the white filter and control (without filter) treatments. In the contrary, the highest LWR was obtained using blue filter in each level of defoliation and density (Table 4). A negative correlation between LWR and CWR at the pollination (-0.61^{**}) and physiological maturity (-0.64^{**}) stages indicated that using blue filter will cause more assimilates allocation to the leaves (higher LWR) and a lower allocation to capitulum (reduction in CWR). Moreover, considering negative correlation of LWR with capitulum dry weight (-0.32^*) and achenes per capitulum (-0.46^{**}) one could say that blue filter can decrease the amount of photosynthates allocated to the reproductive organs by increasing allocation to the leaves and stem (Table 6). The greatest amount of assimilates allocated to leaves (the highest LWR) and stem (the highest stem dry weight) was observed in blue filter treatment with the density of 5 pl m^{-2} without defoliation (Table 4). LIBENSON et al. (2002) reported that low R/FR ratios cause a decline in sunflower yield as the result of decrease in the number of achenes produced in plant. They stated that at high densities, stimulating stem growth in low R/FR ratios may decrease the available resources for the seed yield.

Conclusion

As with other crops, the morphology, physiology, yield and yield components of sunflower are all affected by its density. By increase in plant's population at high densities (crowding), the competition between the plants for growth will lead to taller plants competing for light (IBRAHIM 2012). In the present study, the reduction in radiation penetration into the canopy

through increasing plant density or using blue filter caused a reduction in R/FR ratio through canopy which, in turn, triggered the shade-avoidance mechanisms in sunflower. Under these conditions, the plant managed to increase leaf area and stem length to better benefit from radiation by increasing photosynthate allocated to leaf and stem and also decreasing leaf thickness. On the other hand, these increased allocation to vegetative organs effectively reduced the share of reproductive structures from photo-assimilates, resulting in reduced achene weight, number and capitulum weight. Among these, grain weight was affected more than its number. Decrease in plant density and leaf defoliation causes increase in R/FR ratio through canopy by increasing radiation penetration, thereby moderates shade-avoidance responses to some extent. However, the findings of this study showed that defoliation was not able to completely compensate the decrease in R/FR ratio entering the canopy caused by using blue filter.

Acknowledgment

The authors would like to acknowledge prof. Francisco J. Villalobos (CSIC), for the basic idea of this research. This work was partially funded by University of Birjand.

Accepted for print 4.11.2018

References

- ALIMOHAMMADI R., AZIZOV I. 2011. *Defoliation effects on yield and yield components of sunflower cultivars (Helianthus annuus L.)*. Int. J. AgriScience., 1(7): 361–365.
- ALKIO M., SCHUBERT A., DIEPENBROCK W., GRIMM E. 2003. *Effect of source-sink ratio on seed set and filling in sunflower (Helianthus annuus L.)*. Plant Cell Environ., 26: 1609–1619. doi: 10.1046/j.0016-8025.2003.01077.x.
- ALYABYEV A.JU., LOSEVA N.L., JAKUSHENKOVA T.P., RACHIMOVA G.G. 2002. *Comparative effects of blue light and red light on the rates of oxygen metabolism and heat production in wheat seedlings stressed by heat shock*. Thermochemica Acta, 394: 227–231.
- BABAEI AGHDAM J., ABDI M., SEIFZADEH S., KHIAMI, M. 2009. *Effects of different levels of nitrogen and plant density on yield and yield components of sunflower, Azargol cultivar in Takestan region*. Iranian. J. New Agric. Sci., 14: 1–12.
- BALDISSERA T.C., FRAK E., CARVALHO P.C.D.F., LOUARN G. 2014. *Plant development controls leaf area expansion in alfalfa plants competing for light*. Ann. Bot., 113: 145–157.
- BALLARE, C.L., CASAL J.J. 2000. *Light signals perceived by crop and weed plants*. Field Crop Res., 67: 149–160.
- BALLARE C.L., SCOPEL A.L., JORDAN E.T., VIESTRA R.D. 1994. *Signaling among neighboring plants and development of size inequalities in plant population*. Proc. Natl. Acad. Sci. USA, 91: 10 094–10 098.

- BALOCH J., QASIM KHAN M., ZUBAIR M., MUNIR M. 2009. *Effects of different shade levels (light integrals) on time to flowering of important ornamental annuals*. Int. J. Agric. Biol., 11(2): 138–144.
- BANGE M., HAMMER P.G.L., RICKERT K.G. 1997. *Effect of radiation environment on radiation use efficiency and growth of sunflower*. Crop Sci., 37: 1208–1214.
- BARROS J.F.C. CARVALHO M., BASCH G. 2004. *Response of sunflower (Helianthus annuus L.) to sowing date and plant density under Mediterranean conditions*. Europ. J. Agron., 21: 347–356.
- BOOTH B.D., MURPHY S.D., SWANTON C.J. 2003. *Weed ecology in natural and agricultural systems*. Bristol: CAB International, Wyvern 21 Ltd.
- BRITZ S.J., SAGER J.C. 1990. *Photomorphogenesis and photoassimilation in soybean and sorghum grown under broad spectrum or blue-deficient light sources*. Plant Physiol., 94: 448–454.
- CRUZ-CASTILLO J.G., WOOLLEY D.J., FAMIANI F. 2010. *Effects of defoliation on fruit growth, carbohydrate reserves and subsequent flowering of 'hayward' kiwifruit vines*. Sci. Hort., 125: 579–583.
- FRANKLIN K.A., WHITELAM G.C. 2004. *Light signals, phytochromes and cross-talk with other environmental cues*. J. Exp. Bot., 55: 271–276.
- FUKUDA N., FUJITA M., OHTA Y. 2008. *Directional blue light irradiation triggers epidermal cell elongation of abaxial side resulting in inhibition of leaf epinasty in geranium under red light condition*. Sci. Hort., 115: 176–182.
- GARDNER F.P., PEARCE R.B., MITCHELL R.L. 1985. *Physiology of crop plant*. Ames, USA, Iowa State University Press.
- GHOLINEZHAD E., AYNABAND A., HASSANZADE GHORTAPEH A., NOORMOHAMAD, G., BERNOUSI I. 2009. *Study of the effect of drought stress on yield, yield components and harvest index of sunflower hybrid Euroflor at different levels of nitrogen and plant population*. Not. Bot. Horti. Agrobot. Cluj. Napoca., 37(2): 85–94.
- HEATHER A., GRAHAM H., DECOTEAU D.R. 1997. *Young watermelon plant growth responses to end-of-day red and far-red light are affected by direction of exposure and plant part exposed*. Sci. Hort., 69: 41–49.
- HEUVELINK E. 1999. *Evaluation of a dynamic simulation model for tomato crop growth and development*. Ann. Bot., 83: 413–422.
- HOLT N.M., ZENTNER R.P. 1985. *Effect of plant density and row spacing on agronomic performance and economic returns of non-oil seed sunflower in southeastern Saskatchewan*. Can. J. Plant Sci., 65: 501–509.
- HURD R.G. 1974. *The effect of an incandescent supplement on the growth of tomato plants in low light*. Ann. Bot., 38: 613–623.
- IBRAHIM H.M. 2012. *Response of some sunflower hybrids to different levels of plant density*. APC-BEE Procedia., 4: 175–182.
- KASPERBAUER M.J. 1987. *Far-red light reflection from green leaves and effects on phytochrome mediated assimilate partitioning under field conditions*. Plant Physiol., 85: 350–354.
- KASPERBAUER M.J., KARLEN D.L. 1994. *Plant spacing and reflected far-red light effects on phytochrome-regulated photosynthate allocation in corn seedlings*. Crop Sci., 34: 1564–1569.
- KRIZEK D.T., ORMROD D.P. 1980. *Growth response of grand rapids lettuce and first lady marigold to increased far-red and infrared radiation under controlled environments*. J. Am. Soc. Hortic. Sci., 105: 936–939.
- KUBOTA S., YAMATO T., HISAMATSU T., ESAK S., OI R., ROH M.S., KOSHIOKA M. 2000. *Effect of red-and far-red-rich spectral treatment and diurnal temperature alternation on the growth and development of petunia*. J. Japan. Soc. Hort. Sci., 69(4): 403–409.
- KUREPIN L.V., WALTON L.J. 2007. *Interaction of red to far red light ratio and ethylene in regulating stem elongation of Helianthus annuus*. Plant Growth Regul., 51: 53–61.
- KUREPIN L.V., NEIL EMERY R.J., PHARIS R.P., REID D.V. 2007. *Uncoupling light quality from light irradiance effects in Helianthus annuus shoots: putative roles for plant hormones in leaf and internode growth*. J. Exp. Bot., 58(8): 2145–2157.

- LAMBERS H., CHAPIN F.S., PONS T.L. 2008. *Plant physiological ecology (2nd ed)*. New York, USA, Springer-Verlag.
- LEE J.H., HEUVELINK E. 2003. *Simulation of leaf area development based on dry matter partitioning and specific leaf area for cut Chrysanthemum*. *Ann. Bot.*, 91: 319–327.
- LI S., RAJAPAKSE N.C., YOUNG R.E., OI, R. 2000. *Growth responses of chrysanthemum and bell pepper transplants to photoselective plastic films*. *Sci. Hort.*, 84: 215–225.
- LIBENSON S., RODRIGUEZ V., LÓPEZ PEREIRA M., SÁNCHEZ R.A., CASAL J.J. 2002. *Low red to far-red ratios reaching the stem reduce grain yield in sunflower*. *Crop Sci.*, 42: 1180–1185.
- LINDSTRÖM L.I., PELLEGRINI C.N., AGUIRREZÁBAL L.A.N., HERNÁNDEZ L.F. 2006. *Growth and development of sunflower fruits under shade during pre and early post-anthesis period*. *Field Crops Res.*, 96: 151–159.
- LÜTTGE U. 2007. *Carbon dioxide signaling in plant leaves*. *C. R. Biologies*, 330: 375–381.
- MALLAKAL S.K., MCDONNELL K., DUDLEY S.A., SCHMITT J. 1999. *Effect of red to far-red ratio and plant density on biomass allocation and gas exchange in *Impatiens capensis**. *Int. J. Plant Sci.*, 160(4): 723–733.
- MAZZELLA M.A., ZANOR M.I., FERNIE A.R., CASAL J.J. 2008. *Metabolic responses to red/far-red ratio and ontogeny show poor correlation with the growth rate of sunflower stems*. *J. Exp. Bot.*, 59(9): 2469–2477.
- MILLER J.F., FICK G.N. 1978. *Influence of plant population on performance of sunflower hybrids*. *Can. J. Plant Sci.*, 58: 597–600.
- MORIONDO M., ORLANDINI S., VILLALOBOS F.J. 2003. *Modelling compensatory effects of defoliation on leaf area growth and biomass of sunflower (*Helianthus annuus* l.)*. *Europ. J. Agron.*, 19: 161–171.
- MORRISON M.J., STEWART D.W. 1995. *Radiation-use efficiency in summer grape*. *Agron. J.*, 87: 1139–1142.
- NEZAMI A., KHAZAEI H.R., BOROUMAND REZAZADEH Z., HOSSEINI A. 2008. *Effects of drought stress and defoliation on sunflower (*Helianthus annuus*) in controlled conditions*. *Desert.*, 12: 99–104.
- OLSZEWSKI N., SUN T., GUBLER, F. 2002. *Gibberellin signaling: biosynthesis, catabolism, and response pathways*. *Plant Cell. Suppl.*: S61–S80.
- OYAERT E., VOLCHAERT E., DEBERGH, P.C. 1999. *Growth of chrysanthemum under coloured plastic films with different light qualities and quantities*. *Sci. Hort.*, 79: 195–205.
- POLAT T., OZER H., OZTURK E. 2011. *Responses of hybrid and open pollination sunflowers (*Helianthus annuus* l.) to defoliation*. *Aust. J. Crop Sci.*, 5(2): 132–137.
- POURSAKHY N., KHAJEPOUR M. 2014. *Effect of planting pattern and plant density on growth and yield of sunflower (hisun-36) hybrid*. *Agron. J.*, 104: 54–61.
- PRICE H.J., JOHNSTON J.S. 1996. *Influence of light on dna content of *Helianthus annuus* linnaeus*. *Proc. Natl. Acad. Sci. USA.*, 93: 11264–11267.
- ROSHDI M., REZADOOST S., KHALILI MAHALLEH J., HAJI HASANI ASL N. 2009. *Effects of plant density and defoliation at different developmental stages on yield and yield components of nuts sunflower*. *Iranian J. New Agric. Sci.*, 15: 41–54.
- SANGOI L., GRACIETTI M.A., RAMPAZZO C., BIANCHETTI P. 2002. *Response of Brazilian maize hybrids from different areas to changes in plant density*. *Field Crop Res.*, 79: 39–51.
- SARALA M., TAULAVUORI K., TAULAVUORI E., KARHU J., LAINE K. 2007. *Elongation of scots pine seedlings under blue light depletion is independent of etiolation*. *Environ. Exp. Bot.*, 60: 340–343.
- SCHNEITER A.A., JOHNSON B.L. 1994. *Response of sunflower plants to physical injury*. *Can. J. Plant Sci.*, 74(4): 763–766.
- SCHNEITER A.A., JONES J.M., HAMMOND J.J. 1987. *Simulated hail research in sunflower defoliation*. *Agron. J.*, 79: 431–434.
- SEVERINO L.S., FREIRE M.A.O., LUCENA A.M.A., VALE L.S. 2010. *Sequential defoliations influencing the development and yield components of castor plants (*Ricinus communis* l.)*. *Ind. Crops Prod.*, 32: 400–404. doi: 10.1016/j.indcrop.2010.06.007.
- SMITH H. 1982. *Light quality, photoperception, and plant strategy*. *Ann. Rev. Plant Physiol.*, 33: 481–518.

- TAIZ L., ZEIGER E. 2006. *Plant Physiology. 4th Ed.* Sunderland, Massachusetts, USA, Sinauer Associates Inc.
- TERASHIMA I., HANBA Y.T., TAZOE Y., VYAS P., YANO S. 2006. *Irradiance and phenotype: comparative ecodevelopment of sun and shade leaves in relation to photosynthetic CO_2 diffusion.* J. Exp. Bot., 57: 343–354.
- VAN HINSBERG A.A., VAN TIELDEREN P. 1997. *Variation in growth from in relation to spectral light quality (red/far red ratio) in *Plantago lanceolata* l. In sun and shade population.* Oecologia, 111: 452–459.
- VANDEBUSSCHE F., VAN DER STRAETEN D. 2004. *Shaping the shoot: a circuitry that integrates multiple signals.* Trends Plant Sci., 9: 499–506.
- VOLKOV A.G., DUNKLEY T.C., LABADY A.J., BROWN C.L. 2005. *Phototropism and electrified interfaces in green plants.* Electrochim. Acta., 50: 4241–4247.
- VOLKOV A.G., DUNKLEY T.C., MORGAN S.A., RUFF II D., BOYCE Y.L., LABADY A.J. 2004. *Bioelectrochemical signaling in green plants induced by photosensory systems.* Bioelectrochemistry, 63: 91–94.
- VOS J. 1995. *The effects of nitrogen supply and stem density on leaf attributes and stem branching in potato (*Solanum tuberosum* l.).* Potato Res., 38(3): 271–279.
- WILSON S.B., RAJAPAKSE N.C. 2001. *Growth regulation of sub-tropical perennials by photoselective plastic films.* J. Environ. Hort., 19(2): 65–68.
- XIA S., CHEN S., ZHAO L., WANG, G. 2006. *Density effects on plant height growth and inequality in sunflower population.* Agron. J., 48: 513–519.
- XIONG, J. PATIL G.G., MOE R. 2002. *Effect of dif and end- of- day light quality on stem elongation in *Cucumis sativus*.* Sci. Hort., 94: 219–229.
- YAMADA A., TANIGAWA T., SUYAMA T., MATSUNO T., KUNITAKE T. 2008. *Improvement of *Eustoma grandiflorum* (raf.) Shinn. Cut flower quality for early-autumn shipping with long-day treatment using light sources that delay flower bud formation.* J. Jpn. Soc., 77: 296–303.
- YAMAZAKI H., OI R., HAMANO M., YAMATO Y., MIURA H. 2000. *Inhibition of bulb development of *Allium wakegi araki* by covering with far- red- intercepting film in summer.* J. Japan. Soc. Hort. Sci., 69(3): 250–254.
- YANG F., HUANG S., GAO R., LIU W., YONG T., WANG X., WUA X., YANG W. 2014. *Growth of soybean seedlings in relay strip intercropping systems in relation to light quantity and red:far-red ratio.* Field Crop Res., 155: 245–253.
- YANO S., TERASHIMA I. 2001. *Separate localization of light signal perception for sun or shade type chloroplast and palisade tissue differentiation in *Chenopodium album*.* Plant Cell Physiol., 42: 1303–1310.
- YOUSEFPOOR Z., YADAVI A. 2014. *Effect of biological and chemical fertilizers of nitrogen and phosphorus on quantitative and qualitative yield of sunflower.* Iranian J. Agric. Sci. Sustain. Prod., 24(1): 95–112.
- ZHOU Y., SINGH B.R. 2002. *Red light stimulates flowering and anthocyanin biosynthesis in American cranberry.* Plant Growth Reg., 38: 161–171.

