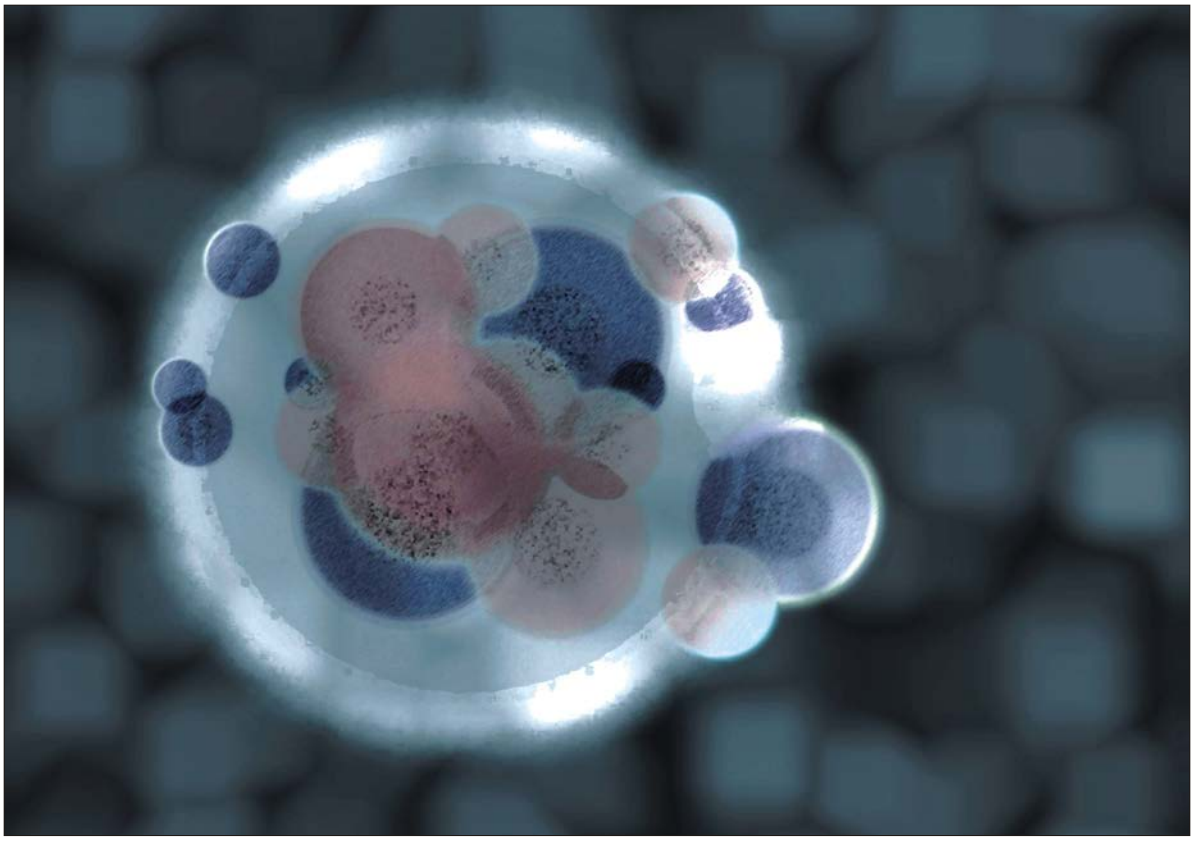

# Journal of Biological Sciences

ISSN 1727-3048

science alert

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Journal of Biological Sciences 7 (2): 263-269, 2007
ISSN 1727-3048


# Photosynthetic Contribution of the Inflorescence and Adjacent Green Tissue to Grain Yield in Four Safflower (*Carthamus tinctorius* L.) Genotypes under Diverse Environmental Conditions

Parviz Ehsanzadeh, Rouia Mahmoudieh and Nasrin Fareed
Department of Agronomy and Plant Breeding, College of Agriculture,
Isfahan University of Technology, Isfahan, Iran

**Abstract:** The hypothesis that grain yield per plant is to some extent proportional to the photosynthetic tissue of inflorescence and adjacent organs was tested on four safflower genotypes under two diverse field conditions, one in summer 2002 and the other in spring 2003. In each four-replicate RCBD field experiment the genotypes Arak 2811, Kouseh, Nebraska-10 and AC Sterling (K12 in 2003) were seeded at 3 m long plots, where each plot consisted five rows, spaced 45 cm apart with plants 7 cm apart on each row. Shading treatment, consisting unshaded control, inflorescence only and inflorescence along with its adjacent two leaves was applied on inflorescences of ten plants per plot from pollination to physiological maturity. Both levels of shading treatment led to significant decreases in 1000-seed weight, seed weight per inflorescence, seed number per inflorescence, seed yield per plant and harvest indices in both years. Averaged over genotypes, 14 and 36% decreases in seed yield per plant due to an imposed source limitation (i.e., the shading treatment) after inflorescence formation were observed in 2002 and 2003, respectively. The imposed source limitation led to 14 and 30% decreases in the safflower plants' harvest indices in 2002 and 2003, respectively, due, apparently, to a reduction in seed size, seed weight per inflorescence and seed yield per plant under the shading treatments. Further studies are recommended to determine the correlation between the photosynthetic area of the inflorescence and related organs of these genotypes with seed yield per plant under normal and stressful conditions and to determine the pattern of redistribution of the photoassimilates with different environmental conditions during safflower grain filling.

**Key words:** Inflorescence, photosynthetic area, *Carthamus tinctorius*, seed yield

## INTRODUCTION

Safflower (*Carthamus tinctorious*) is an oilseed plant and Iran is thought as one of the centers of origin of this cultivated species (Weiss, 2000). The fruit, an achene (commonly known as seed), may contain up to 45% oil, consisting of 70 to 75% linoleic acid. In addition to pharmaceuticals, its oil products could be used in the paint industries. Safflower, accounting for less than one percent of the world annual oilseed production, is considered as a neglected crop plant (Weiss, 2000). Vast genetic variation along with resistance to adverse environmental conditions and the fact that it could be sown both as a spring and as a summer crop in central Iran has, recently, attracted the attention of some Iranian researchers to this neglected crop (Azari and Khajehpour, 2003; Ehsanzadeh and Zarian, 2003).

Although the magnitude of dry matter that can be obtained from an agronomic crop depends on many factors, among basic physiological processes upon which dry matter production of the crop depends is the photosynthetic efficiency of its green surfaces. Furthermore, the amount of economic yield is, partly, a function of synthesis, translocation and accumulation of the photosynthetic products. Among all plant green surfaces, the contribution to fruit (Flore and Layne, 1999) or grain (Fairey and Daynard, 1978) production varies depending on both spatial and temporal proximity of those green surfaces to the reproductive phase and organs and the quality of previously stored assimilates (Lauer and Shibles, 1987; Sawada *et al*., 1995).

A quantitative determination of contribution of growth stages or plant parts adjacent to inflorescence to dry matter production and grain yield should advance our understanding of physiological processes that determine crop yield. Furthermore, the study of these relationships could be important for breeding strategies, because of possible correlations between the photosynthetic

**Corresponding Author:** Parviz Ehsanzadeh, Department of Agronomy and Plant Breeding, College of Agriculture, Isfahan University of Technology, Isfahan, Iran Fax: 98-311-391-3453

surfaces and grain yield per inflorescence. With the exception of the report by Urie *et al.* (1968), indicating 15% decrease in grain yield due to the removal of the safflower upper leaves, no one has reported on the contribution made to grain yield by the photosynthetic surfaces of inflorescence and adjacent organs in this species. Differences, between spring-sown and summer-sown safflower crops, in the magnitude of the mentioned contribution may occur.

Significant contributions to grain yield and differences among genotypes have been reported in other crop species. For awned barley (*Hordeum vulgare* L.) genotypes, photosynthetic activity of the awns continues throughout grain filling and, in some genotypes, maximum photosynthesis rates may occur only few days prior to the physiological maturity (Johnson *et al.*, 1975). Furthermore, removing the top two leaves at the heading stage leads to a decrease in spike dry weight due, mainly, to an imposed limitation of source capacity for photosynthates. Nevertheless, as Kjack and Witters (1974) have reported the extent of contribution made by awns may depend on awn size and morphology. Based on the high correlation coefficients found between grain dry weight and the components of photosynthetic area above the flag leaf node, Simpson (1968) concluded that the photosynthetic area above the flag leaf node is an important determinant of dry matter production in wheat genotypes. In two wheat (*Triticum aestivum* L. em Thell.) genotypes, grown under controlled environmental conditions, ear and flag leaf could contribute approximately 35 and 40%, respectively, to grain yield (Voldeng and Simpson, 1967).

For a number of other crops, the roles of the photosynthetic surfaces of the inflorescence and related organs in grain filling have been established. Evidence of a significant contribution of the corn (*Zea mays* L.) husk and ear leaf in dry matter per plant has been provided by Hesketch and Musgrave (1962) and Sawada *et al.* (1995). In oat (*Avena sativa* L.), differences in the net photosynthetic rate of flag leaf in different genotypes have been reported (Criswell and Shibles, 1971). In common bean (*Phaseolus vulgaris* L.), the $CO_2$-fixing capacity per unit area of the pod may reach 26% of that of the green leaves (Crookston *et al.*, 1974). Leaf removal treatments on sunflower (*Helianthus annuus* L.) have revealed that the magnitude of contribution of individual leaves, to sunflower grain yield, is a function of leaf position on the plant. Schneiter *et al.* (1987) reported that a wide range of defoliation treatments at reproductive stage of sunflower may lead to significant decreases in both individual seed weight and seed yield per plant. While defoliating sunflower at physiological maturity leaves no impact on grain yield or its components, defoliation before the flowering stage may lead to a severe decrease in such grain yield components as 1000-seed weight and seed number per plant (Muro *et al.*, 2001).

Having major morphological differences with aforementioned plants, it seems logical to expect that any proportionality between grain yield and green surfaces of inflorescence and related organs in safflower differs from those found with other crop plants. Therefore, this study was undertaken to determine the contribution of the inflorescence and its adjacent green tissue to grain yield in spring-sown and summer-sown safflower in Isfahan, central Iran.

## MATERIALS AND METHODS

**Experiment 1: Summer 2002:** A four-replicate Randomized Complete Block Design field experiment was conducted at the Lavark Research Farm (Lat. 32° 32'N, Long. 51' 23'E), College of Agriculture, Isfahan University of Technology, Isfahan, Iran in the summer of 2002. Four safflower genotypes, Arak-2811, Kouseh, Nebraska-10 and AC Sterling were seeded under irrigated field conditions where each plot consisted five 3 m long rows, spaced 45 cm apart with plants spaced 7 cm apart within each row. These genotypes were chosen for this experiment partly because they differ considerably in their morphological characteristics, particularly inflorescence size and number per plant (Ehsanzadeh and Zarian, 2003). With the exception of AC Sterling, a genotype obtained from the Canadian collections, the remaining three genotypes constitute the major portion of areas under safflower production in Iran. Plants were seeded in mid-June, 2002, at approximately 5 cm in depth and irrigated immediately. Surface irrigation was carried out after a 100 and 80 mm evaporation from a standard Class-A Evaporation Pan during the vegetative and reproductive growth phases, respectively. Shading treatments were applied using 10×6 cm lightproof, air permeable khaki paper pockets when each inflorescence had, approximately, completed pollination and remained until physiological maturity. The open end of the pocket was closed using a stapler. The three treatments included an unshaded control, shading of the inflorescence only and shading of the inflorescence along with the two upper most leaves of the corresponding branches. All the inflorescences of ten successive plants of the second row in each plot, after leaving a 0.5 m long section as margin, were subjected to a specific shading treatment. The maturation of inflorescence within the shades appeared quite normal and healthy. The basic experimental unit for statistical analysis was the mean value of the ten plants within a single plot.

After physiological maturity on 25th October, 2002, ten plants constituting each experimental unit were harvested at ground level and the number of inflorescences, number of seeds per inflorescence, 1000-seed weight, seed weight per inflorescence, seed yield per plant and harvest index were determined based on 15% moisture content, following drying in an oven at 75°C, for 36 h.

**Experiment 2: Spring 2003:** All materials and methods used were similar to those described for 2002's Experiment, except for:

Genotype AC Sterling was substituted by the K12, a breeding line recently drawn from the local variety Kouseh. This substitution was done due, mainly, to a poor performance, e.g., susceptibility to the diseases, observed from the former genotype in 2002.

The genotypes were seeded on mid-March and harvested on the 3rd week of July 2003, following their physiological maturity.

All the inflorescences of seven successive plants of the second row in each plot, after leaving a 0.5 m long section as margin, were subjected to a specific shading treatment. The basic experimental unit for statistical analysis was the mean value of the seven plants within a single plot. Weather information was obtained from the Isfahan Meteorological Organization.

**Statistical analyses:** Data collected from the two experiments were, separately, analyzed, using the ANOVA procedure of SAS statistical software (SAS In stitute Inc., 1997) and mean separation was performed using Fisher's LSD.

## RESULTS

The synopsis of weather information indicates that while in 2002 monthly maximums of temperature varied from 33.0 to 39.4, for 2003 it ranged from 18.3 to 37.7°C (Table 1).

Genotype affected 1000-seed weight, seed weight per inflorescence, number of seeds per inflorescence, harvest index ($p<0.01$) in both years and seed yield per plant ($p<0.01$ and $p<0.05$ for 2002 and 2003, respectively) (Table 2). In 2002, Kouseh produced smaller seeds, AC Sterling lower seed weight per inflorescence, seed number per inflorescence and seed yield per plant, compared to the other genotypes (Table 3). Kouseh and AC Sterling produced the greatest and smallest numbers of seeds per inflorescence, respectively, while Nebraska-10 and Kouseh had the highest and AC Sterling the lowest harvest indices among all of the genotypes. In 2003, Arak-2811 and Kouseh ranked first and last, respectively, in terms of seed size, while Nebraska-10 and K12 ranked first and last, respectively, with regard to their seed weights and numbers per inflorescence. Furthermore, Nebraska-10 had a higher seed yield per plant and harvest index, compared to the other genotypes.

Shading affected 1000-seed weight, seed weight per inflorescence, number of seeds per inflorescence and harvest index ($p<0.01$) in both years and seed yield per plant ($p<0.05$ and $p<0.01$, respectively, for the two consecutive years) (Table 3). The interaction of genotype x shading was statistically significant only for seed weight per inflorescence ($p<0.05$) and the number of seeds per inflorescence ($p<0.05$) for 2002, while no significant interactions was detected for 2003.

Table 1: Synopsis of weather data for the two growing seasons

| Summer 2002 | | | Spring 2003 | | |
|---|---|---|---|---|---|
| Month | Mean temp. (°C) | Max. temp. (°C) | Month | Mean temp. (°C) | Max. temp. (°C) |
| June | 25.6 | 36.4 | March | 11.4 | 18.3 |
| July | 28.2 | 39.4 | April | 13.8 | 20.6 |
| Aug. | 27.8 | 38.8 | May | 16.6 | 24.3 |
| Sept. | 25.9 | 37.0 | June | 22.8 | 31.3 |
| Oct. | 21.7 | 33.0 | July | 28.5 | 37.7 |

Table 2: Analyses of variances (mean squares) for 1000-seed weight, seed number/inflorescence, seed weight/inflorescence, seed yield/plant and harvest index of four safflower genotypes at three levels of shading

| | | 1000-seed weight | | Seed weight/ inflorescence | | Seed number/ inflorescence | | Seed yield/plant | | Harvest index | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Source of variation | df | 2002 | 2003 | 2002 | 2003 | 2002 | 2003 | 2002 | 2003 | 2002 | 2003 |
| Replication | 3 | 3.97 | 3.50 | 0.014 | 0.062 | 6.03 | 70.70* | 20.20 | 7.88 | 7.00 | 27.95 |
| Genotype (G) | 3 | 134.60** | 28.90** | 0.563** | 0.192** | 774.40** | 213.09** | 15.38** | 9.80* | 112.00** | 50.92** |
| Shading (S) | 2 | 65.70** | 51.40** | 0.151** | 0.882** | 42.14** | 568.94** | 16.25* | 116.84** | 47.00** | 396.38** |
| G x S | 6 | 1.31 | 2.50 | 0.020* | 0.023 | 14.30* | 33.84 | 4.47 | 2.02 | 3.00 | 12.44 |
| Error | 33 | 1.98 | 3.30 | 0.006 | 0.024 | 5.52 | 24.23 | 3.42 | 2.94 | 3.00 | 11.36 |
| CV | | 4.7 | 6.0 | 12.1 | 18.3 | 11.0 | 17.8 | 15.6 | 18.7 | 8.2 | 15.4 |

*, ** Significant at the 0.05 and 0.01 levels of significance, respectively

Table 3: Means* for 1000-seed weight, seed weight/inflorescence, seed number/inflorescence, seed yield/plant and harvest index of four safflower genotypes at three levels of shading

| | 1000-seed weight (g) | | Seed weight/ inflorescence (g) | | Seed number/ inflorescence | | Seed yield/plant (g) | | Harvest index (%) | |
|---|---|---|---|---|---|---|---|---|---|---|
| Genotype | 2002 | 2003 | 2002 | 2003 | 2002 | 2003 | 2002 | 2003 | 2002 | 2003 |
| Arak-2811 | 32.2a | 32.4a | 0.75a | 0.86b | 23.1b | 26.3bc | 13.06a | 9.39ab | 20.62b | 21.4b |
| Kouseh | 25.0b | 28.7c | 0.72a | 0.81bc | 28.6a | 28.1b | 13.46a | 8.45b | 22.87a | 20.6b |
| Nebraska-10 | 31.5a | 30.3b | 0.76a | 1.01a | 23.9b | 33.1a | 14.27a | 10.34a | 23.28a | 24.9a |
| AC-Sterling | 31.3a | | 0.31b | | 9.9c | | 6.51b | | 16.62c | |
| K12 | | 30.6b | | 0.71c | | 23.0c | | 8.46b | | 20.6b |
| LSD (0.05) | 1.2 | 1.5 | 0.06 | 0.12 | 2.0 | 3.9 | 1.54 | 1.37 | 1.4 | 2.7 |
| Shading | | | | | | | | | | |
| Control | 32.3a | 32.6a | 0.74a | 1.11a | 23.3a | 34.2a | 12.98a | 12.21a | 22.7a | 27.4a |
| Inflorescence | 29.5b | 29.5b | 0.60b | 0.67b | 20.6b | 22.6b | 11.37b | 7.06b | 20.4b | 17.7c |
| Inflorescence and Leaf | 28.3c | 29.4b | 0.56b | 0.76b | 20.3b | 25.9b | 11.13b | 8.22b | 19.4b | 20.6b |
| LSD (0.05) | 1.1 | 1.3 | 0.06 | 0.11 | 1.7 | 3.4 | 13.3 | 1.19 | 1.2 | 2.3 |

* Means with the same letter in each column are not significantly different, based on LSD (0.05)

Regardless of the interactions observed in 2002, the two levels of shading treatment, averaged over genotypes and years, led to significant decreases in 1000-seed weight, seed weight per inflorescence, seed number per inflorescence, seed yield per plant and harvest index, though the magnitudes of the decreases differed from one year to the other (Table 3). These decreases were, approximately, 22 and 36 for seed weight per inflorescence, 14 and 38 for seed yield per plant and 14 and 30% for harvest index at the two consecutive years, respectively.

Table 4: Means for seed weight/inflorescence of four safflower genotypes at three levels of shading in 2002

| Genotype | Arak-2811 | Kouseh | Nebraska-10 | AC-Sterling |
|---|---|---|---|---|
| Control | 0.94 | 0.83 | 0.89 | 0.32 |
| Inflorescence | 0.70 | 0.65 | 0.72 | 0.32 |
| Inflorescence and leaf | 0.61 | 0.68 | 0.65 | 0.29 |
| LSD (0.05) | 0.11 | | | |

Table 5: Means for number of seeds per inflorescence of four safflower genotypes at three levels of shading in 2002

| Genotype | Arak-2811 | Kouseh | Nebraska-10 | AC-Sterling |
|---|---|---|---|---|
| Control | 26.8 | 29.8 | 26.8 | 9.6 |
| Inflorescence | 22.2 | 26.6 | 23.2 | 10.4 |
| Inflorescence and leaf | 20.4 | 29.4 | 21.6 | 9.7 |
| LSD (0.05) | 3.4 | | | |

## DISCUSSION

Lower yield components and therefore, seed yield per plant of AC Sterling (Table 3) can be attributed to its susceptibility to powdery mildew (*Erysiphe cichoraceum* DC.). In many kinds of diseases, photosynthesis is reduced due mainly to lessened chlorophyll content and reduced photosynthetic surface along with an accelerated respiration of the host plant (Agrios, 1997). Due to severe infection by the abovementioned pathogen, AC Sterling plants appeared deficient in photosynthetic surfaces and activity particularly during their reproductive growth stages. The low photosynthetic activity of AC Sterling led to the smallest seed sizes, lowest seed weight per inflorescence and seed yield per plant and the poorest harvest index of this genotype among all the genotypes.

Differences of Kouseh, Arak-2811, Nebraska 10 and K12 with regard to their grain yield components are related, at least in part, to morphological differences among these genotypes. Differences, in terms of yield components, between safflower genotypes have been reported by other researchers (Ashri *et al.*, 1974; Abel, 1976).

Shading caused significant decreases in seed weight per inflorescence for 2002 in all of the genotypes, with the exception of AC Sterling, leading to a significant shading x genotype interaction (Table 4). Shading led to significant decreases in the number of seeds per inflorescence for Arak-2811 and Nebraska-10 and no significant changes for AC-Sterling and Kouseh and, therefore, a significant genotype x shading interaction for the 2002 (Table 5). Lack of any significant impact of shading on the seed weight and number per inflorescence in AC Sterling is, probably, related to the infection by powdery mildew. The disease infection, apparently, resulted in a low photosynthetic contribution of the inflorescences and related green surfaces to the grain and dry matter production. Nevertheless, the main cause for the lack of significant decreases under shading in Kouseh is not understood.

Green tissue adjacent to the main sinks at seed filling stage (i.e., inflorescence, bracts and upper leaves of safflower) may play a significant role in providing photosynthate to these sinks (Hopkins, 1999; Gardner *et al.*, 1985), but the magnitude of contribution could vary depending on the flowering behaviour of the crop (i.e., determinate vs. indeterminate), seed or fruit position in the canopy (i.e., upper vs. lower parts) and the environmental conditions experienced during different plant growth stages, particularly grain filling (i.e., mild vs.

warm temperatures). Voldeng and Simpson (1967) and Simpson (1968) concluded that the green tissue above the flag leaf node could play a significant role in grain filling of wheat genotypes. Other workers (Kjack and Witters, 1974; Johnson *et al*., 1975) have reported major contributions to grain yield by photosynthetic tissues adjacent to the inflorescence in different crop species. However, some researchers did not find a significant (Salvador and Pearce, 1988) or large (Cantrell and Geadelmann, 1981) contribution of current husk photosynthesis to grain filling in corn. Meanwhile, evidence indicates that assimilates previously stored in corn husk can play a significant role in its grain filling (Fairey and Daynard, 1978; Salvador and Pearce, 1988).

In the present study, due to the effects of shading on seed size and number, an approximate 14% decrease was observed in both seed weight per inflorescence and seed yield per safflower plant in 2002, while these effects led to an, approximately, 36% decrease in both seed weight per inflorescence and seed yield per plant in 2003. Removal of the upper leaves in safflower in another experiment (Urie *et al*., 1968) has, also, led to a 7% decrease in seed weight, which agrees, to some extent, to the results obtained with this study in 2002. Significant decreases in the harvest indices under shading treatments of the present study, in general and in 2003, in particular, could be attributed to the fact that after inflorescence formation, photosynthates produced by green tissues on the upper portion of the plant are mainly translocated to the reproductive sinks (Simmons and Jones, 1985). It appears that shading resulted in a decrease in photosynthetic activity at the inflorescence level (i.e., limiting the source activity at seed filling stage), which led, in turn, to the decreases in the harvest indices of these safflower genotypes. A determining role of source activity, in grain yield, has been well established (McAlister and Krober, 1958). Furthermore, source-sink ratio during grain filling period plays a determining role in the seed weight of crop plants such as corn (Borras and Otegui, 2001; Borras *et al*., 2002). Also sink-source imbalances may lead to alterations in photosynthesis and its products (Iglesias *et al*., 2002). In soybean, for example, removal of the upper leaves results in an increase in photosynthetic activity of the remained lower leaves (Klubertanz *et al*., 1996). Despite a same degree of source limitation, imposed by shading treatment, at the two years, a more pronounced limitation of the photosynthetic activity at the inflorescence level in 2003 led, apparently, to the more substantial decreases in harvest indices of the safflower genotypes, compared to 2002.

Results of the present work suggest a relatively small contribution of the upper green tissues, particularly the two upper leaves, to the grain yield of the summer-sown safflower in 2002, compared to some crop plants such as wheat (Johnson *et al*., 1974) and barley (Johnson *et al*., 1975) and the spring-sown safflower, i.e., the 2003's experiment. Meanwhile, in some crop plants such as sunflower (Johnson, 1972) and soybean (Klubertanz *et al*., 1996), too, a relatively low contribution of the upper leaves in grain filling have been reported and for safflower (Urie *et al*., 1968) removal of the upper leaves has led only to a decrease of 15% in grain yield. A significant impact of leaf removal on the number of seeds per head in both sorghum (Stickler and Pauli, 1961) and wheat (Mahmood and Choudhary, 1997) has been reported. Whether the inflorescence and its related organs of this set of safflower genotypes differed significantly in their photosynthetic areas or not was not determined in this experiment. Though, it is known that a significant correlation exists between the flag leaf area and grain yield per tiller in wheat (Voldeng and Simpson, 1967). Furthermore, contribution, to grain yield, of green tissue above flag leaf node in cereals may undergo changes with stressful conditions such as drought (Gardner *et al*., 1985). Yet, remobilization and translocation of the previously stored photoassimilates may play a significant role in grain filling, when the source activity is limited (i.e., shading on the upper green tissue in present study) and become insufficient in fulfilling the sink demands (Fairey and Daynard, 1978). Finally, the contribution of the previously stored photoassimilates in grain filling of wheat and barley increases from approximately 5%, under normal conditions, to as much as 50%, under stressful conditions (Gent, 1994).

It seems that, with the present study, the discrepancy observed between the results of the two experiments conducted in 2002 and 2003 is, at least in part, related to the differences between environmental conditions of the two growing seasons (Table 1). While the daily max. temperatures for June and July 2003 were 32.0 and 38.0°C, these temperatures for September and October 2002 were 37.0 and 33.0°C, respectively. Safflower grain filling, in 2002, was coincided with the shorter days and milder daily temperatures characteristic of late summer and early fall in Isfahan. These conditions led, apparently, to a prolonged duration of grain filling along with longer lasting green tissues in lower or at least middle parts of the canopy, thus a relatively lowered photosynthetic contribution of the upper green tissues to grain yield, when compared to the rest of existing green parts in the canopy. The grain filling stage in 2003, on the other hand, was coincided with the longer days and warmer daytime temperatures characteristic to late spring and early summer in Isfahan. These conditions resulted in a shortened duration of grain

filling along with senescing green tissues in middle or at least lower parts of the canopy. Under such conditions, an increased contribution of the upper green tissues (i.e., the inflorescence and the adjacent leaves) to grain filling is not far from one's expectation. While an increase in the photosynthetic activity of the unshaded green tissue of safflower cannot be ruled out, a difference in the extent of redistribution of the photoassimilates during the safflower grain filling in mild days of early fall 2002, relative to the warm days of early summer 2003 cannot be ruled out, too.

Further experiments are needed to determine any possible correlation between photosynthetic areas of inflorescence and related organs and grain yield in different safflower genotypes. Furthermore, the contribution to grain yield of photosynthetic surfaces adjacent to safflower inflorescence under stressful conditions such as drought has to be determined. The redistribution pattern of the photoassimilates during grain filling stage of safflower under different environmental conditions needs to be scrutinized. After conducting such experiments, it may be possible to conclude whether using photosynthetic areas of inflorescence and related organs could be an effective tool for selecting safflower genotypes with a better agronomic performance, particularly under stressful conditions.

## ACKNOWLEDGMENTS

This study was financially supported by the College of Agriculture, Isfahan University of Technology. Scientific inputs from Dr. M.R. Khajehpour and Dr. G.A. Saiedi are appreciated. Mr. Ali Ashrafi and Mostafa Khazaei are thanked for their technical assistances.

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