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EFFECT OF SOURCE-SINK RELATIONSHIP ON YIELD COMPONENTS AND YIELD OF CONFECTION SUNFLOWER (*Helianthus annuus* L.)

Yehoshua Saranga*, Pavel Horcicka** and Shmuel Wolf

Hebrew University of Jerusalem, Faculty of Agriculture, Department of Field Crops, Vegetables and Genetics, P.O. Box 12, Rehovot 76100, Israel.

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SUMMARY

The effect of source-sink relationships on yield and its components was studied in two field trials. Sunflower plants (confection type, cv. DY-3) with small and large heads were treated as follows: seed from the peripheral area of the head were removed at the end of flowering, or leaves were removed soon after appearance (early leaf removal) or at the end of flowering (late leaf removal). Floret number was significantly lower in small vs. large heads, but was not affected by the source-sink manipulations. The percentage of filled seeds in the peripheral and intermediate head zones was 75-80, whereas in the central head zone it was 50-55. Neither head size nor source-sink manipulations had any effect on the percentage of filled seeds. With respect to the applied treatments, seed weight was the most responsive yield component studied. Seed weight was higher in large vs. small sunflower heads; it increased as a result of seed removal and decreased as a result of leaf removal.

Key words: Photosynthesis, source-sink relationship, sunflower, yield, yield components.

INTRODUCTION

One of the most important factors affecting yield and its components is assimilate availability and allocation to reproductive structures, which is primarily determined by leaf area, photosynthetic activity, and the number of competing sinks (Mauney et al., 1978). In different species yield components have different stability, and changes in resource availability can affects mainly one yield component or another. For example, various levels of assimilate supply in

* Corresponding Author.
** Present address: Department of Field Crops, University of Agriculture, Prague 16321, Czech Republic

cotton caused primarily a change in fruit number rather than fruit size (Pettigrew, 1994), whereas in maize they induced major changes in kernel mass rather than kernel number (Lemcoff and Loomis, 1994).

Sunflower (*Helianthus annuus* L.) yield per plant is determined by the number of florets per plant, their fertility and seed weight, all of which are correlated with head and stem diameters and associated with plant density (Punia and Gill, 1994). Low fertility, causing a high percentage of unfilled seed, is a common phenomenon in sunflower (Steer et al., 1986; Merrien, 1992; Punia and Gill, 1994). The occurrence of unfilled seed, sometimes up to 60% of total florets (Steer et al., 1986), may limit yield potential both by reducing seed number and by the assimilates being used to develop their hulls. However, it is possible that a reduction in the percentage of unfilled seed will be compensated for by reduced assimilate allocation to other sinks which may reduce seed weight. Leaf area index (LAI) and leaf area duration are crucial for light interception and photosynthetic rate, and for determining the total amount of assimilate and final yield. Maximum light interception is obtained in sunflower when the LAI reaches a value of 2.5-3 (Merrien, 1992). Alteration of effective leaf area by disease can reduce sunflower productivity; for example, rust infection at various phenological stages influenced the number of seeds per head, the weight of individual seeds and the percentage of oil content and reduced oil yield (Siddiqui and Brown, 1977).

Confection sunflowers (for human feed) are large-seeded cultivars (1000 seed weight ~200g), satisfying specific consumer demands for seed quality such as size, shape, color, easily removable hull, and suitable roasting characteristics. Seed size is of special importance in confection sunflower as it is not only a major yield component, but also an important quality trait. Therefore, manipulation of the crop to increase seed set must not be accompanied by a reduction in seed size. Such a manipulation, if at all possible, must be based on an understanding of the processes underlying seed set and carbon allocation in sunflower.

This study was conducted to investigate the effects of source-sink relationships on the yield and yield components of confection sunflower. Since source-sink relationships may vary between plants with small and large heads, treatments in this study were applied to both types.

MATERIALS AND METHODS

Two field experiments were conducted in 1993 and 1994 at Timurim and Revadim, respectively, both located about 15 km from the southern Mediterranean shore of Israel (about 34.8xE longitude and 31.75N latitude for both locations). Sunflower plants cv. DY-3 were grown in 0.96 m spaced rows at a density of 3.2 plants m^{-2} (as recommended for confection sunflower), unless indicated different. The plants were sprinkler-irrigated, as recommended for commercial sunflower cultivation in that region. Diseases, insects and weeds were effectively controlled.

Table 1: Effects of source-sink manipulations and head size on morphological parameters of confection sunflower (cv. DY-3)

	Head diameter^x (cm)		Leaf	Leaf area^y ($m^2 \cdot plant^{-1}$)	
	1993	1994	number	Small heads	Large heads
Main effect of source-sink manipulation					
Control	19.5 a	24.4 a	25.3 a	0.92 a	1.48 a
Early leaf removal	-	21.4 b	13.1 b	0.65 b	0.82 b
Late leaf removal	20.7 a	22.6 ab	12.9 b	0.43 c	0.74 b
Seed removal	16.7 b	20.8 b	24.8 a	1.01 a	1.60 a
Main effect of head size					
Small heads	15.1 b	19.4 b	18.6 a		
Large heads	23.4 a	25.2 a	19.5 a		

x Data are from the 1994 experiment with exception of head diameter, measured in both years.
y Interaction (source-sink manipulation x head size) was significant only for leaf area and hence detailed data is shown for this parameter, main effects for all the others.
a,b,c Mean separation for each factor within each column by Student-Newman-Keuls multiple range test at P=0.05. Means followed by different letters are significantly different.

Experimental design

In 1993, plants were randomly selected in a commercial sunflower field 28 days after emergence. The selected plants were divided into two predicted head sizes according to leaf size estimations (preliminary observations showed a positive correlation between average leaf area and head size, r^2= 0.93). All plants were selected at the onset of flowering to synchronize flowering period. Source-sink manipulations were applied to these two groups of plants at the end of flowering (soon after the anthesis of all florets of the selected plants), as follows: (1) control, (2) removal of every other leaf from the entire plant (termed hereafter as late leaf removal), and (3) seed removal from the peripheral zone - one third of the head diameter. A randomized factorial design was used with five single plant replicates.

In 1994, different head sizes were induced by growing the plants at two different densities: 3.2 plants m^{-2} to produce small heads and 1.6 plants m-2 to produce large heads (details of actual head sizes in Table 1). Four source-sink treatments were applied in a split-plot design with five replicates: (1) control, (2) early leaf removal - every other leaf from the entire plant was cut off soon after appearance, (3) late leaf removal (as in 1993), and (4) seed removal (as in 1993). Plant densities were applied in main plots, each consisting of 6 rows x 12m, while source-sink treatments were applied in sub plots consisting of a single row, with two untreated border rows. Synchronized flowering plants were marked in each plot, with three plants being harvested at the end of the season.

Leaf area

Leaf area was determined nondestructively at the end of flowering by measuring leaf width (at the widest point) and length, and calculating area as follows:

Leaf area = 0.6981 width length.

This equation was obtained by comparing leaf area measured with an area meter (LI-3100, LI-COR, USA) with leaf area estimated by leaf width and length (r^2= 0.98, n=40).

Photosynthesis

Photosynthetic rate was measured in 1994, using a portable photosynthesis system (LI-6200, LI-COR, USA). Measurements were made three times at 2-week intervals, one week before the onset of flowering, at mid flowering period and a week after flowering termination. The youngest fully-expanded leaf (3rd or 4th from the top) was used to measure photosynthetic rate. Two to three measurement cycles were conducted on each of the measurement days between 10h to 15h, using a specific leaf (one in each sub plot) for the entire day.

Harvest and seed evaluation

Plants were harvested at physiological maturity (55-60 days after flowering) and seeds from individual heads were separated into three zones: peripheral (the zone from which seeds were removed), intermediate and central, each covering a third of the head diameter. In the 1994 experiment, three heads were harvested from each plot, with seeds of each head separated and pooled by location on the head. Filled and unfilled seeds were sorted with an air blower seed cleaner, counted and weighed. Seeds of all three zones (filled+unfilled; including remains of aborted florets) were summed to calculate total floret number.

Statistics

Experimental data were analyzed using the GLM procedure of the SAS statistical software (Joyner, 1985). Means were separated by the Student-Newman-Keuls multiple range test at P=0.05 level.

RESULTS AND DISCUSSION

Plant morphology and photosynthetic capacity

Significant differences in head diameter were obtained as a result of the plant selection in 1993 and the different plant densities in 1994 (Table 1). These differences were largest in 1993, where the average diameter of the small heads was 63% that of the large heads; in 1994, the small heads diameter was 77% that of the large ones. Head diameter was also affected by the sink-source manipulations. The smaller head diameter obtained with the seed removal treatment directly reflected the treatment effect (only the seed-covered zone was measured). Reduced head diameter was induced in 1994 by both leaf removal treatments.

Although the leaf removal treatment reduced the number of leaves to 50% of the control, this proportion was not maintained in terms of leaf area (Table 1). A significant interaction (head size x treatment) was found for the total leaf area measured in 1994. With the late leaf removal treatment, leaf area was about 50% of the control for both head sizes. However, in the early leaf removal treatment, leaf area of plants with large heads was 55% of the control, whereas in plants with small heads it was 70% of the control. Leaf area of the large-headed plants did not increase in response to leaf removal, probably because leaf size was already close to its maximal growth potential. Seed removal from both head sizes induced a slightly higher leaf area than that of controls (not significant).

Average photosynthetic rate of the youngest fully expanded leaf was 35.5, 36.6 and 28 μmol CO_2 $m^{-2}s^{-1}$ a week before, during, and a week after flowering, respectively (detailed data not shown). Photosynthetic rate per unit leaf area was not significantly affected by any of the factors examined on any of the measurement days. Average photosynthetic photon flux densities (PPFD) during the three measurement days were 1530, 1850 and 1720 μmol $m^{-2}s^{-1}$, respectively. Irrigation was applied during flowering and seed set and the plants were not exposed to water stress. Therefore, the reduction in photosynthetic rate after flowering cannot be attributed to changes in PPFD or in plant water status. It is more likely to be a result of reduced photosynthetic efficiency due to leaf senescence.

Yield components and yield

In both years, floret number on the small heads was significantly lower than that on the large heads (Table 2). Residual floret number under the seed removal treatment was 56% and 68% of controls in 1993 and 1994, respectively. Leaf removal treatment consistently induced a small albeit insignificant increase in floret number. The number of florets has been reported to largely depend on environmental factors and management practices imposed at early developmental stages of the plant, such as rust inoculation (Siddiqui and Brown, 1977), fertilization, and plant density (Steer et al., 1986). In our study, various plant densities applied early in the season induced changes in head size and floret number. However, none of the source-sink manipulations applied at later stages affected floret number. Although floret number seems to be positively correlated with head size, the reduction in head size imposed by early leaf removal was not associated with any reduction in floret number, probably due to an early floret initiation.

Table 2: Effects of source-sink manipulations and head size on floret number and percentage of filled seeds in confection sunflower (cv. DY-3)

	Floret number·head^{-1}		Filled seed (%)	
	1993	1994	1993	1994
Main effect of source-sink manipulationx				
Control	1034 a	976 a	73.2 a	68.9 a
Early leaf removal	-	1049 a	-	71.7 a
Late leaf removal	1069 a	1017 a	69.1 a	68.5 a
Seed removal	583 b	669 b	68.2 a	63.3 a
Main effect of head size				
Small heads	662 b	846 b	71.2 a	67.0 a
Large heads	1239 a	1009 a	71.6 a	69.1 a

x Interactions (source-sink manipulation x head size) were not significant and hence only main effects are shown.

a,b Mean separation for each factor within each column by Student-Newman-Keuls multiple range test at P=0.05. Means followed by different letters are significantly different.

The percentage of filled seeds differed considerably between the various sectors of the sunflower heads. In the peripheral and intermediate zones, 75-80% of the seeds were filled, as compared with 50-55% in the central zone (detailed data not shown). However, neither head size nor source-sink manipulations had any effect on the percentage of filled seeds in any of the head zones or over the entire head (Table 2).

The percentage of filled seeds could be affected by one or more of the following factors: insufficient pollination, physiological limitations, or self-incompatibility. In the 1993 experiment, we were unable to increase the percentage of filled seeds by artificial pollination, in addition to natural bee and insect pollination (data not shown). Ben-Porath and Masad (1993), working with the DY-3 cultivar used in this study, also reported that percentage of filled seeds was not affected by enhanced bee pollination. It seems, therefore, that under normal cultivation conditions, with the appropriate density of beehives, pollination does not limit seed set. However, insufficient assimilate supply to the developing seeds may cause seed abortion (Ganeshaiah and Shaanker, 1994). This was not evident in our experiments, where percentage of filled seeds was not affected by source-sink manipulations. Sunflower plants have a system of genetic self-incompatibility (Fick, 1989) which may be a major cause for the unfilled seeds. If there was an effect of source-sink manipulations on seed set, it may have been masked by the effect of self-incompatibility.

Seed weight was significantly affected in most cases (various head sectors and years) by both head size and source-sink manipulations (Table 3). Higher seed weight was obtained in the large sunflower heads. Seed weight increased as a result of seed removal, whereas a lower seed weight was obtained as a result of leaf removal. Early leaf removal seems to have caused an assimilate deficiency resulting in reduced seed weight, whereas late leaf removal did not have a significant effect. On the other hand, removal of seeds from the peripheral zone of the sunflower head caused a surplus of assimilate which in some cases increased seed weight. Seed weight in the peripheral and intermediate head zones was higher relative to the central zone. It is possible that the reduction of seed weight in the central head zone is a result of the high sink strength of the developing seed in the peripheral and intermediate zones.

Table 3: Effects of source-sink manipulations and head size on seed weight of various head sectors of confection sunflower (cv. DY-3)

	Peripheral zone		Intermediate zone		Central zone	
	1993	1994	1993	1994	1993	1994
	1000-seed weight (g)					
Main effect of source-sink manipulationx						
Control	144.1 a	244.3 a	137.1 b	240.5 ab	110.0 b	222.4 b
Early leaf removal	-	214.0 c	-	204.2 c	-	178.1 c
Late leaf removal	148.1 a	230.8 b	137.2 b	228.2 b	101.8 b	207.6 b
Seed removal	(removed)	(removed)	198.7 a	252.9 a	181.0 a	241.0 a
Main effect of head size						
Small heads	138.5 b	217.8 b	141.8 b	219.5 b	117.8 b	197.8 b
Large heads	170.9 a	241.7 a	178.7 a	243.4 a	147.6 a	226.8 a

x Interactions (source-sink manipulation x head size) were not significant and hence only main effects are shown.

a,b,c Mean separation for each factor within each column by Student-Newman-Keuls multiple range test at P=0.05. Means followed by different letters are significantly different.

Yield of the plants with small heads was significantly lower than that of those with large heads. However, because large head size was obtained in 1994 by reducing plant density by 50%, in terms of yield per soil surface area, the small heads were more productive than the large ones.

The impact of source-sink manipulations on yield components and yield depends on the plant's compensatory capacity. Seed removal resulted in 44% and 32% reduction in floret number in 1993 and 1994, respectively (Table 2). Seed yield per plant with this treatment was 16% and 33% lower than that of controls in 1993 and 1994, respectively (Table 4). In 1993, the remaining seeds in this treatment weighed 55% more than controls (Table 3), compensating for the removed seeds. In 1994, the remaining seeds were only 7% higher in weight relative to controls, indicating no compensation for the seed removal.

Early or late removal of 50% of the leaves reduced seed yield by only 10% (not significant) in 1994, and in 1993 late leaf removal did not reduce yield at all (Table 4). The lack of response to late leaf removal can be partially explained by estimate that pre-anthesis assimilates represent 15-27% of the total carbon in

Table 4: Effects of source-sink manipulations and head size on yield of confection sunflower (cv. DY-3)

	Seed yield (g ·plant-1)	
	1993	1994
Main effect of source-sink manipulation		
Control	106.4 a	157.4 a
Early leaf removal	-	144.7 a
Late leaf removal	105.7 a	142.6 a
Seed removal	89.6 a	104.9 b
Main effect of head size		
Small heads	66.2 b	115.7 b
Large heads	152.3 a	159.1 a

x Interaction (source-sink manipulation x head size) were not significant and hence only main effects are shown.

a,b,c Mean separation for each factor within each column by Student-Newman-Keuls multiple range test at P=0.05. Means followed by different letters are significantly different.

sunflower seeds (Hall et al., 1989, 1990). There was no evident compensation for leaf removal by enhanced photosynthetic rate. Leaf removal presumably increased the PPFD reaching the lower leaves, enabling them to increase their activity and compensate for the reduced leaf area. Moreover, after early leaf removal from plants with small heads, the remaining leaves had a larger final area relative to the control, and leaf area per plant was therefore reduced by only 30% (Table 1), which could also contribute to compensation. Redistribution of assimilates between to the seeds (e.g., a change of harvest index) could also contribute to the compensation observed.

Yield of an individual sunflower plant can be expressed as a function of number of florets, percentage of filled seeds and seed weight. Number of florets, known to be affected by treatments imposed at early growth stages, was significantly affected by head size in both years. In this study, source-sink relationships had no effect on seed set, as reflected by the percentage of filled seeds. Seed weight was most responsive to source-sink manipulations, whether they were imposed at the vegetative growth stage (early leaf removal) or later, at the end of flowering (seed removal).

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EFECTO DE LA RELACIÓN FUENTE-SUMIDERO SOBRE LOS COMPONENTES DEL RENDIMIENTO Y EL RENDIMIENTO DE GIRASOL NO OLEAGINOSO (*Helianthus annuus* L.)

RESUMEN

El efecto de la relación fuente-sumidero en rendimiento y sus componentes fue estudiado en dos ensayos de campo. Plantas de girasol (del tipo no oleaginoso cv DY-3) con capítulos pequeños y grandes fueron tratados de la forma siguiente: las semillas fueron separadas al final de la floración, o las hojas fueron cortadas inmediatamente después de la aparición (separación temprana) o al final de la floración (separación tardia). El número de flores fue significativamente más bajo en las cabezas pequeñas que en las grandes pero no fue afectado por las manipulaciones fuente-sumidero. El porcentaje de semillas llenas en las zonas periféricas e intermedias del capítulo fue 75-80 mientras que en la zona central del capítulo fue 50-55. Ni el tamaño del capítulo ni las manipulaciones fuente-sumidero tuvieron ningún efecto en el porcentaje de semillas llenas. En relación a los tratamientos aplicados, el peso de semilla fue el componente de rendimiento que respondió mejor. El peso de la semilla fue más alto en capítulos grandes que en pequeños y se aumentó como respuesta a la separación de semilla y descreció como resultado de la eliminación de hojas.

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EFFET DES RELATIONS SOURCE-PUITS SUR LES COMPOSANTES DU RENDEMENT ET LE RENDEMENT DU TOURNESOL DE BOUCHE (*Helianthus annuus* L.)

RÉSUMÉ

L'effet des relations source-puits sur le rendements et ses composantes a été étudié dans deux essais au champ. Les plantes de tournesol (de type bouche, cv. DY-3) à petits ou gros capitule ont été traitées de la maniére suivante: les graines ont été enlevées à la fin de la floraison, ou bien les feuilles ont été enlevées dès leur apparition (suppression précoce) ou encore à la fin de la floraison (suppression tardive). Le nombre de fleurons a été significativement réduit chez les petits capitules par rapport aux grands, mais n'a pas été modifié par les manipulations source-puits. Le pourcentage de graines pleines a la périphérie et dans les zones intermédiaires du capitule était de l'ordre de 75-80, tandis que dans la zone centrale il était de 50-55. Ni la taille du capitule ni les manipulations source-puits n'ont eu d'effet sur le pourcentage de graines pleines. En ce qui concerne les traitements appliqués, le poids de graines était plus élevé chez les capitules de grande taille par repport aux petits. Le poids de graines a augmenté du fait de la suppression de graines mais a diminué par suit de la suppression des feuilles.