The Effects of Intercepted Solar Radiation on Sunflower (*Helianthus annuus* L.) Seed Composition from Different Head Positions

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ABSTRACT: The effect of intercepted solar radiation during fruit filling on seed weight and oil content from seeds of three sectors of the head in two sunflower (*Helianthus annuus* L.) hybrids of low and high potential oil percentage was investigated. Seed weight in each sector depended on both the level of radiation intercepted (modified by shading and thinning plants) and the genotype grown. A higher level of intercepted solar radiation increased seed weight in each sector. Central seeds of shaded plants showed the lowest weight. The seed and kernel oil content hierarchy among the three sectors was modified only in the hybrid with high potential oil content. For each head sector, variations in seed oil content associated with changes in the level of intercepted radiation could be accounted for by changes in the kernel oil content, not in the kernel/seed ratio. Significant relationships were found between seed oil and kernel oil contents when analyses between treatments ($R > 0.86$) and sectors ($R > 0.92$) were carried out. These relationships together with the growing conditions of plants during seed filling, the genotype, and the seed position on the head are essential factors that should be taken into account when selecting seeds in sunflower breeding programs since they affect the commercial/industrial quality of seeds.

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KEY WORDS: Intercepted radiation, kernel content, kernel oil content, seed oil content, sunflower, sunflower head.

Morphological and physicochemical traits such as a 1000-seed weight, the seed and the kernel oil contents, and the kernel percentage (w/w) define the commercial and industrial quality of sunflower seeds. Lots of seed that are superior with respect to some of these characteristics (e.g., seed oil content) imply higher profits in the commercial process. Some of the quality characteristics mentioned above may be interrelated. For example, the oil concentration in the seed (OS), a term equivalent to oil content, can be expressed as

$$\mathrm{OS} = H \cdot \mathrm{OH} + K \cdot \mathrm{OK} \qquad [1]$$

where H is the hull/seed ratio (w/w), OH is the hull oil concentration, K is the kernel/seed ratio (w/w), where the kernel is the dehulled seed, and OK represents the kernel oil concentration (1).

The 1000-seed weight and other physicochemical traits vary with the position of the seeds in the head. The sunflower head is a capitulum in which flowering starts in the outer part of the head and proceeds toward the center. This means that seeds in the peripheral areas come from flowers developed and fertilized before those in the head center. Therefore, the beginning of fruit filling is subject to the position of the seed in the head (2). The weight per seed, the seed oil content, the kernel oil content, and the kernel/seed ratio were higher in peripheral seeds than at the head center in five field-grown sunflower lines (3). Environmental factors and growing conditions during the seed filling may affect seed quality. The individual weight and the chemical composition of the seeds in the center of the head were modified by removing the seeds located in the periphery, as a result of decreased competition between sinks for assimilates (4). The level of solar radiation intercepted during the seed-filling stage affected the individual weight of seeds inserted in different sectors of the head (5).

The radiation intercepted per plant may vary owing to changes in the incident radiation and/or in the leaf area per plant, thus being modified through crop management (e.g., changes in the sowing date). The level of intercepted radiation modified the weight per seed and the oil content in a hybrid with a high potential oil percentage (6,7). The effect seems to depend on the genotype since the weight per seed of a hybrid with a low potential oil percentage was affected by changes in the radiation, but the oil content remained unaffected (7,8).

Effects of changes in the intercepted radiation on characteristics that may influence the commercial and/or industrial quality of seeds from different head positions have not been investigated. It is unknown if the effect is similar in hybrids with different potential oil percentages. Consequently, the objective of this work was to analyze, in two sunflower genotypes with low and high potential oil content, the effect of the level of solar radiation (corresponding to the photosynthetically active range of the spectrum) intercepted during the fruit-filling stage on the 1000-seed weight, whole seed and kernel oil contents, and the kernel/seed ratio in seeds from different positions of the head. We also investigated the existence of relationships between seed oil content, kernel oil content, and kernel content in each sector of the head and the effects of the level of intercepted radiation on these relationships.

EXPERIMENTAL PROCEDURES

Details of the culture. Two experiments were carried out at the INTA Balcarce Experimental Station, Buenos Aires, Argentina (37°45′ S and 58°18′ W). The two hybrids were DeKalb G-100 (black pericarp with high potential oil content) and Norkin Tordillo (NKT, striped pericarp with low potential oil content). These genotypes showed maximal average

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oil contents of 52 and 47%, respectively, in comparative assays of commercial cultivars at INTA over three seasons (1991–1993). The sowing dates were November 30, 1993 (experiment A), and November 14, 1995 (experiment B). The experiments were randomized split-plot designs with four and three replicates each year, respectively. The densities were 72,000 and 45,000 plants/ha for experiments A and B, respectively. The plants were kept under good nutrient and moisture conditions and free from plagues and diseases. A detailed description of the experiments has been given elsewhere (7).

After the end of flowering (February 22, 1994, and February 2, 1996), the following treatments were applied to cause variations in the level of radiation intercepted during fruit filling: (i) shading with a plastic mesh retaining 50% of the incident radiation (shading, S); (ii) untreated control lots (control, C); and (iii) uniform thinning until a final density corresponding to one-fourth (experiment A) or one-third (experiment B) of the initial density was achieved (thinning, T). Physiological maturity (PM) in G-100 was reached 30, 30, and 34 d after flowering (daf) for treatments S, C, and T, respectively, in experiment A and 39, 45, and 45 daf in experiment B. In NKT, this stage was reached 35, 36, and 36 daf (A) and 41, 40, and 41 daf (B).

Measurements. Global daily incident radiation was measured with a pyranometer (LI-200SB; LI-COR, Lincoln, NE) located 400 m from the experiments. Daily incident radiation corresponding to the photosynthetically active range of the spectrum was calculated as 0.48 × global daily incident radiation. The proportion of solar radiation intercepted by the crop at noon was determined according to Gallo and Daughtry (9) as:

$$1 - \frac{\mathrm{Rb}}{\mathrm{Ro}} \qquad [2]$$

where Rb is the radiation measured below the last green leaf, and Ro is the radiation measured above the canopy. Rb and Ro were measured weekly at solar noon (±1 h), with a line quantum sensor (LI-191SB; LI-COR). The daily proportion of intercepted solar radiation was calculated according to Charles-Edwards and Lawn (10), as:

$$\frac{2 \times \text{proportion of intercepted solar radiation at noon}}{(1 + \text{proportion of intercepted solar radiation at noon})} \qquad [3]$$

In sunflower, this correction allowed a substantial reduction in the error arising from a single measure at noon (11). The daily proportion of intercepted solar radiation between two measurements was calculated by linear interpolation. Daily intercepted solar radiation was calculated as the product of daily incident solar radiation and daily proportion of intercepted solar radiation.

For each replicate of each treatment, five heads were harvested several days after physiological maturity. Each head was divided into three concentric rings (periphery, middle, and center) constituted by approximately 10 parastics (false spirals) of fruits. Fruits from each sector were manually separated from the head, thus gathering the fruits taken from the five selected heads into a unique sample for each sector, treatment, and replicate.

Moisture contents were determined according to Association of Official Analytical Chemists methods (12). Seed weight and hull content were determined for each sector by manual separation and were calculated as the average of triplicates of 100 seeds. Both seed and kernel oil contents were obtained by nuclear magnetic resonance (NMR) with an NMR Newport Analyzer, Magnet Type 10 (Oxford Instruments, Buckinghamshire, England) (13). The kernel oil content of seeds from the central sector could not be determined owing to the small size of the available sample. Analysis of variance was used to determine whether differences between mean values of at least duplicate runs for each treatment and sector were significant at $P < 0.05$. When the F value was significant, the Tukey method was applied to estimate the significance of each treatment. Correlation analysis of the data was performed using SAS (SAS Institute Inc., Cary, NC) (14). Statistical significance of the correlation coefficient (R) was determined at $P < 0.05$.

RESULTS

Growth conditions. Daily mean air temperature and daily mean incident radiation from the application of treatments (TA) to PM of the control lots were 20.9 ± 2.8°C and 19.4 ± 3.0 MJ $\mathrm{m}^{-2}\,\mathrm{d}^{-1}$ in experiment A, and 19.4 ± 3.2°C and 22.0 ± 4.9 MJ $\mathrm{m}^{-2}\,\mathrm{d}^{-1}$ in experiment B.

Cumulative intercepted radiation (MJ plant^{-1}) during the period TA–PM is shown in Table 1. Cumulative intercepted radiation from the end of flowering to PM was, in G-100, approximately six and four times higher in the case of treatment T in comparison with treatment S in experiments A and B, respectively. In NKT, it was six (experiment A) and three (experiment B) times higher. Table 1 also shows that the quantity of radiation intercepted was always greater in experiment B than in experiment A.

1000-Seed weight. The 1000-seed weight decreased from the periphery to the center for both hybrids and in all treatments (Fig. 1). For each treatment and sector, the 1000-seed weight was greater in both years for NKT than for G-100, and it tended to be greater in experiment B than in experiment A, in which the quantity of radiation intercepted was less.

TABLE 1
Cumulative Intercepted Solar Radiation (MJ plant^{-1}) During the Period from the Application of Treatments (TA) to Physiological Maturity (PM) for Each Treatment in Hybrids G-100 and NKT[a]

		Treatment		
Hybrid	Experiment[a]	Shading	Untreated control	Thinning
G-100	A	12.3	22.9	74.3
	B	29.7	67.5	107.0
NKT	A	14.1	27.3	78.8
	B	37.6	68.9	102.4

[a] A, first experiment, 1993–1994; B, second experiment, 1995–1996.

The 1000-seed weight decreased in each sector as the quantity of radiation intercepted decreased (T, C, and S treatments), except for NKT hybrid, experiment B. In the latter case, in which the quantity of plants' intercepted solar radiation was the highest, the 1000-seed weight was not significantly affected by the treatments.

Seed oil content. For each sector, seed oil content was higher in G-100 than in NKT (up to 9% higher in experiment A and 12.7% higher in experiment B) except for the treatment for which the level of intercepted radiation was the lowest (S treatment, experiment A). Seed oil content was maximum in the center and minimum at the periphery in NKT (both experiments) and in G-100, experiment B. In experiment A, in which the quantity of intercepted radiation was lower, oil content in G-100 decreased from the periphery to the center in the case of the S treatment (Fig. 2).

In G-100, the seed oil content increased with the level of intercepted solar radiation in all sectors in experiment A (Fig. 2). In experiment B, in which the level of radiation intercepted was highest, the oil content was lowest for the S treatment, although it was not significantly different from the oil content for the T treatment in the middle and center.

In NKT, the seed oil content in the three sectors was slightly affected by changes in the level of radiation intercepted during filling (Fig. 2), showing smaller differences between treatments than in G-100. In this hybrid, the thinning treatment, representing a higher level of intercepted radiation, tended to correspond to a lower oil content than the other treatments; these differences were significant in experiment B but not in experiment A.

Kernel/seed ratio (w/w)—kernel oil content. Treatments applied significantly affected the kernel oil content of G-100 in both experiments (data shown in Fig. 3). The greatest differences in kernel oil content between treatments were detected in G-100. In experiment A, significant differences were found among the three treatments at the periphery and in the middle of the head. In experiment B, differences between treatments S and C and between treatments S and T were detected for the periphery, and among the three treatments for the middle sector. No effect of the quantity of intercepted radiation on kernel oil content in NKT was observed in any sector.

Kernel/seed ratio (w/w) increased from the periphery to the center in both hybrids (Table 2). In G-100, the level of radiation intercepted did not affect kernel/seed ratio. NKT showed the smallest kernel/seed ratio in the three sectors in treatment T, which represented the highest level of intercepted radiation. Differences detected were significant in experiment A but not in experiment B.

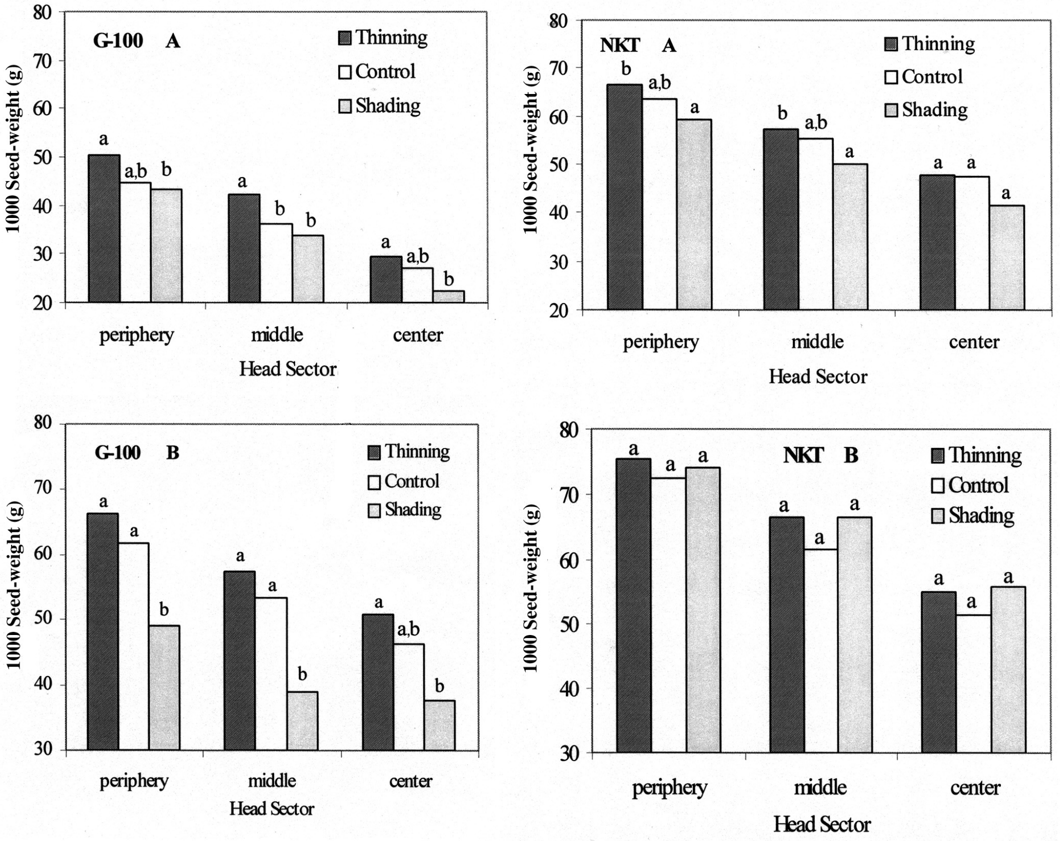

FIG. 1. Seed weight in three sectors of the head in hybrids G-100 and NKT for each of the treatments applied. A, First experiment, 1993–1994; B, second experiment, 1995–1996. Means accompanied by the same letter for each sector are not significantly different at $P < 0.05$ using Tukey's method.

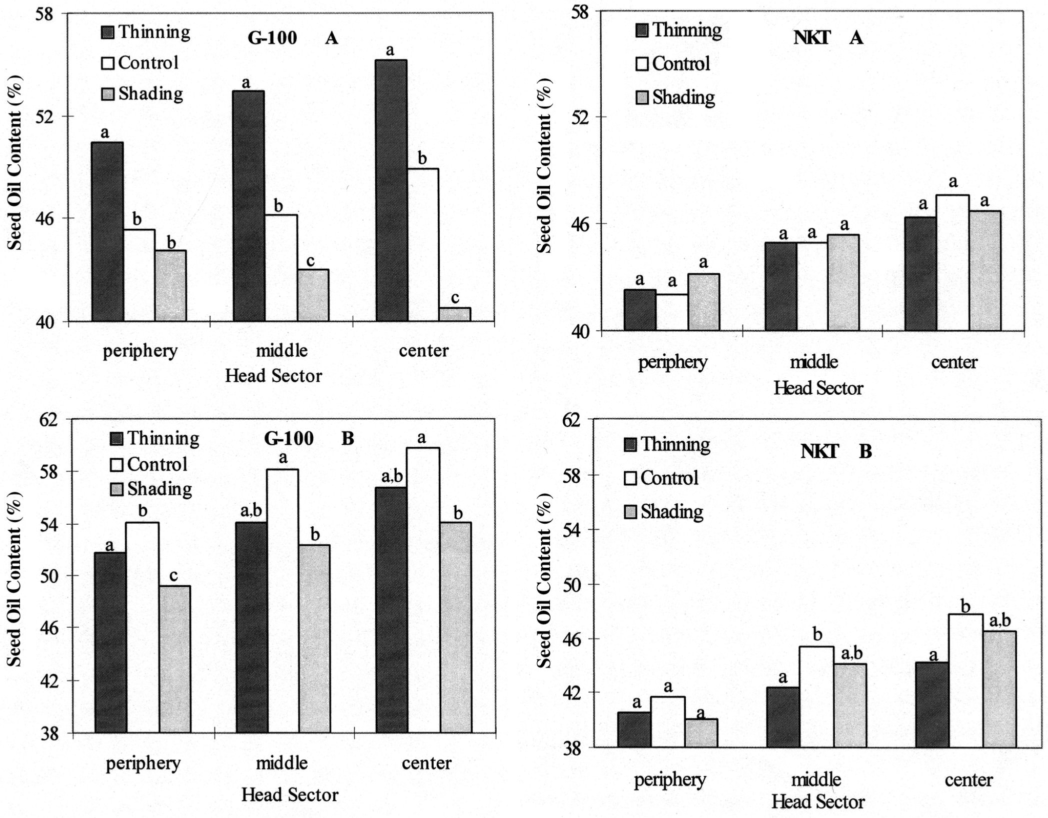

FIG. 2. Seed oil percentage in three sectors of the head in hybrids G-100 and NKT for each of the treatments applied. A, First experiment, 1993–1994; B, second experiment, 1995–1996. Means followed by the same letter for each sector are not significantly different at $P < 0.05$ using Tukey's method.

Relationships between kernel/seed ratio and seed oil content and between kernel oil content and seed oil content. In G-100, the seed oil content in each sector was closely related to the kernel oil content in experiments A ($R = 0.96$ and $R = 0.93$ for the periphery and the middle, respectively) and B ($R = 0.99$ and $R = 0.86$, respectively). For each sector, the variability in kernel oil content accounted for the variability in seed oil content by a common relationship for all treatments and experiments ($R = 0.97$ and $R = 0.94$ for the periphery and the middle, respectively) (Fig. 3). On the other hand, kernel/seed ratio was not related to seed oil content in any of the studied sectors nor when both experiments were analyzed together [$R = 0.13$ and $R = 0.26$ (both not significant) for the periphery and the middle, respectively]. Relationships between these variables were not significant for each experiment separately (for experiment A, $R = 0.41$ and $R = 0.16$ for the periphery and the middle, respectively; for experiment B, $R = 0.14$ and $R = 0.62$ for the periphery and the middle, respectively). Coincidentally, the correlation analysis showed that variations in seed oil content for each treatment and sector were, in general, accounted for by the variability in kernel oil content; close correlations were obtained for the S treatment ($R = 0.92$ and $R = 0.94$ for the periphery and the middle, respectively) and the C treatment ($R = 0.93$ and $R = 0.94$ for the periphery and the middle, respectively); the relation was lower and not significant for the T treatment [$R = 0.74$ (periphery) and $R = 0.55$ (middle)].

Variations in seed oil content between sectors were mainly accounted for by variations in kernel oil content when both experiments were analyzed together ($R = 0.90$, 0.92, and 0.80 for S, C, and T treatments, respectively). In spite of an increase of the kernel/seed ratio from the periphery to the center of the head (Table 2), no significant relationship was found with seed oil content in any treatment ($R = 0$, 0.44, and 0.20 for treatments S, C, and T, respectively). Despite the lower range of variation found in seed oil content, these results were not substantially altered when both experiments were analyzed separately (data not shown).

In NKT, the low variability in seed oil content between treatments (see Fig. 2) did not allow any relationship to be established for each sector between seed and kernel oil contents or between seed oil content and kernel/seed ratio. For the S and C treatments, the variability in seed oil content between sectors was accounted for by the kernel oil content but with low correlation coefficients ($R = 0.57$ and 0.56, respectively) when both experiments were analyzed together. No significant relationship was found in the case of the T treatment ($R = 0.40$). In most cases, no relationship was found between seed oil content and kernel/seed ratio when both experiments were analyzed separately nor when they were analyzed together [highest value of $R = 0.24$ (not significant)]. Only the T treatment in experiment B showed a significant relationship ($R = 0.92$).

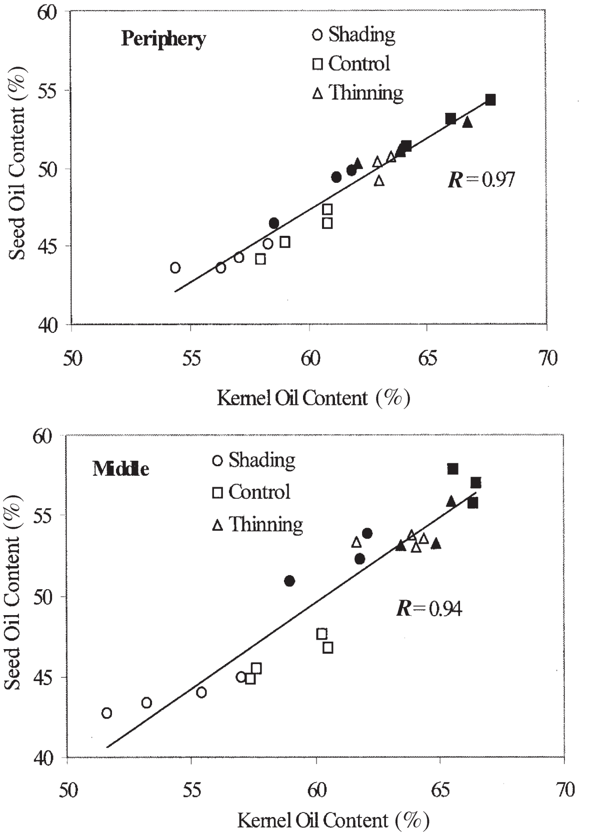

FIG. 3. Seed oil percentage as a function of kernel oil percentage in G-100. Open and filled symbols of the same shape represent the same treatment; open symbols correspond to experiment A and filled symbols to experiment B.

TABLE 2
Kernel/Seed Ratio (w/w) in Three Sectors of the Head in Hybrids G-100 and NKT^a

		G-100		NKT	
Sector	Treatment^b	A	B	A	B
Periphery	S	0.741^a	0.743^a	0.685^a	0.663^a
	C	0.726^a	0.746^a	0.650^b	0.663^a
	T	0.746^a	0.739^a	0.636^b	0.651^a
Middle	S	0.747^a	0.747^a	0.719^a	0.696^a
	C	0.738^a	0.739^a	$0.680^{a,b}$	0.696^a
	T	0.749^a	0.760^a	0.667^b	0.678^a
Center	S	0.769^a	0.776^a	0.765^a	0.724^a
	C	0.762^a	0.779^a	0.712^{ab}	0.727^a
	T	0.767^a	0.782^a	0.699^b	0.705^a

[a] Values followed by the same letter for each sector are not significantly different at $P < 0.05$ using Tukey's method. A, first experiment (1993–1994); B, second experiment (1995–1996).
[b] S, Shading; C, control; T, thinning.

DISCUSSION

The 1000-seed weight decreased from the periphery to the center for both sunflower hybrids investigated in this study. This is in agreement with results reported by many authors (2–4,15–17). Variations in the quantity of intercepted solar radiation modified 1000-seed weight in every sector and in both hybrids (except in NKT, experiment B). In spite of these changes, the hierarchy in 1000-seed weight among the sectors remained the same in all cases. The greater weight of seeds nearer the periphery may be due to a larger supply of nutrients or to less competition among seeds as a consequence of the greater available space per seed in the receptacle (4,18).

Seed oil content increased or decreased from the periphery to the center of the head, depending on the level of radiation intercepted and the genotype. In our experiments, variation in the level of intercepted radiation affected aerial dry matter, dry matter partitioning into seeds, and reserve remobilization (7), suggesting that the carbon nutrition level of the plant was modified by the treatments applied. In G-100, a decrease in the level of intercepted radiation modified the hierarchy in oil content but not the hierarchy in 1000-seed weight among different sectors of the head. However, in NKT, seed oil content increased from the periphery to the center of the head in all cases; the level of intercepted solar radiation did not affect this trend. Changes in the level of radiation intercepted during the filling stage of seeds and/or effects of genotype could explain why seed oil content has been reported to decrease from the periphery to the center by some authors (3,15,17), whereas others have reported an increase (2,16). Changes of seed quality attributes linked to the position of seeds on the head should be considered in sunflower breeding programs (3). The growing conditions of plants during seed filling should be considered in these programs as they can modify the hierarchy of seed oil content among different sectors of the head and so alter the results of the selection.

Sunflower seed differs from seeds of other oilseed crops in that the hull is an important component of its weight and the oil concentration in the hull is low (1). As can be deduced from Equation 1, significant changes in seed oil content may be caused by changes in the relative proportions of hull weight and seed weight or in the concentration of oil in the hull (19). In G-100, more than 74% of the variability in seed oil content was accounted for by the variability in kernel oil content, which exhibited large variations in seed oil percentage between experiments and treatments. Variations in seed oil content for a specific treatment and between sectors were also due to variations in the kernel oil content. No clear relationships were found between the oil percentage of seeds and kernel/seed ratio. Despite a lower variability in seed oil content between treatments and experiments, the NKT hybrid showed similar trends to G-100. All these results agree with reported findings that variations in the oil percentage of seeds between different sectors of the head originated from variations in the kernel oil percentage and not in the kernel content (20).

Kernel/seed ratio increased from the periphery to the center in both hybrids. This is opposite to the results found for five sunflower cultivated lines (3). Variations in the level of intercepted solar radiation did not affect this ratio in the hybrid of high potential oil percentage (black hull and lower proportion of hull in whole weight seed) whereas in hybrids with low potential oil percentage this ratio was sometimes modified by the treatments.

Variations in the level of intercepted radiation affected 1000-seed weight in the three sectors of the head (up to 48% in the same sector) without any effect (G-100) or with a very low effect in some cases (NKT) on kernel/seed ratio. It is very important to note that the hull weight is defined at the beginning of the seed filling stage, before the kernel weight is defined (21,22) and soon after the treatments were applied (23). The low variation in kernel/seed ratio found in this work suggests that the final size of the kernel could be determined by the final size of the hull.

An overall analysis of our results shows that the quality of seeds inserted in different sectors not only depends on the genotype but also may be modified by environmental conditions during the fruit filling and by the interaction between the environment and the genotype. The level of radiation intercepted during the seed filling may affect the commercial/industrial quality of seeds inserted in different head sectors. The effect is different according to the variable considered (seed weight or oil content), depending not only on the level of radiation intercepted but also on the genotype grown. This shows the absence of simple relationships between the position in the head and the oil content in seed and kernel as well as between the seed weight and these variables, even for the same cultivar. On these results, monitoring before harvest would be an interesting tool to use to obtain seeds with proper qualities, especially in breeding programs.

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