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YIELD OF DIFFERENT HEAD POSITIONS OF SUNFLOWER (*Helianthus annuus* L.) AND ITS RELATIONSHIP WITH VASCULARIZATION

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SUMMARY

This work was aimed to study, under different levels of radiation intercepted by the plants during the seed filling stage, the relationship between yield and vascularization in three concentric positions of the capitulum. At the end of flowering, we applied shading (to reduce intercepted radiation) and thinning (to increase it) to three culture plots: a shaded plot, a thinned plot and a shaded and thinned plot. One additional untreated plot was used as control. We harvested heads at flowering and at physiological maturity. We delimited on them three positions: outer, middle and inner. Portions of each position were extracted from physiological maturity heads and their yield components were determined. The remaining heads were fixed in F.A.A., soaked in paraffin, and transversely cut at seed insertion to measure vascularization variables (phloem and sieve tubes area, number of tranverse and longitudinal bundles and sieve pores diameter). The head area unit was used as a base in all measurements. Shading reduced dry weight in the three positions. The middle position showed the highest yield and the inner showed the lowest in the four plots. The yield of the former was high because its lower individual seed weight (decreasing from periphery to center in all plots) was compensated by a higher number of filled seeds. However, average sieve pores radius was similar among positions, and phloem and sieve tubes areas were similar among positions and treatments, which could not account for the differences in yield per head area unit between positions. This enables us to conclude that this variation would not be produced by vascularization lack.

Key words: **sunflower, head position, yield, seed filling stage**

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INTRODUCTION

The number of seeds and the individual seed weight, as yield components of the sunflower plant (*Helianthus annuus* L.), show a great variability among the outer, middle and inner positions of the head. Individual seed weight decreases from periphery to center (Goffner *et al.*, 1988; Karadogan *et al.*, 1998). The number of filled seeds at the center is usually also low, which means an important decrease in yield.

The low number of filled seeds at the center of the head (in other words, the low yield of this position) has been atributed to a deficient vascularization of it (Durrieu *et al.*, 1985). These authors report that vascular bundles enter the head by the periphery and that the center of the receptacle is made up of a medular parenchyma without bundles. Thus, outer seeds are fed directly by the capitulum bundles whereas inner seeds are supplied by branches that the peripheral bundles generate. The same authors also found that many of these bundles end with saccules or granules and therefore they would not be able to supply assimilates to the seeds. They suggest that this would cause a qualitative and quantitative gradient (from periphery to center) in seed nutrition. Against these results, some studies on plants fed with ^{14}C (Goffner *et al.*, 1988) and others with seed removal or defoliation (Steer *et al.*, 1988) suggest that vascularization of the inner position of the capitulum would not be restrictive for the transport of assimilates to the inner seeds.

The supply of assimilates to seeds and flowers of different head zones depends both on the relationship between source (mainly leaves and carbon reserves of the stem, Hall *et al.*, 1990) and sink and on the characteristics of the phloem in between (Farrar and Gunn, 1996). When calculating the flux of sucrose from source to sink, the phloem characteristics (sieve tubes area and sieve pores radius) are considered according to a new focus (Farrar and Williams, 1991; Farrar and Gunn, 1996) based on the equation of Poiseuille:

$$Js = \frac{C \cdot \delta P \cdot A \cdot r^2}{8\eta \cdot l} \qquad [1]$$

The flux *Js* of sucrose or any other solute depends on its concentration *C*, the turgor pressure difference between source and sink δP, the cross-sectional area of phloem *A*, the sieve pores radius *r*, the viscosity η of the sieve tubes contents, and the length *l* of the phloem. This equation has been used to explain experimental results (Minchin *et al.*, 1993; Aguirrezábal *et al.*, 1993). However, the description of sunflower head by Durrieu *et al.* (1985) has not been verified yet through the quantification of the characteristics of the phloematic tissue that it enables.

In this work, we analyzed the relationship between phloem quantity and phloematic tissue characteristics of three concentric head positions and their seed yield. Unlike previous surveys on this topic (Steer *et al.*, 1988; Goffner *et al.*, 1988), all the measured variables were based on the capitulum area. The phloem characteristics used in equation [1], *i.e.*, sieve tubes area and sieve pores radius, were specially studied. Finally, in order to obtain a substantial variation in yield, we modified the amount of photosynthetically active radiation (PAR) intercepted by the plants during the seed filling stage, which strongly affects the individual seed weight and the number of seeds in the studied hybrid (Andrade and Ferreyro, 1996; Dosio *et al.*, 1997).

MATERIALS AND METHODS

A typic argiudol soil was seeded with the hybrid Dekalb G100 in Balcarce (Argentina). The culture had a density of 7.2 plants/m^2 and was mantained under good hydric and mineral conditions. Further details of the culture management are given by Dosio *et al.* (1997). In this work, the experimental design was completely randomized.

At flowering end (MO stage, Merrien, 1992), we applied treatments to modify the amount of intercepted radiation per plant: shading to take intercepted radiation to 50% and thinning to take density to 1.8 pl/m^2. The culture was divided into four plots, each one with a combination of the two treatments: (i) a shaded plot (hereafter S treatment), (ii) a thinned plot (T treatment), (iii) a shaded and thinned plot (ST treatment), and (iv) a plot kept untreated as control (UC treatment). The global radiation (GR) was registered with a pyranometer (SIAP Biometallic, model PL1) placed 400 meters away from the experiment and the incident photosynthetically active radiation (PAR, 400-700 nm) was calculated as 0.48 GR. The coefficient of interception for each plot (CI) was estimated as 1 - (Ru/Ro), where Ru is the radiation measured under the last green leaf and Ro is the measurement over the canopy. The Ru and Ro values were measured with an integration bar (Line Quantum Sensor, LI-COR, Lincoln, NE) and were registered in a data storage central (LI-COR 1000). The measurements were done once a week following the Gallo and Daugthry (1986) technique, calculating the intermediate values by linear interpolation. Daily intercepted PAR was calculated as the product of PAR and CI. The plants in T, ST and S treatments intercepted respectively 256, 133 and 72% of the amount of radiation intercepted by the plants in the UC treatment during the seed filling stage (46.8 MJ/plant).

We harvested three heads at flowering end and 24 (six per treatment) at physiological maturity (M2 stage). The latter ones had similar diameters (150 $\pm$12 mm). In 12 of these M2 stage heads (three of each treatment), we delimited three positions (outer, middle and inner) proportionally to the diameters and determined dry seed weight yield and number of filled and empty seeds on a 100 mm^2 portion of each.

The other 12 M2 heads were immediately fixed in F.A.A. From each one of them we cut three 6 mm thick transects (radial portions) and delimited and separated the outer, middle and inner position sections. Each section was dehydrated in an ascending alcoholic series and soaked in Tissuemat type paraffin. The samples were cut with a Minot type microtome (Leitz Wetzlar), transverse and 20 mm thick (making sure that they were parallel to seed insertion). The first transverse cut was done at seed insertion (level 0) and the second at 300 μm from the former (level 300). The cuts were stained with blue toluidine. We determined the number of vascular bundles per head area unit (40x) in the three positions. The bundles disposed parallel to the cut surface were considered longitudinal and the ones disposed perpendicular to the cut surface were considered transverse. Lines parallel to the head radius were drawn on each 2 mm away from the other and the length over which each line intercepted phloematic tissue was measured (100x). We calculated the phloem area in each cut as the relationship between the sum of phloem-intercepting lengths and the sum of the lines' lengths. In preliminary experiences, phloem area had been measured on photographs using an image analyser. These last experiences showed that our method of transects correctly estimates differences above 10%. The sieve tubes area was measured in the same way. Finally, we cut other three transects of these heads and made them diaphanous using the technique of Dizeo de Strittmater (1973) in order to macroscopically observe the vascularization.

We also determined the average sieve pores diameter in the three MO stage heads. Three preparations were made out of each position of the heads as described. We measured the diameter of the pores of ten sieve plates in each preparation using an inmersion objective (1000x). We then obtained the average pore diameter in each sieve plate by measuring all the pores that intercepted two perpendicular transects and calculated from it the radius of the pores assuming that they were circular.

RESULTS

Yield and yield components in different head positions

The yield per head area unit varied among positions and treatments (Figure 1). The middle position showed the highest values in all treatments, the outer position showed slightly lower values and the inner position showed the lowest. The highest variation between treatments due to variations in intercepted PAR showed at the inner position, in which the T treatment (higher interception) reached 163, the ST treatment 124 and the S treatment (lower interception) 68% of the UC treatment yield.

The middle position showed the highest number of filled seeds per head area unit in all treatments (Figure 2). The outer position showed slightly lower values and the inner one showed the lowest. The number of empty seeds increased (Figure 3) and the individual seed weight decreased from periphery to center in all treatments. The thinning treatment showed the highest average dry weight of individual seeds in the three positions (data not shown).

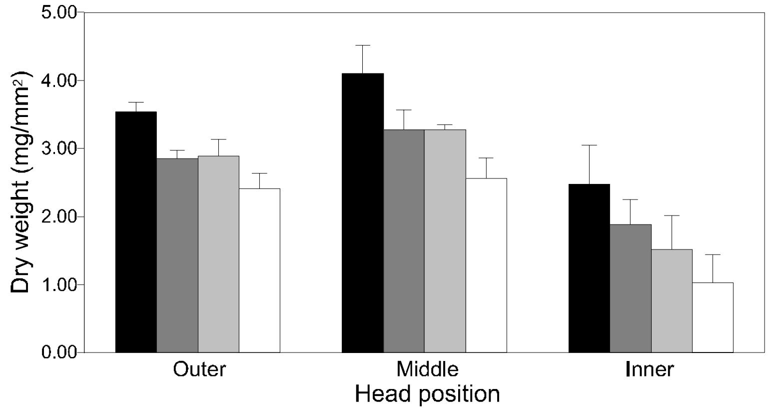

Figure 1: Average dry weight yield per head area unit (g/mm^2) of three concentric head positions (outer, middle and inner) in four treatments with different incident radiation levels: shaded (white bars), thinned (black bars), shaded and thinned (dark gray bars), and untreated control (light gray bars). The standard error for each position and treatment is represented by vertical bars.

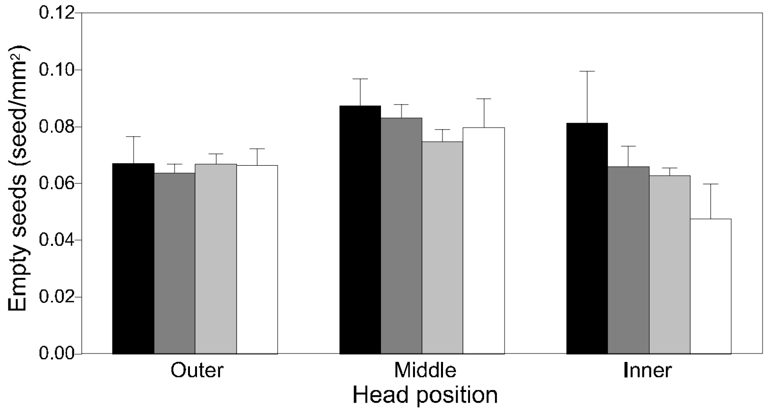

Figure 2: Average number of filled seeds per head area unit (seeds/mm^2) of three concentric head positions (outer, middle and inner) in four treatments with different incident radiation levels: shaded (white bars), thinned (black bars), shaded and thinned (dark gray bars), and untreated control (light gray bars).

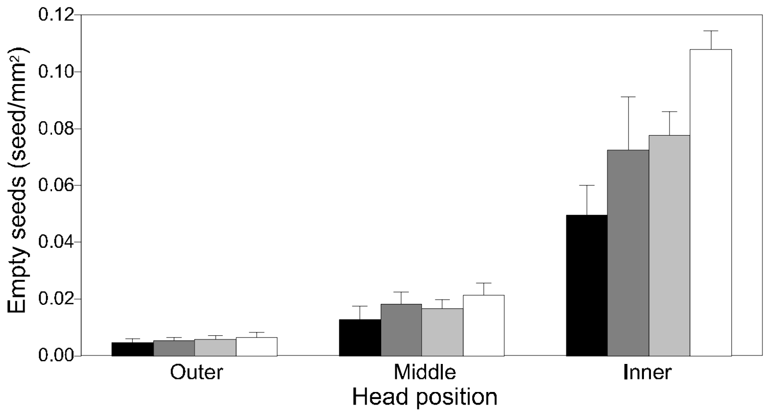

Figure 3: Average number of empty seeds per head area unit (seeds/mm^2) of three concentric head positions (outer, middle and inner) in four treatments with different incident radiation levels: shaded (white bars), thinned (black bars), shaded and thinned (dark gray bars), and untreated control (light gray bars).

Anatomic studies

The receptacle is hollow at the center and the parenchyma tissue near the hole is not vascular. The vascular bundles take a peripheral course throughout the receptacle (Figure 4). They enter the head by the periphery, reach the seed insertion zone and turn to the center, running parallel to the upper surface. Some of these bundles ramify into thinner tubes which feed the seeds and other sinks. In the cuts of the vascular zone, we found bundles parallel (longitudinal) and perpendicular (transverse) to the cut surface. However, neither granules nor saccules were found (cf. Durrieu *et al.*, 1985).

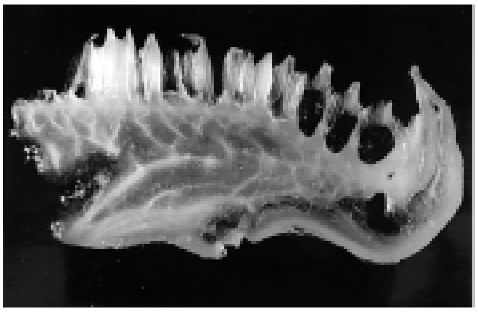

Figure 4: Radial cross-section photograph of a sunflower head. Once made diaphanous through the technique of Dizeo de Strittmater (1973), its transparent vascular bundles are clearly visible.

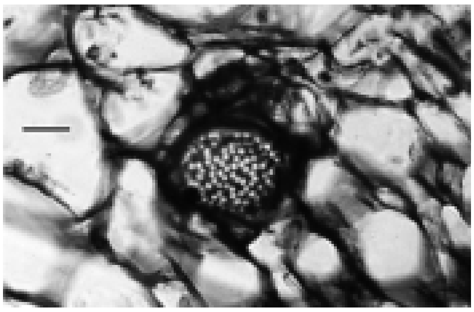

Figure 5: Cross-section photograph of phloem showing a sieve plate with sieve pores, after being stained with blue toluidine. Bar = 10 µm.

In MO stage, the pores of the sieve plates were clearly visible in the three positions, suggesting that they were already functional (Figure 5). The average pore radius was similar in the three positions (Table 1).

Table 1: Average values of phloem area, number of longitudinal and transverse vascular bundles, and sieve tubes area per head area unit and sieve pores radius in three head positions at flowering end. Secondary values show the standard error.

	Outer position	Middle position	Inner position
Phloem area ($\mu m^2/mm^2$)	20000 ± 4500	20100 ± 3400	21200 ± 3100
Transverse vascular bundles (bundles/mm^2)	0.216 ± 0.018	0.233 ± 0.009	0.40 ± 0.063
Longitudinal vascular bundles (bundles/mm^2)	0.044 ± 0.0057	0.044 ± 0.009	0.042 ± 0.01
Sieve tubes area in transverse bundles ($\mu m^2/mm^2$)	4400 ± 748	4320 ± 778	6400 ± 895
Sieve tubes area in longitudinal bundles ($\mu m^2/mm^2$)	6100 ± 1150	6100 ± 1014	5600 ± 742
Sieve pores radius (μm)	0.464 ± 0.049	0.466 ± 0.042	0.458 ± 0.052

The average phloem and sieve tubes areas were similar in the outer and middle positions and larger in the inner one, considering that the number of filled seeds was not definitely fixed and the head was still expanding (maximum diameter was reached near seven days after MO). The number of transverse vascular bundles per head area unit was similar in the outer and middle positions and almost twice in the inner position. Finally, there were more transverse bundles than longitudinal ones in this stage (around 5 times more in the outer and middle positions and 10 times more in the inner one).

Table 2: Average number of longitudinal and transverse vascular bundles per head area unit in three head positions at physiological maturity. Values shown for four treatments with different intercepted radiation and two cut levels (0 and 300 µm away from seeds insertion). Secondary values show the standard error.

Treatment	Position	Transverse bundles per mm^2		Longitudinal bundles per mm^2	
		0 µm level	300 µm level	0 µm level	300 µm level
Shaded	Outer	0.172 ±0.028	0.142 ±0.033	0.064 ±0.021	0.063 ±0.016
	Middle	0.173 ±0.023	0.142 ±0.024	0.040 ±0.014	0.037 ±0.019
	Inner	0.173 ±0.022	0.150 ±0.017	0.046 ±0.017	0.038 ±0.011
Untreated control	Outer	0.179 ±0.010	0.154 ±0.020	0.069 ±0.026	0.067 ±0.022
	Middle	0.173 ±0.014	0.161 ±0.017	0.055 ±0.026	0.048 ±0.031
	Inner	0.178 ±0.014	0.158 ±0.014	0.044 ±0.017	0.032 ±0.014
Shaded & thinned	Outer	0.166 ±0.018	0.130 ±0.017	0.059 ±0.028	0.040 ±0.023
	Middle	0.165 ±0.010	0.135 ±0.018	0.053 ±0.019	0.049 ±0.047
	Inner	0.163 ±0.018	0.126 ±0.022	0.042 ±0.019	0.044 ±0.026
Thinned	Outer	0.177 ±0.022	0.164 ±0.029	0.050 ±0.020	0.034 ±0.019
	Middle	0.177 ±0.025	0.154 ±0.025	0.047 ±0.007	0.027 ±0.015
	Inner	0.172 ±0.028	0.158 ±0.027	0.041 ±0.02	0.032 ±0.02

In M2 stage, when head expansion had finished, the number of transverse vascular bundles per head area unit was similar in the three positions, for each level (0 and 300 µm) and each treatment. The number of longitudinal bundles did slightly decrease from the outer to the inner position (Table 2). Little vascular branching between 0 and 300 µm levels was suggested by a slight decrease in the number of transverse bundles of the latter. Also phloem and sieve tubes areas were similar in all positions and treatments for each level (Table 3).

Table 3: Average phloem area per head area unit in three head positions at physiological maturity. Values shown for four treatments with different intercepted radiation and two cut levels (0 and 300 μm away from seeds insertion). Secondary values show the standard error.

Treatment	Position	Phloem area (μm²/mm²)	
		0 μm level	300 μm level
Shaded	Outer	18500 ±2500	16300 ±900
	Middle	19000 ±2100	15900 ±1500
	Inner	18900 ±2500	15300 ±2000
Untreated control	Outer	18200 ±1400	16000 ±2100
	Middle	19500 ±1800	15100 ±2500
	Inner	17400 ±2000	14900 ±2500
Shaded & thinned	Outer	18600 ±2500	15700 ±2300
	Middle	19000 ±2100	15100 ±2400
	Inner	18900 ±2500	15600 ±1800
Thinned	Outer	19800 ±1900	16200 ±1800
	Middle	21000 ±2600	15600 ±1900
	Inner	19000 ±2000	15800 ±1600

Sieve tubes area was greater in longitudinal than in transverse bundles (Table 4). Also in this stage the number of longitudinal bundles was smaller than the number of transverse ones. The outer position showed a lower number and a greater area of longitudinal bundles than the inner position, which suggests that these bundles ramify into thinner bundles in their way from the periphery to the center of the head.

Table 4: Average sieve tubes area per head area unit in longitudinal and transverse bundles at physiological maturity. Values shown for four treatments with different intercepted radiation. Secondary values show the standard error.

Treatment	Position	Sieve tubes area in transverse bundles (μm²/mm²)	Sieve tubes area in longitudinal bundles (μm²/mm²)
Shaded	Outer	3480 ±371	6494 ±893
	Middle	3522 ±629	5808 ±716
	Inner	3485 ±576	5677 ±1118
Untreated control	Outer	3297 ±346	6675 ±1013
	Middle	4132 ±689	5827 ±700
	Inner	2552 ±571	4947 ±726
Shaded & thinned	Outer	3178 ±511	6714 ±614
	Middle	3095 ±471	7506 ±597
	Inner	3575 ±749	7001 ±1097
Thinned	Outer	4008 ±789	7594 ±644
	Middle	4006 ±973	7750 ±1069
	Inner	3083 ±546	6275 ±612

None of the anatomic variables studied (phloem and sieve tubes areas, number of vascular bundles and sieve pores diameter) were affected by the treatments.

DISCUSSION

The application of treatments provided an important range of intercepted radiation through which we studied the yield and vascularization in the outer, middle and inner concentric positions of the head. We found that increases and decreases of intercepted PAR raised and reduced yield and its components (individual seed weight and number of seeds) while they did not affect the vascularization.

Irrespective of treatment, existed found variations among head positions in yield per head area unit. The middle position showed the greatest dry weight per head area unit in all treatments, which was mainly a consequence of the number of filled seeds per head area unit. Individual seed weight decreased from periphery to center in all treatments. A similar tendency has been found by many authors (Lencrerot *et al*., 1973; Goffner *et al*., 1988; Steer *et al*., 1988; Merrien, 1992; Karadogan *et al*., 1998).

The yield per head area unit of each head position seems not to be limited by the amount of phloem able to supply carbohydrates to its seeds, as at least three of our results suggest:

1. Phloem area and number of vascular bundles in MO stage was similar in the outer and middle positions but higher in the inner, which suggests that vascularization is not responsible for the lack of filling in many inner seeds.
2. The inner position in the thinned treatments had similar yield per head area unit as the outer position in the shaded treatments. This yield decreases when intercepted radiation is low suggesting that the inner seeds are weaker than the outer ones in the nutrition competition. Goffner *et al*. (1988) arrived at a similar conclusion feeding sunflower plants with ^{14}C; during the first three weeks after the flowering, the ^{14}C assimilated by the plants was mainly accumulated in the outer position.
3. The phloem area and the number of vascular bundles in the M2 stage were similar among positions and treatments, despite of great differences in yield, which suggests that outer and inner seeds would be fed by a similar amount of sieve tubes. In agreement with these results, Steer *et al*. (1988), using restrictive pollination techniques and removing the external seeds from the head, found that the vascularization of the inner position was able to feed with organic and inorganic nutrients this position.

Despite of what Durrieu *et al*. (1985) describe, we did not find interruptions of vascular bundles. Although the longitudinal bundles structures were similar to those found by these authors, they would not be real interruptions. The absence of saccules and granules could be attributed to genotypical differences between our cultivar and that used by Durrieu *et al*. (1985).

Finally, we did not find differences between positions in sieve pores radius, one of the variables in equation [1]. As the cross-sectional area of phloem was not different among positions, the differences in growth of seeds between them could be accounted for, according to Farrar and Williams (1991), by their differences in phloem path length or in source-sink turgor pressure difference.

In conclusion, this work shows that differences in yield between different head positions cannot be attributed to lack of vascularization.

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RENDIMIENTO EN DIFERENTES POSICIONES DEL CAPÍTULO DE GIRASOL (*Helianthus annuus* L.) Y SU RELACIÓN CON LA VASCULARIZACIÓN

RESUMEN

El objetivo fue estudiar, bajo diferentes niveles de radiación interceptada por las plantas durante la etapa de llenado de frutos, la relación entre el rendimiento y la vascularización en tres sectores concéntricos del capítulo. Al final de la floración, aplicamos tratamientos de sombreado y raleado a tres parcelas de cultivo: una parcela sombreada, una raleada y una sombreada y raleada. Una parcela sin tratar se utilizó como testigo. Se muestrearon capítulos en fin de floración y en madurez fisiológica. Se delimitaron en ellos tres sectores: periférico, medio y central. Se extrajeron porciones de cada sector de capítulos muestreados en madurez fisiológica, se determinaron el rendimiento y sus componentes. Los capítulos restantes fueron cortados transversalmente en la inserción de los frutos para medir variables de la vascularización (superficie de floema y de tubos cribosos, número de haces vasculares transversales y longitudinales y diámetro de poros cribosos). Para todas las mediciones se usó como base la unidad de superficie de capítulo. El sombreado redujo el peso seco en los tres sectores. El sector medio mostró el rendimiento más alto y el central el más bajo en las cuatro parcelas. El rendimiento del primero fue alto porque su menor peso individual de frutos fue compensado por un mayor número de frutos llenos. Sin embargo, el radio promedio de poros cribosos fue similar entre sectores, y las superficies de floema y de tubos cribosos y el número de haces vasculares por unidad de superficie de capítulo fueron similares entre sectores y entre tratamientos, lo que no pudo dar cuenta de las diferencias en rendimiento por unidad de superficie de capítulo entre sectores. Esto nos permite concluir que esta variación no sería producida por una vascularización deficiente.

LE RENDEMENT DES DIFFERENTS ZONES DU CAPITULES DU TOURNESOL (*Helianthus annuus* L.) Y SON RELATION AVEC LA VASCULARISATION

RÉSUMÉ

L'objet a été étudier la relation entre le rendement et la vascularisation dans trois zones concentriques du capitule sous des differents niveaux du rayonnement intercepté par plante pendant la periode du remplissage des fruits. Au stade fin floraison nous avons apliqué à trois parcelles des traitements d'ombrage ou d'éclaircissage. Une quatrième parcelle a été gardée sans aucun traitement (contrôle). Des capitules ont été echantillonés aux stades de fin floraison et de maturité physiologique. On a delimité sur ceux-ci trois zones concentriques: peripherie, milieu et centrale. Dans des capitules en maturité physiologique, nous avons mesuré le rendement et ses composantes sur les trois zones. Les capitules qui restaient ont été coupés de facon transversale à niveau de l'insertion des fruits pour mesurer la vascularisation. Toutes les variables ont été mesurées par unité de surface du capitule. L'ombrage a reduit le poids sec dans les trois zones. Dans tous les traitements, la zone du milieu presenta le rendement le plus forte et celle du centre le plus faible. Le rendement du milieu a été plus forte que celui de la peripherie malgré le moindre poids individuelle de leurs fruits parce que celui-ci a été compensé par un

nombre de grains pleins plus forte. Cependant, le rayon moyen des pores cribeux a été similaire dans toutes les zones du capitule. Les surfaces du phloème et des plaques cribeuses ont été aussi similaires entre zones et entre traitements. Des differences dans la vascularisation du capitule ne peuvent donc rendre compte des differences en rendement par unité du surface du capitule entre zones et traitements. On peut donc conclure que les variations du rendement chez des differentes zones du capitule ne sont pas dues à une déficience dans la vascularisation.