HELIA, **16**, Nr. 18, p.p. 21-30 (1993)

EFFICIENCY OF CARBON ASSIMILATION AND WATER UTILIZATION IN SEVERAL NS SUNFLOWER LINES AND HYBRIDS

Plesničar M., Sakač Z., Panković D., Ćupina T., Škorić D.

Institute of Field and Vegetable Crops, 21000 Novi Sad, M. Gorkog 30, Yugoslavia.

SUMMARY

The rate of CO_2 assimilation, photosynthetic efficiency and assimilate accumulation were measured in 15 field-grown NS sunflower (*Helianthus annuus* L.) lines and hybrids. Transpiration and water use efficiency were also measured in sunflower leaves in order to evaluate the behavior of the examined genotypes under water stress.

Photosynthetic efficiency, determined at saturating CO_2 and at low light intensity, was high in sunflower leaves. At a high light intensity and ambient CO_2, however, the rate of carbon assimilation was 1/3 of the potential rate of photosynthesis at saturating CO_2. The tested sunflower genotypes differed in the efficiency of water use and transpiration at a high light intensity and ambient CO_2. Our results on water use efficiency and/or transpiration efficiency can be used as indicators of hybrid sunflower adaptability to arid conditions.

Key words: Sunflower, leaves, photosynthesis, stomatal conductance, photosynthetic water use efficiency

INTRODUCTION

Carbon assimilation is a result of photosynthetic processes in leaves and it is directly associated with plant productivity. Plants differ in genetic potential for carbon assimilation. For example, in conditions of high temperature and light intensity, the C4 plants have higher rates of photosynthesis than the C3 plants. Differences within individual plant species, however, have not been studied extensively and the biochemical and physiological reasons for these differences have not been satisfactorily explained (Gimenez et al., 1992). Environmental factors may also affect the assimilation intensity considerably. In many parts of the world plant productivity is significantly reduced in arid conditions. This is why large efforts have been invested in the study and improvement of plant tolerance to water stress (Virgona et al., 1990).

The object of this investigation was to measure the rate and efficiency of photosynthesis and assimilate accumulation in leaves of fifteen field-grown NS sunflower lines and hybrids. Plant reaction and adaptability to arid conditions was estimated on the basis of the measurements of transpiration, stomatal conductance and water use efficiency.

MATERIAL AND METHODS

The investigation included five sunflower (*Helianthus annuus* L.) lines (RHA-SNRF 17, RHA-58, RHA-SNRF, OCMS-22, CMS-Ha-V-8931-3-4) and ten sunflower hybrids (NS-H-26 RM, NS-H-43, NS-Helios, NS-H-54, NS-H-100, NS-H-101, NS-H-130, NS-H-132, NS-H-160, NS-H-162).

Sunflower plants were grown in 3.5 m x 13 m plots at the experimental field at Rimski Šančevi in 1991. The sowing density was 45000 plants/ha. The border rows were omitted from the measurements, which were done at seven-day intervals from the 60th to the 120th day after sowing.

Photosynthesis and transpiration were measured in field conditions, in the 20th and 25th leaf of three plants, from 9 to 11 AM, using Portable Photosynthesis System LI 6000 (LI-COR, USA). Photosynthesis and transpiration were measured within a temperature range of 23 - 33°C and a light intensity range of 1000 - 1800 μmol quanta m^{-2} s^{-1}. After these measurements, the same leaves were sampled for the measurements of sugar content (HPLC OPTILAB 5931, HSRI detector) (Sakač et al., 1992).

Photosynthesis was also measured in laboratory on discs (10 cm2) of 20th and 25th leaf, at 25°C and saturating CO_2 (5%) in dependence of light intensity, with an LD-2 oxygen electrode (Hansatech, King's Lynn, UK) (Walker, 1990). The data obtained were used for the calculation of photosynthetic efficiency (QY) and maximum rate of photosynthesis (A_{max}). Transpiration efficiency (the ratio of photosynthesis to transpira-

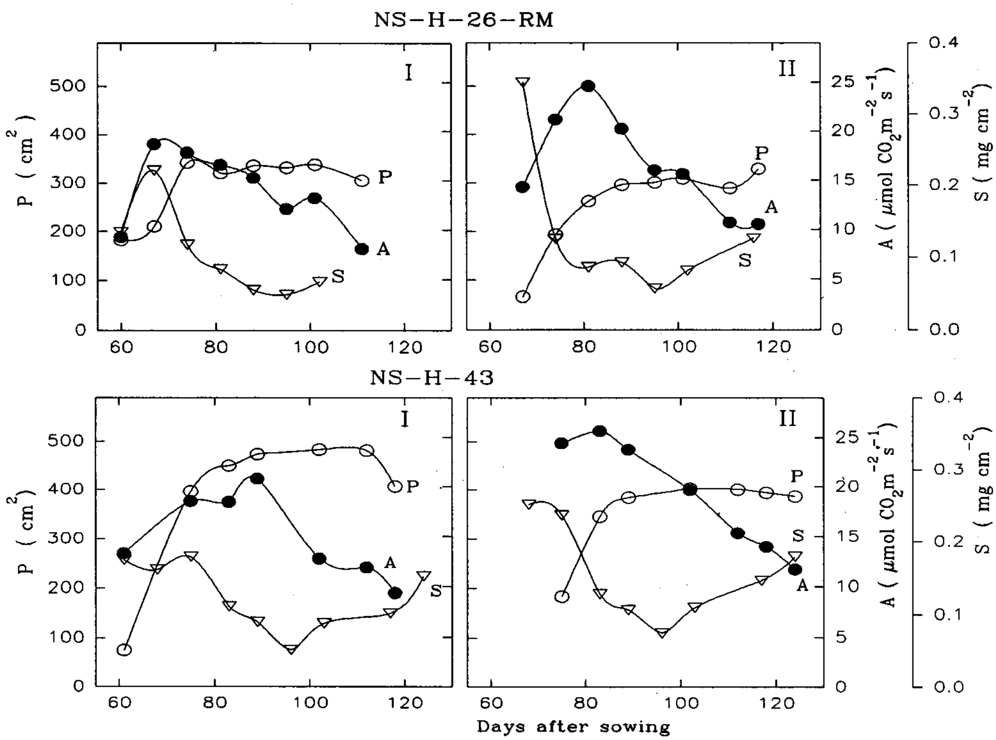

Figure 1. Leaf area (○), assimilation rate (●) and sugar content (▽) in leaves 20 (I) and 25 (II) of hybrids NS-H-26 and NS-H-43 in the course of plant anthesis and grain filling

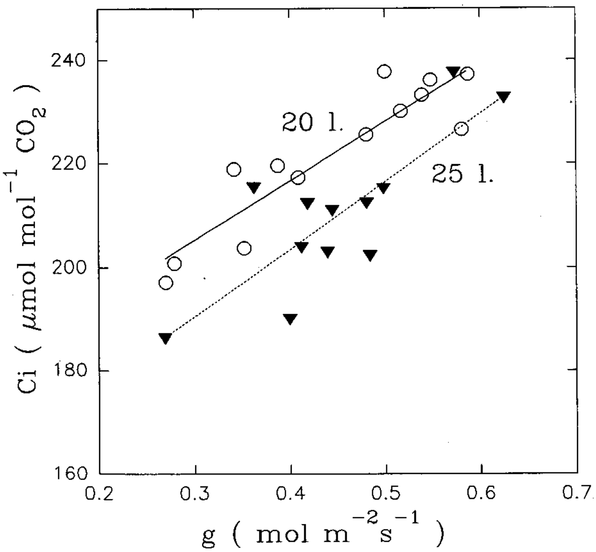

Figure 2.
Relationship between intercellular CO_2 concentration (Ci) and stomatal conductance (g), measured under conditions of light-saturated photosynthesis in leaves 20 (○) and 25 (▼) in field-grown sunflower genotypes

tion) and water use efficiency in leaves (the ratio of photosynthesis to stomatal conductance) were calculated on the basis of the field measurements of photosynthesis and transpiration.

RESULTS

Rate of photosynthesis increases with leaf development to reach the maximum value before the leaf reaches its maximum size. Later on it decreases, as shown in Figure 1 for the 20th and 25th leaf of the hybrids NS-H-26 and NS-H-43. The results obtained for the other hybrids were similar, the times when maximum photosynthesis and maximum leaf area were attained depending on the length of vegetation period of the hybrid in question. Intensity of photosynthesis and leaf area increase from basal leaves to those at the top third of the stem, the 20th and 25th leaf are included among the latter.

Figure 1 shows also the changes in sugar content that occurred in the 20th and 25th leaf during the reproductive stage of plant development. After reaching the maximum value before maximum leaf area was achieved, sugar content changes in harmony with changes in intensity of photosynthesis.

CO_2 uptake in the course of photosynthesis is functionally connected with the release of H_2O through stomata in the course of transpiration. High positive correlations were found between CO_2 concentration and stomatal conductance in the 20th and 25th leaf, r=0.91 and r=0.81, respectively (Figure 2).

Tables 1 and 2 show the mean values of photosynthesis and transpiration effected by the 20th and 25th leaf of the tested lines and hybrids. It is evident that in both ambient and optimum conditions the rate of photosynthesis is lower and the CO_2 content higher in the 20th than in the 25th leaf, while the values for stomatal conductance and transpira-

Table 1. Photosynthesis and transpiration measurements (mean values) for leaf 25 of NS-sunflower lines and hybrids in the reproductive stages of plant development (80 - 120 days after sowing).

Genotype	Intercelular CO_2	Transpiration	Stomatal conductance	Photosynthesis	
				at 0.03% CO_2	at 5% CO_2
	ppm	mmol H_2O $m^{-1}s^{-1}$	mol $m^{-2}s^{-1}$	μmol CO_2 $m^{-2}s^{-1}$	μmol O_2 $m^{-2}s^{-1}$
RHA-SNRF-17	186.12 ± 22.97	3.32 ± 0.91	0.27 ± 0.16	17.33 ± 4.39	49.74 ± 4.95
RHA-58	232.43 ± 29.17	5.74 ± 2.15	0.63 ± 0.27	19.91 ± 4.43	50.14 ± 2.86
RHA-SNRF	-	-	-	-	-
OCMS-22	-	-	-	-	58.98 ± 8.29
L-1	215.24 ± 20.26	4.61 ± 2.28	0.36 ± 0.19	12.09 ± 5.01	50.18 ± 11.07
NS-H-26-RM	189.86 ± 39.06	3.04 ± 1.77	0.40 ± 0.13	16.29 ± 6.09	50.36 ± 12.39
NS-H-43	169.33 ± 27.99	3.31 ± 1.38	0.35 ± 0.13	19.68 ± 5.04	65.32 ± 9.23
NS-HELIOS	210.90 ± 35.05	3.39 ± 0.78	0.44 ± 0.20	19.59 ± 5.75	56.69 ± 9.24
NS-H-101	237.43 ± 27.28	2.85 ± 0.96	0.57 ± 0.35	14.26 ± 5.51	53.62 ± 7.51
NS-H-54	215.09 ± 32.35	3.03 ± 1.06	0.50 ± 0.18	18.67 ± 4.92	60.21 ± 15.41
NS-H-100	212.33 ± 25.48	2.91 ± 1.28	0.48 ± 0.19	16.49 ± 4.14	56.39 ± 7.76
NS-H-130	203.77 ± 17.37	4.50 ± 1.57	0.41 ± 0.18	18.84 ± 5.02	63.43 ± 7.00
NS-H-132	202.16 ± 40.49	4.36 ± 0.61	0.48 ± 0.27	19.24 ± 3.00	58.67 ± 10.63
NS-H-160	202.81 ± 19.09	4.78 ± 2.82	0.44 ± 0.20	18.32 ± 5.89	56.70 ± 9.99
NS-H-162	212.19 ± 35.05	3.88 ± 7.54	0.42 ± 0.16	19.02 ± 4.87	63.60 ± 5.80

Table 2. Photosynthesis and transpiration measurements (mean values) for leaf 20 of NS-sunflower lines and hybrids in the reproductive stages of plant development (80 - 120 days after sowing).

Genotype	Intercelular CO_2	Transpiration	Stomatal conductance	Photosynthesis	
				at 0.03% CO_2	at 5% CO_2
	ppm	mmol H_2O $m^{-1}s^{-1}$	mol $m^{-2}s^{-1}$	μmol CO_2 $m^{-2}s^{-1}$	μmol O_2 $m^{-2}s^{-1}$
RHA-SNRF-17	197.14 ± 34.43	2.99 ± 1.27	0.27 ± 0.15	14.22 ± 4.87	-
RHA-58	209.13 ± 26.00	3.98 ± 1.47	0.60 ± 0.31	19.16 ± 4.73	43.41 ± 9.99
RHA-SNRF	200.79 ± 27.24	4.54 ± 1.18	0.28 ± 0.14	13.43 ± 4.81	41.21 ± 4.40
OCMS-22	225.45 ± 22.48	5.69 ± 3.58	0.48 ± 0.19	15.63 ± 4.85	58.41 ± 13.83
L-1	229.94 ± 11.57	4.93 ± 2.19	0.52 ± 0.17	15.58 ± 4.74	46.36 ± 10.23
NS-H-26-RM	217.31 ± 39.67	2.64 ± 1.20	0.41 ± 0.41	13.86 ± 4.43	41.30 ± 14.47
NS-H-43	203.72 ± 27.48	2.28 ± 0.71	0.35 ± 0.14	15.29 ± 4.99	42.66 ± 7.98
NS-HELIOS	219.53 ± 50.38	2.68 ± 1.19	0.39 ± 0.18	14.66 ± 7.38	46.36 ± 13.06
NS-H-101	237.69 ± 43.24	3.12 ± 1.06	0.50 ± 0.28	14.62 ± 3.99	42.48 ± 8.91
NS-H-54	237.19 ± 25.44	2.59 ± 1.13	0.59 ± 0.39	14.05 ± 3.72	48.49 ± 15.01
NS-H-100	246.10 ± 18.84	3.37 ± 1.38	0.91 ± 0.46	14.37 ± 3.90	46.40 ± 8.66
NS-H-130	218.89 ± 29.83	3.18 ± 0.82	0.34 ± 0.21	14.53 ± 4.24	46.09 ± 5.78
NS-H-132	236.06 ± 32.99	3.62 ± 0.96	0.55 ± 0.31	13.25 ± 5.06	43.76 ± 10.87
NS-H-160	226.45 ± 24.01	4.46 ± 1.42	0.58 ± 0.24	16.65 ± 5.14	44.38 ± 10.93
NS-H-162	233.14 ± 28.57	4.35 ± 2.86	0.54 ± 0.21	14.90 ± 4.84	48.91 ± 10.93

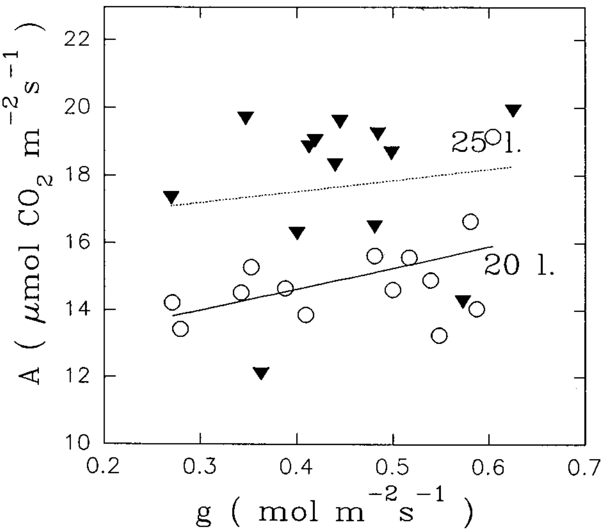

Figure 3.
Relationship between light-saturated assimilation rate (A) and stomatal conductance (g) at atmospheric CO_2 concentration in field-grown sunflower plants. Each point is the mean of several measurements for leaf 20 (○) and 25 (▼) of a genotype during the reproductive stages of plant development.

tion do not exhibit significant differences between the two leaf positions. The tested genotypes displayed large differences in stomatal conductance (from 0.27 to 0.91 mol $m^{-2}s^{-1}$) and leaf transpiration (from 2.28 to 5.69 mmol H_2O $m^{-2}s^{-1}$). The rate of photosynthesis increased by 20% only as the stomatal conductance in the 20th leaf changed from 0.27 to 0.60 mol m^{-2} s^{-1}, the rate of photosynthesis increased still less in the 25th leaf (Figure 3).

Light response of photosynthesis was measured in controlled conditions of optimum temperature (25°C) and saturating CO_2 concentration (5%). Figure 4 shows the light response curves for the 25th leaf of the hybrids NS-H-26 and NS-H-43. Maximum photosynthetic rates of the genotypes tested ranged between 50.36 (NS-H-26) and 65.32 (NS-H-43) (Table 1). The values of maximum photosynthetic efficiency, determined by the slopes of the curves , were the same (0.08) for all genotypes. Relationship between potential maximum rates of photosynthesis and the rates measured in the ambient conditions in the field was linear (Figure 5), indicating that the ambient conditions allowed 30 to 40% of the photosynthetic potential of leaf to be utilized.

High water use efficiency of leaf, defined as a ratio of photosynthetic rate and stomatal conductance (Freeden et al., 1991), indicates a quality necessary for plant adaptation to arid conditions. Figure 6 shows that water use efficiency decreases considerably with increasing stomatal conductance ($r=-0.93$ for the 20th leaf and $r=-0.81$ for the 25th leaf), photosynthesis changes only slightly under the same conditions (Figure 3). The hybrid NS-H-43 and its male parent (SNRF) exhibited much higher water use efficiency by the leaf than the other tested genotypes. This is in agreement with the previously observed drought tolerance of this sunflower hybrid.

Transpiration efficiency decreased with the increase in transpiration of the 20th and 25th leaf. The highest efficiency was shown by NS-H-43 (Figure 7).

Sugar accumulation in mature sunflower leaves is a result of sucrose synthesis in leaf in the process of photosynthesis and its translocation from leaves into other plant parts. Accordingly, sugar content in the 25th leaf, when expressed in mg/cm2, is high and fairly uniform in relation to that in the 20th leaf (Figure 8). The lines had a somewhat higher

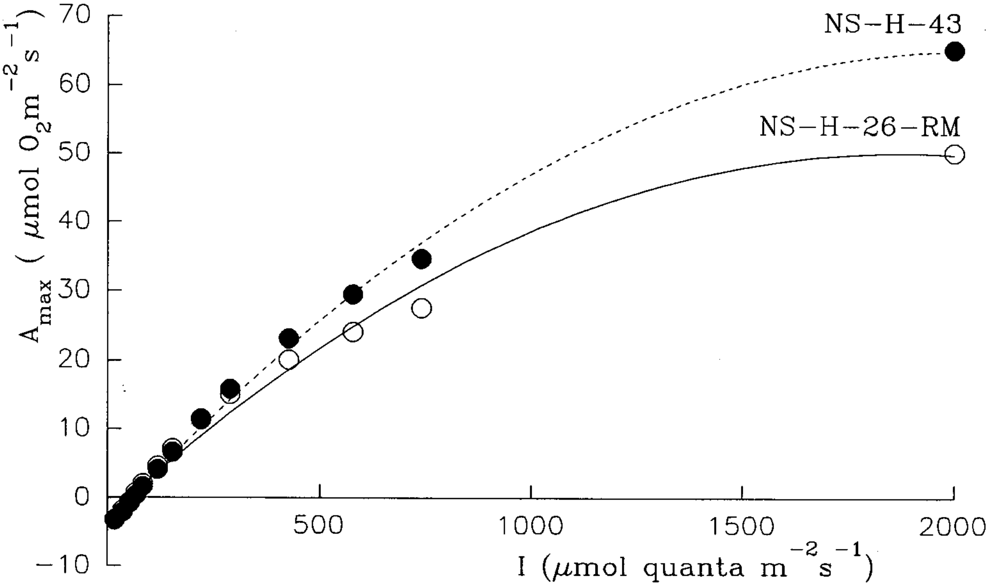

Figure 4. Light response curves of photosynthetic O_2 evolution at CO_2 saturation of two sunflower hybrids NS-H-26 (○) and NS-H-43 (●). Measurements were done on several leaf discs from leaves 25, at 25°C in LD-2 electrode.

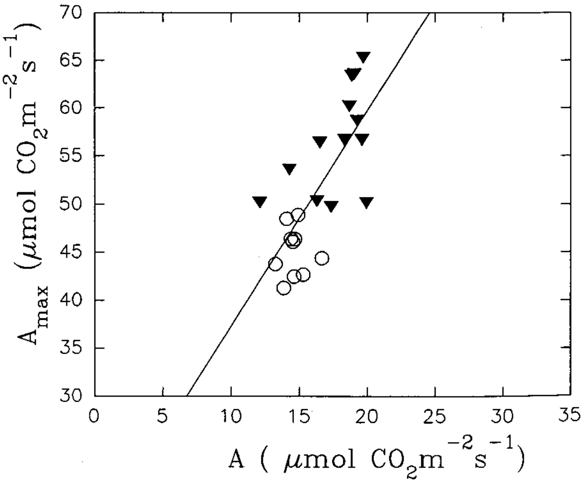

Figure 5.
Relationship between light- and CO_2-saturated assimilation rates (A_{max}) and light-saturated assimilation rates measured at ambient CO_2 (A) for leaves 20 (○) and 25 (▼) of sunflower plants. Each point is the mean value of several measurements on one genotype.

sugar content in leaves than the hybrids. On the other hand, the leaves of the former were much smaller than those of the latter. Sucrose held 30 to 50% of the total sugar content.

The yield of the hybrids in the small-plot trials ranged fairly uniformly around 4 t/ha.

DISCUSSION

It is well known that young fully developed leaves in the upper part of a plant have the highest photosynthetic capacity and, therefore, they are the major producers of assimilates at all stages of plant development. Reduced rate of photosynthesis in old leaves is, among other things, due to an increased stomatal resistance (McWilliam, 1974).

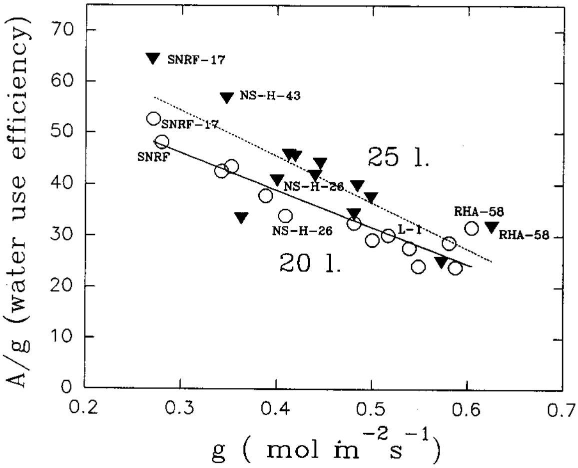

Figure 6.
Ratio between light-saturated assimilation (A) and stomatal conductance (g) as a measure of photosynthetic water use efficiency (A/g) is presented in dependence of stomatal conductance for leaves 20 (○) and 25 (▼) of tested sunflower genotypes.

Our results show that, in field conditions, rates of photosynthesis in corresponding leaves of the tested genotypes did not differ much during the reproductive stage of plant development. Significant differences occurred in stomatal conductance of examined leaves (Tables 1 and 2). Our results showed that the increase of CO_2 in leaf was due to an increase in stomatal conductance and a decrease in CO_2 utilization by chloroplasts. A high positive correlation between CO_2 concentration in the leaf and stomatal conductance (Figure 2) supports the findings of Wise et al. (1990, 1992) for field-grown sunflowers.

Under conditions in which conductance does not have a significant effect on photosynthetic rate, we succeeded in establishing differences in transpiration efficiency and water use efficiency in leaves of field-grown sunflower genotypes (Figures 6 and 7). Water use efficiency was in high negative correlation with the stomatal conductance in the 20th and 25th leaf of all genotypes. The highest efficiencies were exhibited by the hybrid NS-H-43 and its male parent SNRF. These were brought about by the relatively

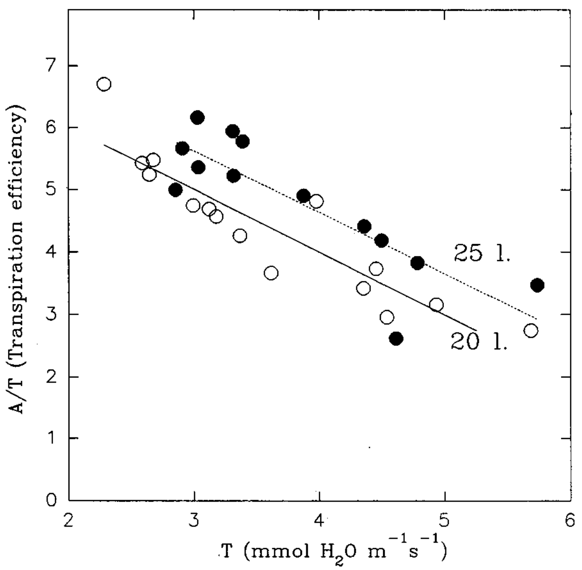

Figure 7.
Transpiration efficiency (A/T) as a function of transpiration (T) for leaves 20 (○) and 25 (●) of tested sunflower genotypes. Each point is the mean value of several measurements in the field on the leaves of one genotype.

low stomatal conductances of these genotypes. The highest values of stomatal conductance and the lowest efficiencies were shown by the parent lines of the hybrid NS-H-26. The hybrid itself had intermediate values of these two parameters.

Genetic variation of transpiration efficiency has been observed long time ago (Brigs and Shantz, 1914). Changes in transpiration efficiency of a leaf may be due to changes in

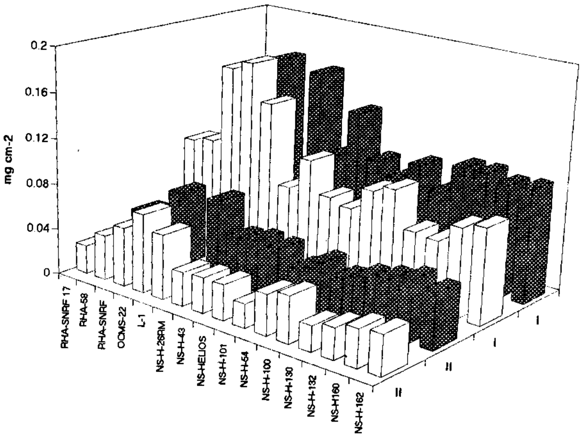

Figure 8.
Content of soluble carbohydrates (I) and sucrose (II) in leaves 20. (□) and 25. (▒) of NS sunflower lines and hybrids. Each bar is the mean value of 5-7 measurements, 3 repetitions, in the course of reproductive stages of plant development.

either rate of photosynthesis, stomatal conductance , or both (Farquhar et al., 1982). In this experiment, the differences in transpiration efficiency and water use efficiency were mostly due to the differences in stomatal conductance that existed among the genotypes. The results indicate that stomatal conductance is evidently the factor of the observed drought tolerance of the hybrid NS-H-43 and the sensitivity of the hybrid NS-H-26.

Although the photosynthetic rates measured in leaves of the field-grown sunflower hybrids were uniform and relatively high, they were three times lower than the corresponding potential values obtained in controlled conditions of optimum temperature and saturating light and CO_2. The differences observed between the potential and actual photosynthetic rates indicate that the photosynthetic capacity of leaves could be increased (Walker, 1992).

At the beginning of its development the leaf is only an assimilate sink, to turn into an assimilate sink and source later on. Before reaching its maximum area, the leaf becomes exclusively a source of assimilates. Increased sugar content in leaves may be a result of increased sugar synthesis or reduced translocation into other plant parts. At the stage of intensive leaf growth increased sugar content results from an increased photosynthetic rate and sugar synthesis and a reduced sugar translocation. When maximum leaf area is attained, a reduction in sugar content results from a decreased photosynthesis and sugar synthesis and an increased translocation (Dale and Milthorpe, 1983).

CONCLUSIONS

At low light intensities and saturating CO_2 the tested genotypes had a high photosynthetic efficiency. In the field conditions and at high light intensities, however, only 30 to 40% of the photosynthetic potential of sunflower leaves is utilized.

The field-grown sunflower hybrids differed in the water use efficiency and transpiration efficiency. These parameters may be used as indicators of hybrid sunflower adaptability to arid conditions.

REFERENCES

Briggs, L.J., Shantz, H.L., 1914. Relative water requirements of plants. J. Agric. Res. 3: 1-64.

Dale, J.E. and Milthorpe, F.L., 1983. General features of the production and growth of leaves, In: Dale, J.E. and Milthorpe, F.L. (Eds), The growth and functioning of leaves, Cambridge University Press, Cambridge, pp. 151-178.

Farquhar, G.D., O'Leary, M.H. and Berry, J.A., 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust. J. Plant Physiol. 9: 121-137.

Freeden, A.L., Gamon, J.A. and Field, C.B., 1991. Responses of photosynthesis and carbohydrate partitioning to limitations in nitrogen and water availability in field-grown sunflower. Plant Cell Environ. 14: 963-970.

Gimenez, C., Mitchell, V.J. and Lawlor, D.W., 1992. Regulation of photosynthetic rate of two sunflower hybrids under water stress. Plant Physiol. 98: 516-524.

McWilliam, J.R., English, S.D. and McDougall, G.N., 1974. The effect of leaf age and position on photosynthesis and the supply of assimilates during development in sunflower. Proc. Sixth Int. Sunflower Conference, Bucharest, pp. 173-179.

Sakač, Z., Ćupina, T., Plesničar, M. and Panković, D., 1992. Odnos izmedju intenziteta fotosinteze, transpiracije, akumulacije asimilata i prinosa kod NS hibrida suncokreta. Zbornik radova Poljoprivrednog fakulteta u Novom Sadu 20: 433-447.

Virgona, J.M., Hubick, K.T., Rawson, H.M., Farquhar, G.D. and Downes, R.W., 1990. Genotipic variation in transpiration efficiency, carbon -isotope discrimination and carbon allocation during early growth in sunflower. Aust. J. Plant Physiol. 17: 207-214.

Walker, D.A., 1990. The use of oxygen electrode and fluorescence probes in simple measurements of photosynthesis, Oxygraphics Limited, Sheffield, pp. 1-203.

Walker, D.A., 1992. Excited leaves. New Phytol. 121: 325-345.

Wise, R.R., Frederick, J.R., Alm, D.M., Kramer, D.M., Hesketh, J.D., Crofts, A.R. and Ort, D.R., 1990. Investigation of the limitations by leaf water deficit in field-grown sunflower (*Helianthus annuus* L.). Plant Cell Environ. 13: 923-931.

Wise, R.R., Frederick, J.R., Alm, D.M., Kramer, D.M., Hesketh, J.D., Crofts, A.R. and Ort, D.R., 1992. Corrigendum: Investigation of the limitations by leaf water deficit in field-grown sunflower (*Helianthus annuus* L.). Plant Cell Environ. 15: 755-756.

EFICIENCIA DE LA ASIMILACIN DEL CARBONO Y UTILIZACION DE AGUA EN VARIAS LINEAS E HBRIDOS DE GIRASOL

RESUMEN

Les tasas de asimilacin de CO_2, eficiencia de la fotosntesis y acumulacin de asimilados fueron medidas on 15 lneas e hbridos de girasol bajo condiciones de campo. La transpiracin y eficiencia del uso del agua fueron medidas tambin en las hojas para evaluar el comportamiento de los genotipos examinados bajo estrs hdrico.

La eficiencia fotosinttica, determinada bajo saturacin de CO_2 y baja intensidad de luz fue alta en las hojas de girasol. Bajo intensidad de luz alta y CO_2 ambiental la tasa de asimilacin de carbono fue 1/3 de tasa potencial de fotosntesis bajo saturacin de CO_2. Los genotipos de girasol examinados en condiciones de campo mostraron diferentes eficiencia del uso de agua y transpiracin en condiciones de alta intensidad de luz y CO_2 ambiental. Nuestros resultados sobre eficiencia del uso del agua y/o eficiencia de la transpiracin pueden ser utilizados como indicadores de la adaptabilidad de los hbridos NS-H-43 a la sequa.

EFFICACITÉ DE L'ASSIMILATION DU CARBONE ET DE L'UTILIZATION DE L'EAU CHEZ PLUSIEURS HYBRIDES ET LIGNES NS DE TOURNESOL

RÉSUMÉ

Le taux d'assimilation du CO_2, l'efficacité photosynthétique et l'accumulation d'assimilate ont été mesurée sur quinze lignées et hybrides de tournesol NS cultivés au champ. La transpiration et l'efficacité d'utilisation de l'eau ont été également mesurées sur des feuilles de tournesol afin d'évaluer le comportement des génotypes étudiés sous stress hydriques.

L'efficacité photosynthétique déterminée à CO_2 saturant et faible intensité lumineuse s'est revélée élevée pour les feuilles de tournesol. A haute intensité lumineuse et CO_2 ambiant, le taux d'assimilation du carbone représentait dependant le tiers du taux potentiel de photosynthése à CO_2 saturant. Les génotypes étudiés en condition de champ ont montré différents niveaux d'efficacité d'utilisation d'eau et de transpiration sous haute intensité lumineuse et CO_2 ambiant. Nos résultats sur l'efficacité d'utilisation d'eau et / ou le taux de transpiration peuvent être utilisés comme indice d'adaptabilité de l'hybride de tournesol NS-H-43 à la sécheresse.