Bioproduction and Leaf Area Development (*Helianthus annuus* L.) II. Quantitative Relationship in a Savanna Dry Season[1]

*J.J. San José, M. Cabrera**

ABSTRACT

Growth characteristics of sunflower (*Helianthus annuus* L.) were determined for the varieties Manfredi, Local of Kenia and Record, cultivated and irrigated during the dry season in a savanna climate. Photosynthetic production dynamics in the cultivated varieties were analyzed as a function of the sowing season. Results indicate a differential dependence of the productive capacity of plant genotype on environmental factors of the growing season. A discussion based on the assimilate partitioning process in sunflower and on the reduction in plant density due to the lodging effect of heavy rains, characteristic of the wet season, interprets the differences observed.

RESUMEN

Las características de crecimiento del girasol (*Helianthus annuus* L.) fueron determinadas en las variedades, Manfredi, Local de Kenia y Record, cultivadas e irrigadas durante la temporada de sequía de un clima de sabana. La dinámica de la producción fotosintética de las variedades, fue analizada en función de la temporada de siembra. Los resultados indican que parece existir una dependencia diferencial de la capacidad productiva de los genotipos en función de los factores ambientales, característicos de la temporada de crecimiento. Una discusión, basada en el proceso de partición de asimilados en girasol y en la reducción de la densidad de plantas debido al acame por efecto de las lluvias, es formulada para tratar de explicar las diferencias observadas.

INTRODUCTION

Sunflower has been traditionally used in temperate regions as a source of raw material for good quality table oil, presenting an oil production second in world ranking (26) Furthermore, recent studies in biomass production indicate that it may also be used as high quality forage, silage, fuel energy (2) and liquid fuel for diesel engines used in farm operations (4).

New established and selected sunflower cultivars seem to be better adapted to extreme tropical conditions than any other oil-seed crop. Furthermore, recently developed hybrids with superior qualities and yields after the practical cytoplasmatic male-sterile system (3) could be of basic interest for the region.

Although local crop practices and environmental factors affecting oil percent and composition during the period of sunflower development have been investigated rather extensively (24), scant information is available about sunflower adaptation to tropical regions. In spite of this situation, present results on yields of sunflower and other oilseed crops growing in low fertility soil and water stress conditions (6) suggest that cultivation be extended to the savannas. This is true especially in the vast lowland savannas of northern South America, with acid soils very low in nutrient content and a pronounced rainfall seasonality with four to six months of dry season and 1 300 to 2 200 mm rainfall (20). Under these ecological conditions, yield comparisons among sunflower cultivars planted in the Orinoco Llanos indicate a potential yield in achenes of up to 3.4 t/ha with an oil content ranging from 52 to 64% (16). This information is undergoing an intensive re-examination because of our critical shortage of oilseed crops, mainly due to economic constraints. Thus, agricultural strategies and crop yield have been analyzed, especially in relation to the comparative response of sunflower to seasonal climatic changes in the savanna.

The object of this work is to study growth of different sunflower varieties (Manfredi, Local of Kenia and Record) planted in the Trachypogon savannas of the Orinoco Llanos during the dry season, under an irrigation scheme. Conventional growth analysis and functional approach techniques were used to compare the environmental growth response of sunflower in the wet and dry seasons.

1 Received for publication 24 March, 1987
We are grateful to Dr Justiniano Velázquez for his challenging ideas and suggestions. We also wish to thank M.Sc. Marta Barrios and Miss Jane Mechan for their help in the preparation of this manuscript. The work was carried out during the tenure of a "Consejo Nacional de Investigaciones Científicas y Tecnológicas Grant" (CONICIT-Venezuela SIDF DC. FORT-I-EBLL).

* Centro de Ecología Instituto Venezolano de Investigaciones Científicas. Apartado 1827, Caracas 1010-A, Venezuela.

MATERIALS AND METHODS

An experimental site, similar to that described in Part I of this series, was established at the Calabozo Biological Station, Venezuela (8°56'N; 67°36'W) at the beginning of the dry season. The site was divided into four plots (50 x 50 m^2), which were fertilized as follows: one with 1 t/ha NPK 12:12:17/2 (IVP) and the other three with 2.5 t/ha from the same stock. Certified seeds of the cultivar Record were planted in two plots treated with different levels of fertilizer (1.0 and 2.5 t/ha), and the cultivars Local of Kenia and Manfredi were planted in the other two plots fertilized with 2.5 t/ha. Seeds of these trials were planted on February 3rd at 0.25 m intervals and spaced in rows of 0.8 m (62 000 plants/ha).

During the growth period of the sunflower cultivars, experimental plots were irrigated using a sprinkler system. Thus, irrigation supplied water to replace the loss through evaporation and to maintain soil water content at a water potential higher than −0.03 MPa as monitored by three series of nylon units (Bouyoucos) inserted at 0.30 and 0.60 m depths. Block resistance was measured daily with a Beckman bridge model RN–2B. Twice a month, soil samples were taken at various depths from three diferent places and water content was measured by drying at 105°C to a constant dry weight. These values were used to adjust block resistance measurements to soil water content and dry weight percentage. In addition to these procedures, commercial tensiometers were placed in the row nearest the center of each plot to directly measure the soil water matric potential at 30 and 60 cm depths. Irrigation frequency varied between three and occasionally four times a week.

One week after planting, five samples (1.0 m long and 0.8 m between rows) of the aboveground crop biomass were harvested at random and each separated into stems, petioles, assimilatory and non-assimilatory leaves and inflorescences. Each sample was dug up with soil to a depth of 0.5 m; belowground biomass was separated by the flotation method (15) and oven-dried at 80°C to a constant dry weight. Leaf area was measured with a portable photoelectric planimeter (Lambda Mod. 3050A). This process was repeated approximately every two weeks.

Sunflower growth characteristics were calculated from dry weight and leaf area data of the samples using the classical and functional growth analysis techniques described by Blackman (5), Briggs *et al.*, (7), Richard (19), Kvet *et al.*, (13), Ondok (16), Evans (9), Causton and Venus (8) and Hunt (11)

RESULTS

1. Changes in crop dry weight and leaf area development of sunflower cultivars during the savanna dry season.

Dry matter accumulations (Fig. 1) in the varieties Manfredi, Local of Kenia and Record were not significantly different throughout the dry season (Kruskal-Wallis test in 22). Thus, between 68 and 73 days after planting, the cultivars reached a maximum plateau value of 1376 ± 140 g/m^2.

The distribution of dry weight (W) (Fig. 2) in the different plant organs was similar between the cultivars Local of Kenia and Record and, at maximum mean biomass accumulation, assimilates were diverted

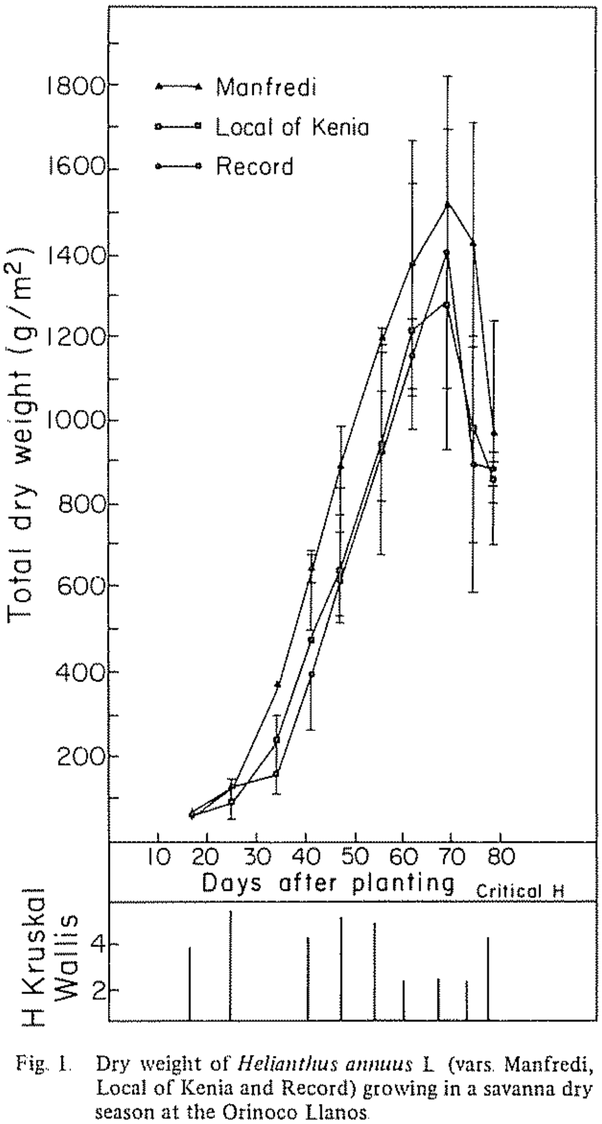

Fig. 1. Dry weight of *Helianthus annuus* L. (vars. Manfredi, Local of Kenia and Record) growing in a savanna dry season at the Orinoco Llanos.

into leaves, petioles, stems, roots and inflorescences (14, 41, 40, 17 and 17 percent, respectively). On the other hand, cultivar Manfredi showed a different W distribution with a significantly higher weight percentage in stems and inflorescences (34 and 28 percent of the total biomass, respectively) as compared with the two other cultivars.

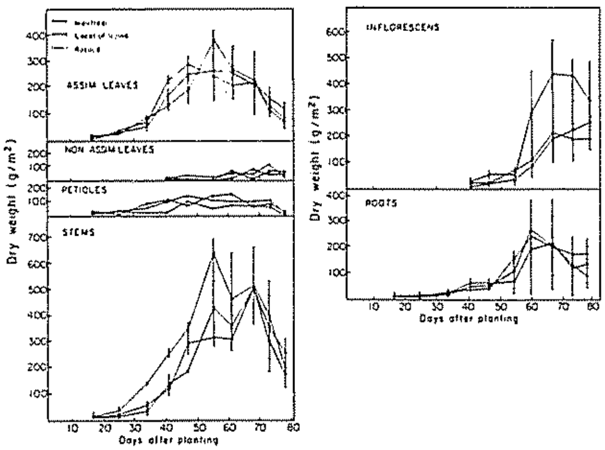

Fig. 2. Dry weight of *Helianthus annuus* L. (vars. Manfredi, Local of Kenia and Record) growing in a savanna dry season at the Orinoco Llanos.

Growth analysis characteristics of the sunflower cultivars, based on dry weight and leaf area, indicate that the crop growth rates (CGR) (Fig. 3e) of the cultivars followed similar patterns. Maximum CGR of Manfredi, Local of Kenia and Record were 42, 45 and 40 $g/m^2/day$ at 47, 61 and 55 days after planting, respectively. However, the W for these cultivars recorded from 34 to 61 days coincided (ANOVA with regression) with a linear regression, and after applying the STP test (21) it was found that the set of regression coefficients did not differ significantly from one another. The assumption of bivariate normally distributed data was tested by the Kolmogorov-Smirnov test (21). Therefore, the mean CGR for the varieties was 37.4 $g/m^2/day$ ($r^2 = 0.90$; $F = 134.4$; $S(y/x) = 120.3$).

Mean net assimilation rate of the cultivars (NAR) (Fig. 3a) decreased with crop age. At the begining of the season, varieties Manfredi and Record showed an NAR 2.4 times greater than the cultivar Local of Kenia (28 $g/m^2/day$). After 48 days, NAR was similar for all cultivars.

Leaf area ratio (LAR) (Fig. 3b) increased with plant age until 55 days after planting, and in the varieties Manfredi, Local of Kenia and Record it reached values of 33, 44 and 40 cm^2/g at 47, 55 and 34 days after planting, respectively. Local of Kenia maintained this relatively high value (circa 30 cm^2/g) during the first six weeks. At the end of the growth period, the three curves presented the same tendency.

Development of leaf area in the varieties is shown in Fig. 3d. The maximum LAI occurred in the Local of Kenia (4.3 m^2/m^2) at 55 days after planting, while in Manfredi and Record the values were 3.1 and 3.4 m^2/m^2, respectively. Leaves began to die in the bottom of the canopy after 41 days and this process was predominant after 61 days, when LAI apparently decreased.

The relative growth rate of the varieties Manfredi, Local of Kenia and Record (RGR, Fig. 3c) decreased throughout the season from values of 0.110; 0.100 and 0.037 g/g/day to 0.010; 0.007 and 0.028 g/g/day, respectively, at the end of the season.

2. Functional approach to sunflower growth analysis.

After testing different growth curves using the functional approach (8, 11), the Gompertz function (28, 18) appeared to reproduce the course of sunflower growth with reasonable accuracy, as shown by the fit of dry weight data of the varieties to a statistical regression curve. The parameters ($W = Ae^{-be^{-kt}}$) calculated (A = asyntotic value; b = position of the curve along the time axis and k = the rate constant inversely determining the spread of the curve along the time axis) are shown in Table 1. Rate constants were compared to study the effect of the experimental treatments (genotypes

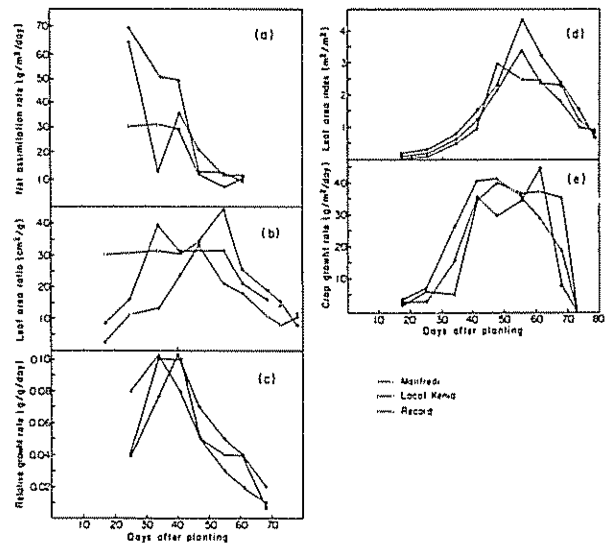

Fig. 3. Net assimilation rate (a), leaf area ratio (b), relative growth rate (c), leaf area index (d) and crop growth rate (e) of *Helianthus annuus* L. (vars. Manfredi, Local of Kenia and Record) growing in a savanna dry season at the Orinoco Llanos.

Table 1. Parameters of the Gompertz function ($W = Ae^{-be^{-Kt}}$) fitted to sunflower dry weight of the varieties Manfredi, Local of Kenia and Record: wet and dry seasons of a Trachypogon savanna at the Orinoco llanos.

Variety		Treatment	A (g/m^2)	K/day	b (g/m^2)	Inflection point		r^2
						t	w	
a)	Manfredi sel.10	wet season*	1 047	0.057	9.7	39.9	385	0.94
b)	Manfredi sel.10	dry season	1 501	0.065	15.9	42.6	552	0.96
c)	Local of Kenia	dry season	1 247	0.054	9.3	41.3	458	0.95
d)	Record	dry season	1 003	0.062	11.4	39.3	369	0.93
e)	–	1 963**	3 590	0.040	18.5	72.8	624	0.98
f)	–	1 964**	2 399	0.040	11.9	61.9	763	0.99

* Data from the first part of this work.

** Data from KREH'S experiments (12)

and seasons) on sunflower growth, by using the linear regression test for slope equality: covariance analysis (21). The results of this test indicate that for the set of k regression coefficients, the sum of squares among computed k's ($SS_{among\ k's}$=0.31) was lower than the critical sum of squares and therefore there was stability in the magnitude of k for the studied genotypes growing under different seasonal conditions.

3. Yield and components of the different varieties

There were no significant yield differences (Table 2) between the varieties planted and irrigated during the savanna dry season; thus the mean value was 2.5 t/ha ± 0.9. On the other hand, oil content was higher in the variety Record (44% in achenes and 60% in almonds) than in Manfredi (38 and 55%, respectively) or Local of Kenia (39 and 51%, respectively), although these differences were not correlated with yield or head diameter. However, despite an absence of yield differences, the higher oil content reported in the variety Record was negatively related to the trend of seed production in the varieties studied.

An attempt was made at interpreting the yield in the different varieties as a function of the season and genotpyes, by simultaneously comparing the present data with results obtained in Part I of this series. Thus, the differences were tested by a functional analysis of variance (22) applied to a factorial experimental design of treatments. The analysis of variance of yield data indicated that comparison among varieties and between seasons differed significantly. Variance homogeneity was previously tested by Bartlett (21, 22).

DISCUSSION

It was found that the functional trends of the growth indexes, calculated for the genotypes growing during the dry season, were relatively similar. Thus, accumulation of dry matter presents three phases: the first occurs until 34 days after planting, characterized by a development of control processes in the partioning of carbon assimilates mainly in stems and leaves. During this phase, crop growth rate (CGR) was mainly proportional to maximum net assimilatory rate. In the second phase, a maximum plateau of CGR for the varieties (CGR = 34 $g/m^2/day$) was evidently related to LAI development until 64 days after planting. However, as the season proceeded, the sink strength capacity of the inflorescences to assimilate seems to control plant development, especially the size of the assimilatory surface (LAI) and the activity of the assimilate source as expressed by the NAR. The latter increases at the end of the season (third phase), as reported for other sunflower varieties (17, 27). The dynamic process of the source sink relationship, controlled by the inflorescence sink from early in the season, was referred to as a "continuous inflorescence partitioning priority" in Part I of this series

Comparison of dry matter accumulation in the varieties cultivated during the wet and dry season fails to reveals any significant differences (Kruskal-Wallis test among the primary data harvested after 55 days of planting. However, early in the season, mean CGR was higher in the varieties planted during the dry season (37 $g/m^2/day$) as compared with those cultivated during the wet season (21 $g/m^2/day$). This difference asociated with a NAR seems to be related to seasonal changes, mainly as a result of a higher radiation regime during the dry season. Thus Wilson (27) showed that NAR of sunflower growing in arid climates was more than twice than other studied crops. However, low sensitivity of the relative growth rate (0.061 and 0.055 g/g/day for the wet and dry season, respectively) to enviromental changes, as a comparison of production efficiency of plant genotypes among the seasons, indicated a considerable advantage for the sunflower community in adapta-

Table 2. Yield and components in sunflower varieties planted and irrigated during the dry season of the Trachypogon savannas in the Orinoco llanos.

Variety		Yield (g/m^2)	Harvest (%)	Head (mm)	Oil content (%) Achenes	Almonds	Lodging (%)
a)	Manfredi sel.10	2.8 ± 1.4	0.28	147.3 ± 9.4	38	55	26
b)	Local of Kenia	2.6 ± 0.9	0.29	139.0 ± 10.5	39	51	21
c)	Record	2.2 ± 0.9	0.25	141.4 ± 11.3	44	60	23

ting to prevailing conditions of the savanna climate. These results seems to be associated with a compensatory effect of the NAR and leaf area ratio owing to variations in the specific leaf area. Thus the capability of expansion in space of sunflower leaves during the dry season was lower than in those leaves formed during the wet season.

The statistical analogy found among the "constant rates" ($K = 0.06\ day^{-1}$) calculated from the Gompertz function for the varieties growing under different seasons appears to be coherent with previous results, and an indication of the functional adaptability of this crop. Thus, genotypes presented a similar range of growth at equal time intervals, as described by the Gompertz function (27, 18). This analogy in the sunflower community was previously reported for a lower level of organization: leaves of *Pelargonium* ($K = 0.06\ day^{-1}$), growing under considerably different conditions (1). However, it will be necessary to obtain a greater amount of detailed data on sunflower growth before a generalization can be formulated. This postulation is supported by the fact that lower values of K seem to be associated with highly productive cultivars. From Kreh's data (12), a mean K of 0.04 day^{-1} was calculated for two sunflower trials, with a mean duration of growth periods, mean leaf area duration and mean biomass duration of 150 days, 538 m^2/m^2/growth period and 196125 $g/m^2/m^2$/growth period as compared with mean values of 78 days, 93 m^2/m^2/growth period and 44700 g/m^2/growth period, respectively, for the studied varieties growing in the savannas.

An analysis of the effect of enviromental factors (seasonal changes) and agricultural treatments (irrigation) on the yield of sunflower genotypes, indicated that there are differences in community function among the sunflower varieties as a function of the savanna season. These results were based on randomly chosen samples which differed in plant density due to the lodging effect of the heavy rains characteristic of the wet season. Analogous results were found when the Harvest Index (H), as expressed by the ratio of harvested seed dry weight to total dry weight of the genotypes, was analyzed. The results indicated that, during the dry season, dry weight was similarly distributed among the achenes and the vegetative structures. By contrast, during the wet season H was relatively lower in the varieties Local of Kenia and Record, as compared with Manfredi. However, a possible differential partitioning process, diverting a greater amount of assimilates to the reproductive organs, was masked by the lodging effect on seed yield and dry matter accumulated by the crops.

As previously pointed out, this situation seems to be common for fields of sunflower cultivated in tropical conditions. Thus, Suarez and Herrera (23) observed that for trials of sunflower cultivated in Cuba, up to 58 percent of the heads were empty and the mean lodging was higher than 31 percent. This situation could be controlled by varying the plant density rate and introducing new genotypes. Thus, Mazanni (personal comunication) has been successfully testing new varieties with a low lodging percentage in localities with heavy rains and high winds.

Despite the effect of lodging on dry matter production of sunflower during the wet season, irrigated sunflower fields are a valid option for increasing yields in the Orinoco Llanos, with a herbaceous layer production of 6 t/ha/year and extensive cattle raising with a low carrying capacity ranging from 0.2 to 0.5 U.A./ha/year. Thus, mean achene production of the studied varieties under irrigation (2.5 ± 0.9 t/ha) was analogous to the mean values reported for experimental trials in savannas with high fertility soils (14). Results indicate that in irrigated fields the varieties analyzed show a good adaptation to potential savanna conditions and new varieties, resistant to lodging, have to be introduced for improving sunflower yield during the wet season. However, the rate of sunflower CO_2 uptake is very sensitive to the length of the rainless periods which occur during the wet season (19); therefore a supplementary irrigation scheme must be implemented.

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