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

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ABSTRACT

Growth characteristics of sunflower (*Helianthus annuus* L.) were determined for the varieties Manfredi, Local Kenia and Record, cultivated during the wet season in a savanna climate. Plant adaptations to prevailing conditions were studied, and growth indexes for the Manfredi variety were established by using conventional growth analysis and functional approach techniques. Crop growth rate (CGR) of the Manfredi variety was mainly proportional to leaf area index (LAI) development until it reached a maximum (29 g/m²/day) at the beginning of the growth season (0-48 days after planting). Thereafter, the rapid senescence of leaf biomass was offset by an increase in net assimilation rate (NAR) in such a way that the CGR remained within similar values. Thus NAR (assimilate source) might be controlled by the sink strength of the inflorescens: "a continuous inflorescence partitioning priority." Furthermore, this partitioning strategy appears to be associated with an exponential decrease of the relative growth rate according to the Gompertz function fitted to the data.

COMPENDIO

Las características de crecimiento del girasol (*Helianthus annuus* L.) fueron determinadas en las variedades Manfredi, Local de Kenia y Record, cultivadas durante la temporada de sequía de un clima de sabana. Las adaptaciones de las plantas a las condiciones prevalecientes fueron estudiadas, y los índices de crecimiento de la variedad Manfredi establecidos mediante el análisis convencional de crecimiento y las técnicas funcionales. Los resultados indican que la tasa absoluta de crecimiento (TAC) de la variedad Manfredi fue proporcional al desarrollo de índice de área foliar, hasta que la TAC alcanzó un máximo (29 g/m²/día) al comienzo del período de crecimiento (0-48 días después de la siembra). Luego ocurrió una rápida senescencia de la biomasa foliar, la cual fue compensada por un aumento en la tasa neta de asimilación (TNA); en tal forma que la TAC permaneció dentro de similares valores. Así, la TNA (fuente de asimilados) es aparentemente controlada por la "fuerza de sumidero" de la inflorescencia mediante una "prioridad caracterizada por una partición continua hacia la inflorescencia". Esta estrategia departición parece estar asociada con una disminución exponencial de la tasa relativa de crecimiento, de acuerdo a la función Gompertz.

INTRODUCTION

Sunflower (*Helianthus annuus* L.) is a plant native to the temperate regions of North America; it has also been introduced to Europe, the USSR, Argentina and Turkey, which are now main producers (29). Nevertheless, in the last two decades, sunflower has been recognized as a potential commercial crop in the American tropics (6). In African (40) and Asian countries, (5), it is already grown on a commercial scale with varying degrees of success.

In tropical countries, the potential of sunflower for food production has recently gained new prominence because of a huge shortage in the supply of groundnuts. In Venezuela, sunflower has been used for ornamental purposes and cultivated on a small scale for birdfeed (35). Newly established and selected cultivars now seem to be well adapted to prevailing agroclimatic conditions (15, 16, 36, 37), with a potential yield of up to 4 t/ha and oil content ranging from 52 to 64 percent. This high primary production potential makes sunflower a valid alternative in the environmental conditions of the tropics. They are of particular interest in the vast areas of the Orinoco Llanos covered by *Trachypogon* savannas (28) and traditionally used for extensive cattle grazing, despite a low carrying capacity, estimated between 0.2 and 0.5 A.U./ha. These ecological constraints on primary productivity (28) suggest that sunflower, a plant which is adaptable to different environments (22), is a valid option as a source of raw material for the production of vegetable oil (38). It is also promising for animal feed, due to high forage yield (7.1-9.2 t/ha of dry matter) with more than 19% protein (30, 43).

The purpose of this paper is to study growth and dry matter production of sunflower, planted in the *Trachypogon* savannas during the wet season, in order to determine plant adaptations to prevailing savanna conditions. Sunflower yield is evaluated on the basis of production of its achene and seasonal biomass, both of which are considered sources of protein and fuel.

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MATERIALS AND METHODS

The experiment was set up at the Calabozo Biological Station (8°56'N; 67°36'W), from June to September. Site altitude was 98 m, average daily temperature 27.4°C, and annual precipitation 1234 mm. Soil analyses were made on level terrain with an upper layer of fine sediment (sandy-clay-loam 1 m thick), underlain by a hardpan horizon defined as lithoplinthic by Smith *et al.* (31). The experimental site (1 ha) was fertilized with 1 t/ha of NPK 12:12:17/2 (IVP) and divided into two plots (50 x 50 m^2).

On June 23rd, certified seeds of the Manfredi Sel. 10 and Local Kenia varieties (FONAIAP) were planted separately in each plot at 0.25 m intervals and spaced in rows of 0.80 m (62000 plants ha^{-1}). One week after planting, five samples (1 m long and 0.8 m between rows) of the aboveground crop biomass of the Manfredi variety were harvested at random and samples separated into stems, petioles, assimilatory and non-assimilatory leaves and inflorescens. Using the flotation method (17), the below-ground biomass of each sample was separated from soils dug up to a depth of 0.5 m, and all samples of plant biomass were 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.

Growth characteristics of the Manfredi variety were processed from dry weight and leaf area data (primary values) of the samples using the classical and functional growth analysis techniques described by Blackman (2), Briggs *et al.* (3), Richards (24), Kvet *et al.* (14), Ondok (20), Evans (8), Causton and Venus (4) and Hunt (12).

Doses of fertilizer were applied as locally recommended for sunflower yield (19), and the nutrient effect was re-examined during the months of September to November, to measure the effect of the extremely poor oxisols of the savannas, using a Latin square design An NPK 12:12:17/2 (IVP) fertilizer gradient 1-4 t/ha (an increase of 0.5 t/ha; eight treatments) was obtained by treating each plot (10 x 10 m^2) separately Certified seeds of the Record variety (FONAIAP) were planted on July 30 at 0.25 m intervals and spaced in rows of 0.8 m (62000 plants/ha). A single classification analysis of variance (32) was applied to test the differences among observed results; variance homogeneity had been previously tested by Bartlett (33).

Seed oil percentages were determined with a nuclear magnetic resonance technique (11) on a random sample of approximately 10 g of seed expressed as a percentage (10% moisture basis).

RESULTS

Response of the Manfredi variety to the savanna wet season, expressed as a function of biomass dry weight (W) and leaf area development.

Changes in crop dry weight during the season

Data indicate that, in the initial 28 days after planting, W in the Manfredi cultivar accumulated slowly as determined by the differentiation and development of leaf tissue (Fig. 1). The differentiated leaves then contributed substantially to assimilation, and there followed an immediate phase of rapid growth, until total W reached a maximum plateau value of 1004 g/m^2 between 69 and 76 days after planting (Mann Whitney U Test, 32). Thereafter, the accumulated dry weight rapidly decreased to 75 percent of the maximum value 82 days after sowing.

The dry weight accumulation in plant organs followed a similar pattern to that of total biomass. Assimilatory leaves reached maximum dry weight (158 g/m^2) 55 days after sowing, followed by a slow decrease until the end of the season. Stem dry weight was the highest in proportion throughout the growth period, and visual inflorescens (capitula) appeared 48 days after planting, and only two weeks later showed a higher proportion (26%) of total dry weight than roots and leaves. The total percentage distribution of W in the different plant organs at the end of the growth period (the time of maximum dry weight accumulation) showed that most of the W produced was diverted into the stems (45%). A similar proportion of W was accumulated in inflorescens (24%) and stems (17%) combined, whereas less than 11% was found in harvested roots and leaves.

The ratio of stem/root dry weight (S/R) increased to 15 at 48 days after sowing and held steady thereafter at values around 11. The Harvest Index (H) was 24 percent, and yield was 1.8 t/ha ± 1.1 in achenes. In the Local Kenia cultivar, the effect of lodging was apparently due to heavy rains during the season, which hampered sunflower analysis based on continuous sampling at different time intervals.

Analysis of growth characteristics of the Manfredi variety based on dry weight and leaf area

Calculated values of mean Crop Growth Rate (CGR) (Fig. 2e) increased slowly (1.7-4.2 g/m^2/

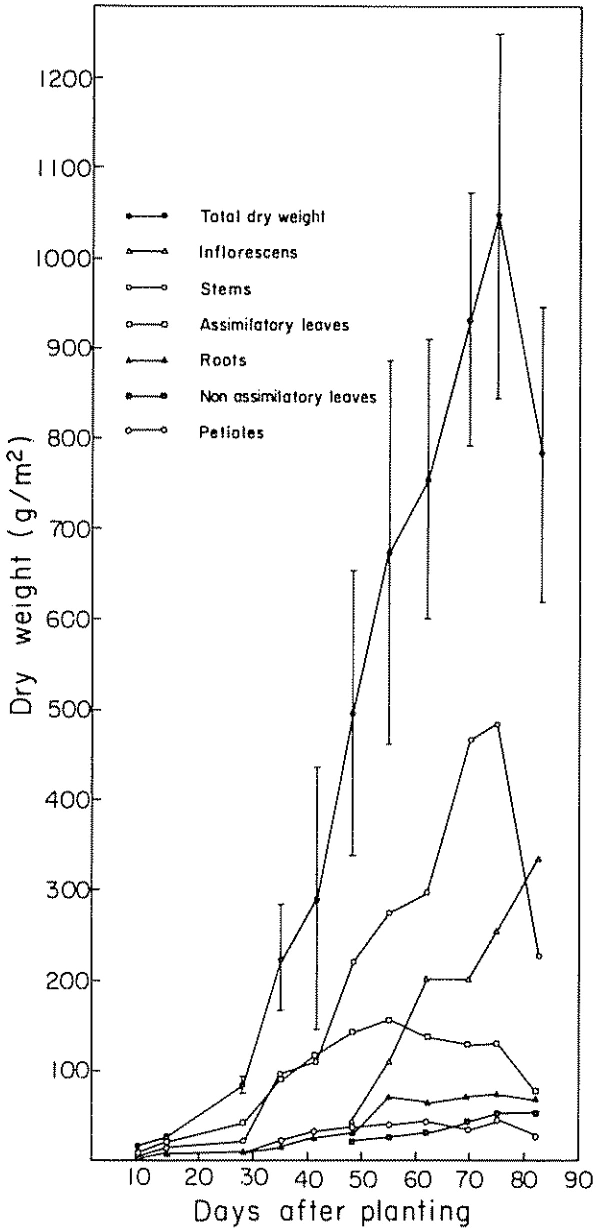

Fig. 1. Dry weight of *Helianthus annuus* L. (var. Manfredi) growing in a savanna wet season in the Orinoco llanos

day) during the first three weeks, with a subsequent period of rapid growth lasting until the end of the growth period, 76 days after sowing. Maximum CGR (29 $g/m^2/day$) was reached 48 days after sowing; however, despite apparent differences in CGR during this period, the data for the 48th, 55th and 69th days coincided (ANOVA with regression, 32) with a linear regression, and the monotonic mean growth was 21 $g/m^2/day$ ($r^2 = 0.99$). The assumption of bivariate, normally distributed data was tested by Kolmogorov Smirnov (32).

Net Assimilation Rate (NAR) (Fig. 2a) as a function of crop age showed two clearly defined phases. In the first, NAR decreased up to 41 days after planting; thereafter it increased from 7 to 15 $g/m^2/day$, 48 days after sowing, when a relatively large amount of dry matter was diverted to the inflorescens. This last change in NAR suggests that, during this interval, the dry weight ratio of assimilatory leaf area to senescent leaves remained similar. NAR then decreased at the end of the growth period

The leaf area ratio (LAR) (Fig. 2b) increased with plant age until 28 days after sowing, when it reached a value of 129 cm^2/g. Thereafter, it decreased to 6 cm^2/g, recorded at the end of the growth period

The development of the leaf area index (LAI) (Fig. 2d) over the course of the season indicates that between 48 and 55 days after sowing LAI reached a plateau value (2), followed by a rapid decrease. The mean relative growth rate (RGR) Fig. 2c) decreased from 0.14 to 0.02 g/day at the end of the season, as a function of the time lapse after planting. The trend of this index was apparently exponential.

Changes in the proportion of assimilatory tissue during crop development, after the visual onset of the inflorescens, were expressed by the allometric relationship (α) between the relative growth rate of reproductive structure biomass (mean RGR = 0.078 g/g/day) and vegetative biomass (mean RGR = 0.061 g/g/day). This measurement showed that the carbohydrate sinks are active simultaneously, beginning early in the growth period. Thus, flowering formation was strongly associated with an α 1.27, reflecting a preferential translocation of carbohydrates from the sources to the capitula, the latter acting as stronger carbohydrate sinks than other organs.

Functional approach to sunflower growth analysis

Different growth curves were tested using the functional approach (12, 4), and the Gompertz function (24, 41) appeared to reproduce the course of sunflower growth with considerable accuracy after data was fitted by methods of statistical regression ($Y = 2.22-0.6X$, $r^2 = 0.94$; $S(Y/X) = 0.30$ and $F = 117.60$). This approach will be used in the second phase of the study to test the effect of experimental treatments (varieties and seasons) on sunflower growth by comparing numerical values of the

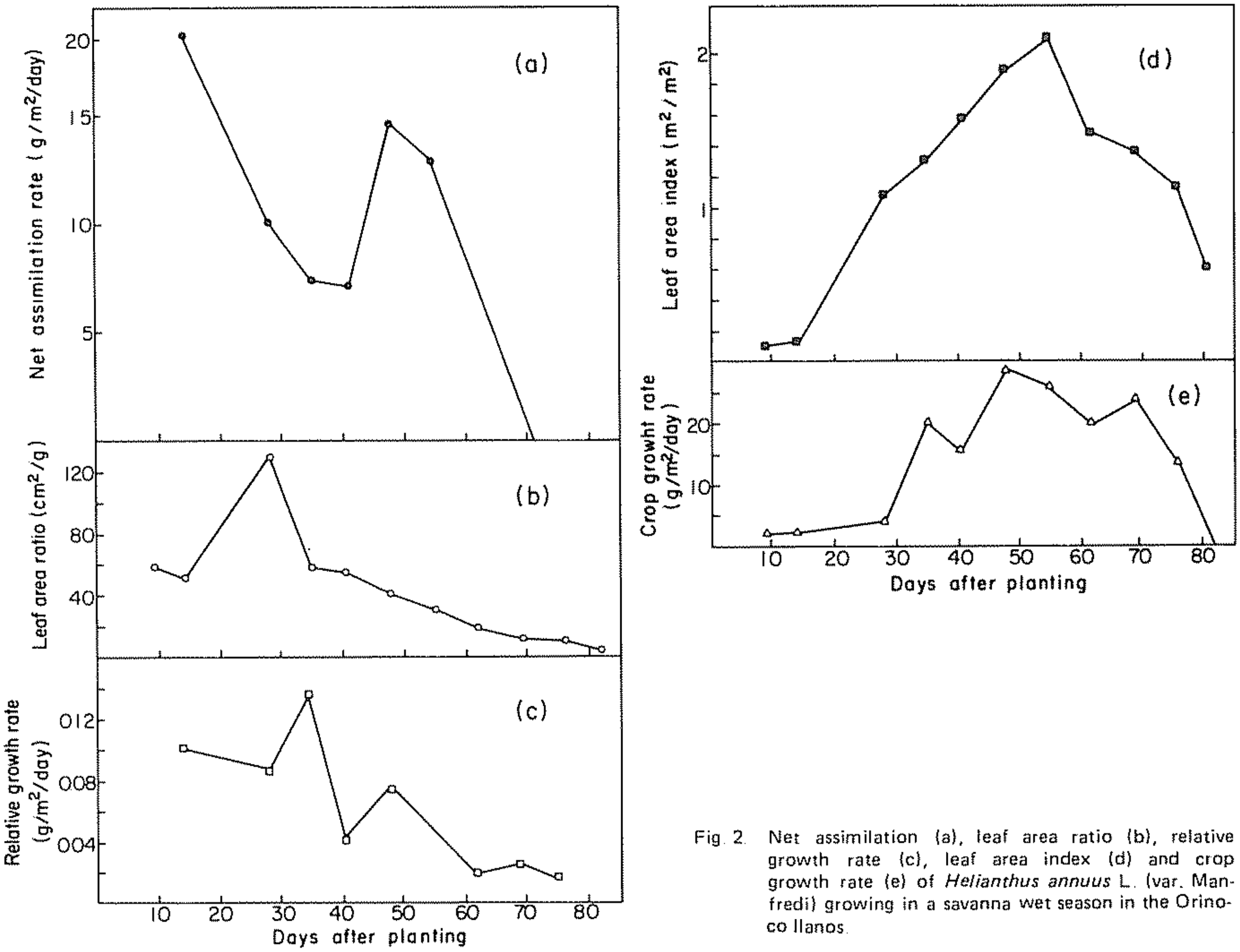

Fig. 2. Net assimilation (a), leaf area ratio (b), relative growth rate (c), leaf area index (d) and crop growth rate (e) of *Helianthus annuus* L. (var. Manfredi) growing in a savanna wet season in the Orinoco llanos.

constant rate. Parameters were calculated from the fitted Gompertz curve $(W = Ae^{-be^{-kt}})$ where: A is the asyntotic value (= 976.47 g); b the position of the curve along the time axis (= 9.21); and k the rate constant, inversely determining the spread of the curve along the time axis (= 0.06 day^{-1}).

Effect of fertilizer gradient on sunflower (Var. Record) yield

The ANOVA test for the Latin square design (32) showed that the different fertilizer treatments (1-4 t/ha) did not have a significant effect on the yield of the Record variety (F treatments = 1.46; $F_{0.01}$ = 3.47 and $F_{0.05}$ = 2.42). The weight of achenes harvested in the fertilized plots ranged from 0.46 to 0.70 kg/m^2 with a mean value of 0.61 kg/m^2 and Sd = 0.14 kg/m^2. The homogeneity of variance was previously tested by Bartlett (33) (X^2 calc. = 14.93; $X^2_{0.01}$ = 16.18).

Sunflower yield and components

Inflorescence weight increased in a linear fashion throughout the season, and when physiological maturity was reached, in the case of the Manfredi variety, 43% of the total dry matter produced was diverted into inflorescens. The harvest index was 24%.

Yield of the Manfredi variety (Table 1) was significantly higher than that of the two other varieties studied. In spite of these yield differences, no head diameter compensation was observed. Oil content was higher in the varieties Local Kenia and Record than in the Manfredi variety. This suggests that oil content may have been negatively associated with yield and head diameter. However, all varieties produced seeds of at least 40% oil content in all trials. The oil content determines price premiums for sunflower seeds (25).

Table 1. Yield and components in sunflower varieties growing during the wet season of the *Trachypogon* savannas in the Orinoco llanos.

Variety	Yield (g/m²)	Harvest index (%)	Head diameter (mm)	Oil content		Lodging (%)
				achenes	almonds (%)	
a) Manfredi sel. 10	1.88 ± 1.1	0.24	136.8 ± 9.3	31	43	21
b) Local Kenia	0.60 ± 0.2	0.19	96.4 ± 8.6	34	46	47
c) Record	0.71 ± 0.2	–	59.5 ± 7.5	37	56	45

DISCUSSION

The Manfredi variety showed a unimodal growth rate throughout the season, with crop growth rate (CGR) mainly proportional to leaf area index (LAI) development from the beginning of the growth period until a maximum was reached 48 days after planting. Thereafter, in spite of a rapid senescense of leaf biomass, CGR maintained similar values due to an increase in net assimilation rate (NAR) (15.4 g/m^2/day). Briggs *et al.* (2) also reported this NAR subsidiary maxima coinciding with the appearance of flower development. This situation might be related to a control of NAR by the sink strength of the inflorescens. Thus, increase in source activity of the Manfredi variety could be due to greater inflorescence-sink activity, since there is a balance between the production rate of new leaves and the onset of leaf senescence (which maintains the LAI).

The CGR of the Manfredi variety reached a maximum (29 g/m^2/day) when the leaf area index was 1.9 and NAR 15.4 g/m^2/day, 48 days after planting. This maximum value was 41% lower than the potential (42 g/m^2/day) indicated for sunflower under intensive agricultural production (39). However, comparisons of Manfredi growth characteristics with relatively through data from Kreh's experiments (13) indicate that, although NAR was 1.7 times greater than reported by Kreh (13), the difference in CGR was due to stronger development of LAI as a possible reflection of higher plant density (compare 62 000 plants/ha for the Manfredi crop with 80 000 plants/ha in Kreh's experiment). Therefore, in this comparison, sunflower planted in the *Trachypogon* savannas presents a high potential yield associated with an increase in LAI proportional to plant density, since seed production seems to be correlated with crop LAI at anthesis (23). However, an attempt to increase CGR by changing plant density could be a precarious solution for increasing seed production in sunflowers, since seed yield and oil concentration appear to be higher at relatively low population densities (25 000 to 50 000 plants/ha) (1).

Results of dry weight distribution for the Manfredi variety showed a three-way phase distribution pattern. In the first phase (until 41 days after sowing), dry weight was mainly diverted to the leaves, reaching 45 percent of the total. In the second phase, the visual onset of inflorescence development occurred 48 days after planting; the dry weight accumulated in the stems steadily increased to 52 percent of the total, and the assimilatory leaf biomass maintained a constant rate of accumulation. The increase in leaf dry weight after the development of the inflorescens was offset by the death of crop basal leaves. In the third and final phase of the growth period, inflorescence activity as an assimilate source increased and dry weight reached 42 percent of the total crop weight 76 days after sowing. Thus, mean RGR of inflorescens (0.066 g/g/day) was about double that of roots, stems and leaves (0.033, 0.027 and 0.026 g/g/day, respectively).

Previous results with the distribution of newly produced dry matter in the community, as expressed by the relative growth rate (RGR) of plant organs, had indicated that carbohydrate sinks in simultaneous activity were partially centered in inflorescence growth beginning early in the season; "a continuous inflorescence partitioning priority strategy". These findings seem to be a common characteristic in carbohydrate partitioning of dry matter in sunflower (3, 9, 7). Thus, the decline in growth energy of the systems, at a constantly proportional rate according to Gompertz functions (24), could be related to inflorescence development. Sunflowers have a capacity for continuous growth increase, thus exceeding the growth of the organs and acting as an effective sink competitor for a limited supply of assimilates. The energy required for plant maintenance and growth and related respiratory processes must also be involved.

Little primary data are available and it is therefore difficult to generalize about the sunflower growth trend, but it appears that the Gompertz function might be suitable to describe *Helianthus* growth. Thus, Kreh's data (13) were significantly fitted by us and the equation for two trials (in different years, 1963 and 1964) were $W = 3\,590.77e^{-18.54\;-0.04\,t}$ and $W = 2\,399.40e^{-11.94\;-0.04\,t}$

The yield of sunflowers planted during the wet season was 1.88, 0.60 and 0.71 t/ha for the cultivars Manfredi, Local Kenia and Record, respectively. The highest yield in Manfredi was analogous to the mean value reported for experimental plantations in Venezuela and temperate latitudes (2.1 t/ha in Mazzani and Voinea (16) and 2.8 t/ha in Owen (21)); however, it was lower than the potential (4 t/ha) specified for this crop. This difference might be a result of the lower total radiation occurring during the wet season, when atmospheric conditions reduce in total amount of radiation as compared with the dry season (20 MJ/m^2/day/vs 31 MJ/m^2/day). These results seem to be related to the linear relationship between NAR and radiation, previously established for *Helianthus* (22).

However, in spite of a reduction in the mean seasonal radiation, studies on energy and gas exchange within a sunflower canopy of the Manfredi variety (27) indicate that during the rainless days of the wet season the loss of sensible heat exceeded 50% of the available energy during midday, and this was associated with reduced CO_2 uptake by the upper canopy leaves. Therefore, during brief periods, water deficits in the savanna soil became severe enough to produce a reduction in source strength (CO_2 assimilation) and **a fortiori** in source size (leaf area index, LAI), as shown by Yegappan (42) under experimental conditions. Supplementary irrigation seems to be necessary to maintain an adequate water balance in the sunflower community and consequently a high crop yield. However, in certain sunflower cultivars, it has been observed that, upon relief of stress, leaf area increases in specific leaves (34). These crops could adapt better to the savanna conditions where rainless periods occur during plant growth.

A further factor in the differences in yield reported here could be the significant effect of lodging, which occurred in the Local Kenia cultivar due to the heavy rains typical of the savanna wet season. This effect may be partially controlled by plant population and spacing; for example, Robinson *et al.* (25) found that lodging in sunflower was a function of population density for cultivars ranging between 17 000 to 62 000 plant/ha. Uniformly spaced single plants seemed to lodge least, and at harvest they produced capitula with the lowest moisture percentage and seeds of the highest yield and oil percentage (26). Compensatory responses to these changes in plant population can occur in sunflower (18).

Reports on the performance of sunflower in savannas used for extensive cattle grazing indicate a possible improvement in savanna yield. This is associated with the greater amount of energy allocated to reproductive structures as compared with vegetative structures: an "r strategist" in temporarily unstable environments (10). This is the basis for developing appropriate cropping strategies and research for a better understanding of sunflower response to savanna conditions.

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Notas y comentarios

Flores explosivas promueven la polinización

Las flores polinizadas por insectos generalmente emplean el gentil arte de la seducción. . . dulce néctar, suave perfume, atractivos colores, interesantes formas, nutritivo polen. Pero la orquídea tropical americana *Catasetum* está provista de una antipática sorpresa dentro de sus perfumadas flores. Estas explotan bolsas de polen sobre las abejas visitantes con tal fuerza que deja a los insectos permanentemente asustados.

Catasetum es de todas maneras algo inusual. A diferencia de la mayoría de los géneros vegetales, tiene separadas, en diferentes plantas, sus flores masculinas y femeninas. Y como Charles Darwin descubrió, la flor masculina tiene una asombrosa pistola escondida en su centro. Cuando un insecto se posa en la flor, colecta perfume del labio en el que aterriza. Pero metiéndose más adentro, frota la antena de la flor, un cuerno sensitivo al toque, que provoca el disparo de dos bolsas de polen (polinios) situadas en la parte superior.

Sólo toma una fracción de segundo la pistola para disparar. Pero la fuerza es sorprendente; los sacos de polen, que pesan menos de un décimo de gramo, son disparados a una velocidad de unos 300 centímetros por segundo. Y como Darwin descubrió en su propia persona, al ser golpeado en la cara por un *Catasetum* en explosión, el impacto es bastante doloroso. Los polinios se pegan entonces tenazmente a su blanco con una viscosa goma.

¿Y cómo se siente una abeja después de que ha sido golpeada? Gustavo Romero y Craig Nelson, del Departamento de Biología de la Universidad de Indiana, encontraron que las abejas golpeadas con polinios nunca olvidaban la experiencia. Aunque las abejas inspeccionaban regularmente las flores masculinas, no aterrizaban en ellas otra vez. En lugar de eso, se dirigían a las flores femeninas, que aunque son de tamaño y forma diferentes, emiten el mismo perfume atractivo.

Una vez que una abeja aterriza sobre las féminas, los polinios le son quitados por una hendidura en la parte receptiva del órgano sexual femenino. La cisura entonces se hinchaba cerrándose, y así la planta era polinizada exitosamente (**Science**, vol. 232, p. 1538).

La violencia es claramente importante para la polinización de *Catasetum*. Si las abejas no estuvieran asustadas de volver a entrar en una flor masculina, ellas estarían recogiendo polinios de otras flores machos, con la consecuencia de que sería imposible el sacar uno de estos sacos por las flores femeninas. Romero y Nelson explican todo el fenómeno de la violencia como un resultado de la intensa competencia entre las plantas masculinas por conseguir "parejas". Como se producen más machos que hembras de *Catasetum*, un macho necesita desanimar a su abeja polinizadora para que no se interese por sus competidores.

La abeja distingue los machos de las hembras, a pesar de que huelen igual, por diferencias visuales. El tamaño, forma y color de las flores femeninas son bastantes distintos. En realidad, los sexos fueron una vez clasificados equivocadamente como géneros distintos. El viejo género *Catasetum* Richard es la forma masculina, *Monachanthus* Lindley es la forma femenina, y en algunas especies de *Catasetum*, la forma hermafrodita se designó como *Myanthus* Lindley.

La evolución de la violencia probablmente fue marchando mano a mano con estas diferencias sexuales. Así, en las plantas de *Catasetum* con las menores diferencias entre los sexos, los polinios tienen menor fuerza (un 10 por ciento del peso de la abeja). Pero, en especies como *C. pileatum*, las diferencias entre los sexos es la más grande y los polinios son disparados con tal fuerza (28 por ciento del peso de la abeja) que pueden hacer blanco en el polinizador cuando éste ha comenzado a volar. **Adalberto Gorbitz.**