PHYSIOLOGICAL AND MORPHOLOGICAL ADAPTATIONS IN TOMATO INTERCROPPED WITH *TAGETES ERECTA* AND *AMARANTHUS HYPOCHONDRIACUS*

ADAPTACIONES FISIOLÓGICAS Y MORFOLÓGICAS EN TOMATE ASOCIADO CON *TAGETES ERECTA* AND *AMARANTHUS HYPOCHONDRIACUS*

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SUMMARY

Intercropping is an alternative strategy to traditional application of agrochemicals for plant disease management. Intercropping tomato plants (*Lycopersicon esculentum* Mill.) with marigold (*Tagetes erecta* L.) resulted in significantly less foliar and fruit damage by *Alternaria solani.* Such reductions were explained by the allelopathic effect of marigold on *A. solani* conidia germination, by the reduction in daytime hours with relative humidity ≥ 92 %, and by providing a physical barrier against conidia spreading. Physiological adaptations and anatomical modifications of tomato plants due to shading by marigold might also have some effect on *A. solani* infection. Therefore, in this study we measured net photosynthesis rate, respiration rate, stomatal conductance, chlorophyll content, leaf thickness, plant height, leaf area, specific leaf area and fruit yield of tomato plants intercropped with marigold or the native pigweed (*Amaranthus hypochondriacus* L.), or grown as a single crop. Tomato plants intercropped with marigold (T-M) or pigweed (T-P) grew longer stems (26 to 33 %), thinner leaves (33 to 35 %), and lower specific leaflet area (61 to 69 %) than plants grown alone (T). Also, tomato plants intercropped with marigold had a higher (P ≤ 0.05) net photosynthetic rate (48 and 64 %) and chlorophyll content (4 and 9 %) than T-P and T treatments, at 10 weeks after tomato transplant (WATT). From 19:00 to 23:00 h the T-M doubled (P ≤ 0.05) the respiration rate compared to the non-intercropped tomato plants. The amount of leaf sections with starch grains in the parenchyma cells was higher (P ≤ 0.05) in T-P (50 %) and T (86 %) treatments than in treatment T-M. Compared to treatments T-P and T, T-M produced more (P ≤ 0.05) fruits (100 and 148 %, at 8 WATT), inflorescences (46 and 25 %, at 6 WATT) and fruit yield (100 and 148 % at 15 WATT).

Index words: *Alternaria solani, Lycopersicon esculentum*, *Tagetes erecta*, intercropping, photosynthesis.

RESUMEN

La asociación de cultivos es una alternativa al uso de agroquímicos para el manejo de enfermedades. En plantas de tomate (*Lycopersicon esculentum* Mill.) se redujo el daño foliar y de frutos inducido por *Alternaria solani* cuando estuvieron asociadas con cempasúchil (*Tagetes erecta* L.). Dicha reducción se ha explicado por el efecto alelopático del cempasúchil en la germinación de los conidios de *A. solani*, por la reducción en el número de horas por día con una humedad relativa ≥ 92 %, y por el efecto de barrera física de esta especie que interfiere con la dispersión de los conidios. Las modificaciones fisiológicas y anatómicas de las plantas de tomate por el sombreado en la asociación con cempasúchil podrían tener algún efecto sobre el nivel de infección de *A. solani*. Por ello en este estudio se midió fotosíntesis neta, respiración, conductancia estomática, contenido de clorofila, grosor foliar, altura de planta, área foliar, área foliar específica y rendimiento en plantas de tomate asociadas con cempasúchil o alegría (*Amaranthus hypochondriacus* L.) y en tomate sin asociar. Las plantas de tomate asociadas con cempasúchil (C-T) o alegría (A-T) presentaron mayor altura (26 a 33 %), hojas más delgadas (33 a 35 %), y menor área foliar específica (61 a 69 %) que el tomate sin asociar (T). Pero sólo el tomate asociado con cempasúchil superó (P ≤ 0.05) en tasa de fotosíntesis neta (48 y 64 %) y contenido de clorofila (4 y 9 %) a los tratamientos A-T y T, a las 10 semanas después del transplante del tomate (SDTT). De las 19:00 a las 23:00 h, C-T duplicó (P ≤ 0.05) su tasa de respiración en comparación con T. La cantidad de cortes foliares con gránulos de almidón en el parénquima fue mayor (P ≤ 0.05) en los tratamientos A-T (50 %) y T (86 %) que en C-T. En comparación con los tratamientos A-T y T, C-T produjo más (P ≤ 0.05) frutos (100 y 148 % respectivamente, a las 8 SDTT), más inflorescencias (46 y 25 % respectivamente, a las 6 SDTT) y más rendimiento (64 y 42 % respectivamente, a las 15 SDTT).

Palabras clave: *Alternaria solani*, *Lycopersicon esculentum*, *Tagetes erecta*, asociación de cultivos, fotosíntesis.

INTRODUCTION

Intercropping is an alternative strategy to traditional application of chemicals for plant disease management (Thurston, 1992; Altieri, 1999). The most beneficial intercropping systems make use of plants with antimicrobial properties. Marigold (*Tagetes erecta* L.), a traditional

Recibido: 27 de Octubre del 2005.
Aceptado: 26 de Enero del 2007.

flower in México for the All Saints Day celebration, has been recognized for its fungicidal, nematocidal and insecticidal properties due to the presence of thiophenes in all its tissues (Jacobs *et al.*, 1994; Montes and García, 1997; Riga *et al.*, 2005). Tomato plants (*Lycopersicon esculentum* Mill.) intercropped with marigold have shown significantly less foliar and fruit damage by *Alternaria solani* Elis and Martin, Jones and Grout than the non-intercropped tomato (Zavaleta-Mejía and Gómez, 1995; Gómez-Rodríguez *et al.*, 2003). According to Gómez-Rodríguez *et al.* (2003), the beneficial effects of marigold when intercropped with tomato can be attributed to three protective mechanisms: 1) By the allelopathic effect of marigold on *A. solani* conidia germination; 2) By reducing the period with relative humidity ≥ 92%, thus diminishing conidial development; and 3) By providing a physical barrier against conidia spreading. Physiological adaptations and anatomical modifications due to shading on tomato plants intercropped with marigold could also have some effect on *A. solani* infection (Rojas-Martínez *et al.*, 1999).

Because of its shading effect, intercropping may influence the canopy net carbon assimilation rate and the expression of some morphological characteristics, such as stem length and leaf thickness (Taiz and Zeiger, 2002; Redfearn *et al.*, 1999). Crops are able to sense nearby plants by detecting the far-red light reflected by them, even before the associated plants provide shade. Exposure to far-red light can eliminate phytochromes that absorb this radiation, so plants can adjust their growth to avoid shading by elongating the stems and projecting new leaves above the light-obstructing structures (Robson *et al.*, 1996).

Leaves grown under shade are larger and thinner than leaves grown under sunlight, while the latter have smaller and denser stomata, presumably to better regulate water vapor losses and CO_2 assimilation under full sunlight. Sunlight leaves are two to three times thicker than shaded leaves, due to the formation of larger or additional layers of palisade cells and a well developed spongy mesophyll (Taiz and Zeiger, 2002). The anatomical adaptations in response to shading, frequently represent a reduction in photosynthetic capability of up to five times compared to sunlight leaves (Salisbury and Ross, 1994).

Since the physiological adaptations and anatomical modifications due to shading of tomato plants when intercropped with marigold, might also have some effect on *A. solani* infection, the objective of this work was to evaluate the effect of intercropping on several physiological and anatomical features in tomato plants. This information might assist tomato growers in selecting an intercropping system for plant disease management as alternative strategy.

MATERIALS AND METHODS

1997 Growing season

Experimental conditions. The study was performed under field conditions at the Experimental Research Station of the Colegio de Postgraduados in Texcoco, México. Treatments included: Tomato (cv. 'Río Grande') alone (T), tomato intercropped with marigold (T-M) and tomato intercropped with pigweed (T-P). When intercropped the species were alternated along the row and rows were 100 cm apart with 50 cm between plants, while in non-intercropped tomato rows were 100 cm apart with 30 cm between tomato plants. Marigold and pigweed (cv. 'L-125') seedlings (30 days-old) were planted during the second week of April, 30 d before planting the tomato seedlings. Previous studies (Zavaleta-Mejía and Gómez, 1995; Rojas-Martínez *et al.*, 1999) had established these planting dates, fertilization rates and plant distances for optimal tomato crop health and yield when intercropped with marigold. The pigweed has not been reported with antifungal properties and thus it was used as intercropping control for comparing with marigold in this experiment.

Treatments were randomly assigned to three 26 m x 6 m plots, and divided into four quadrants (replications). The experimental units consisted of 3-row plots, 13 m long and 1 m between rows. Prior to planting, the soil was disinfested with dazomet (Basamid®, Basf Mexicana, S. A. de C. V.) at 38 g a.i. m^{-2} to prevent root diseases. Pigweed and marigold plants were fertilized individually with 80N-40P-00K, with one half of the N applied 8 d after planting (third week of April) and the other half 30 d later (third week of May), while all the P was applied in the third week of April. Tomato plants were also fertilized with 150N-60P-00K, by applying the N in two equal halves, at 8 and 30 d (third week of May and first week of June, respectively); as in the other treatments, all the P was applied in the first application. The effects of these intercroppings on *A. solani* infection were also evaluated but reported elsewhere (Gómez-Rodríguez *et al.*, 2003).

Physiological variables. Instantaneous net photosynthesis and respiration rates, and stomatal conductance were recorded in nearly simultaneous lectures in one tomato plant per replication, with a portable LI-6200 photosynthesis system provided with a 0.25 L assimilation chamber (LI-COR, Inc., Lincoln, NE, USA) at 5, 8 and 10 weeks after tomato transplant (WAT). Each measurement started with the photosynthetic rate once a steady state was reached (variable time); immediately afterwards the chamber and the leaf were completely darkened by covering them with a flannel for 90 s (*i. e.*, 30 s after the CO_2 had started to increase at a constant rate) and until then the measurement of the respiration rate was actually started. In both rates the time programmed for actual CO_2 monitoring was 15 s. At 5 WAT, the readings were taken every 4 h over a 24 h period; at 8 and 10 WAT, the readings were taken only at 11:00 and 15:00 h. Total leaf chlorophyll content was recorded in four plants per replication, with a SPAD 502 chlorophyllmeter (Minolta, Japan) at 5, 8 and 10 WAT. In all cases, readings were taken on the terminal leaflet of the third leaf, counted from the plant apex.

Morphological variables. Plant height and number of leaves and inflorescences per tomato plant were recorded every 15 d, starting at 2 WAT, for a total of four measurements. Fruits per plant were recorded at 6 and 8 WAT in three plants per replication. Leaf area per plant was measured at 6 WAT in at least two plants per replication, one per species in the intercropped plots; the leaf area per leaflet registered at 10 WAT was estimated from three terminal leaflets from fifth leaf sampled from one plant per replication, measured with an LI-3100 integrator (LI-COR, Inc., Lincoln, NE, USA). Dry leaf weight per leaflet was measured after the leaflets were oven dried at 70 °C until constant weight. Specific leaf area per leaflet (SLAF) expressed as $cm^2\ g^{-1}$ was calculated by: SLAF = leaf area/leaf dry weight.

Leaf thickness was recorded on the terminal leaflet of the fourth leaf in a plant per replication, at 12 WAT. A 1 cm^2 leaf tissue section, located at 1.5 cm from the bottom (0.5 cm from each side of the main vein), was taken from each leaflet. Transverse sections 40 μm thick from each leaflet tissue, obtained with a freeze microtome (Model 880, American Optical, USA), were mounted in glycerol 25 % (v/v). Thickness was measured on both sides of the main vein with an ocular micrometer (Carl Zeiss, Germany) at 10X amplification, under a microscope (Carl Zeiss, Germany).

Fruit yield. Ripe tomato fruits from plants of the central row in each replication were harvested and weighed at 12 and 13 WAT; at 15 WAT both green and red fruits were harvested. Total fruit yield per plant was estimated from these data.

1999 Growing season

Experimental conditions. Intercropped treatments and agronomic management were the same as in 1997, except for a few differences described below. In 1999, the 30 day-old marigold and pigweed (cv. 'Nepal 96') seedlings were transplanted 30 and 15 d before tomato seedlings, respectively, which were transplanted during the first week of May. Pigweed plants were trimmed one month after transplant in order to produce similar foliage as that of marigold. Treatments were randomly assigned to three 17 m x 8 m plots, and divided into four quadrants (replications). The experimental_units consisted of 8-row plots, 4 m long with 1 m between rows.

Physiological variables. Instantaneous net photosynthesis rate and stomatal conductance were recorded on the terminal leaflet of the third leaf in 12 tomato plants per treatment, with an LCA - 2 (ADC; England, UK) portable photosynthesis device provided with a 0.25 L assimilation chamber, at 10 WAT. Readings were started at 11:00 am and taken for two consecutive days, using the same variables as in 1997 readings.

Histochemical tests with potassium iodine and the periodic acid-Schiff reaction were performed at 10 WAT, for detecting starch grains in tomato leaves. For the potassium iodine test, a portion of the leaf samples used for leaf thickness were exposed to a few drops of potassium iodine for 20 min and then washed with distilled water (Johansen, 1940). Leaf sections were mounted in glycerol 25 % (v/v) and the stained sections were counted.

For the periodic acid-Schiff reaction, the third leaf was collected from eight plants per treatment located in central rows. Three terminal leaflets were collected per leaf, and from them only eight leaflets were processed per treatment. A leaf tissue section, located at 1.5 cm^2 from the bottom (0.5 cm from each side of the main vein), was taken from each leaflet. A 1 cm^2 leaf tissue section from each leaflet was fixed in FAA [a mixture of 500 mL absolute ethyl alcohol, 100 mL formaldehyde 40 % (v/v), 50 mL glacial acetic acid, and 350 mL distilled water], and observed under a microscope (Curtis, 1986). A bright pink color indicated the presence of starch grains and the number of stained sections was scored.

Morphological variables. Tomato leaf area and leaf dry weight were recorded on three terminal leaflets of the fourth leaf, at 10 and 12 WAT, obtained from two leaves in 18 plants per treatment. Leaf thickness was measured on the terminal leaflet of the fourth leaf, in 10 plants per treatment, at 10 WAT. Both processing and observation of leaf tissue samples were done as described for the 1997 growing season.

Statistical analysis

Each experiment was analyzed as a randomized complete block, and an analysis of variance was performed on each variable, and when it reported significant differences among treatments a means comparison test was applied using the Student's *t*-test. All analyses were performed using the Statistical Analysis System software (Windows 6.11, 1995, USA).

RESULTS

Physiological variables

Stomatal conductance of intercropped tomato plants was similar to that of non-intercropped tomato in all sampling dates in 1997, but in 1999 it was significantly greater when intercropped with marigold than in the other two treatments, T-P and T (Table 1). The net photosynthetic rate of tomato leaves at 10 WAT was significantly greater when intercropped with marigold (T-M) than in the non-intercropped tomato, by 78 % in 1997 and by 64 % in 1999. In 1999, net photosynthesis was 48 % greater in the T-M treatment than in the tomato intercropped with pigweed (T-P) (Table 1). However, in previous dates (5 and 8 WAT) there were no significant differences in photosynthesis among treatments.

Only at 10 WAT in 1997, the tomato plants intercropped with marigold had significant higher chlorophyll content than the non-intercropped plants (9 %) and than tomato intercropped with pigweed (4 %) (Table 2).

When intercropped with marigold or pigweed, tomato plants had a similar leaf respiration rate during daylight hours (except at 11:00 h) than tomato grown as a single crop. During the night (19:00 and 23:00 h), the intercropped tomato plants with marigold had a significant increase in respiration rate over the non-intercropped tomato plants (Figure 1).

Both staining tests showed the presence of starch in mesophyll chloroplasts and in leaf main vein (Figure 2). The lowest frequency of leaf sections with starch granules (73 %) occurred in the T-M treatment (Table 2).

Morphological variables and fruit yield

Intercropped tomato plants (T-M and T-P) were 33 % taller at 4 WAT and 26 % at 8 WAT than the non-intercropped tomato (T), and T-P tomato plants were 27 % taller at 6 WAT than the T treatment (Table 3), but there were no significant differences among treatments in the number of leaves per plant (data not shown). A significantly higher number of tomato inflorescences was recorded in T-M than in the other two treatments, at 4 WAT (54 to 70 %) and 6 WAT (25 to 46 %); however, at 8 WAT the mono-cropped tomato had a similar value as T-M (Table 4). The number of fruits per plant was also significantly higher in T-M than in T-P at 6 WAT, and higher than in T-P and T at 8 WAT (Table 4). Fruit yield at harvest (15 WAT) was significantly higher in T-M than in T-P and T (Table 4), even though tomato plant density in

Table 1. Stomatal conductance (μmol H_2O m^{-2} s^{-1}) and instantaneous net photosynthetic rate (μmol CO_2 m^{-2} s^{-1}) in tomato leaves grown intercropped with marigold (T-M) or pigweed (T-P) and non-intercropped (T), for the 1997 and 1999 growing seasons.

Treatment	Stomatal conductance†				Photosynthetic rate†			
	1997			1999	1997			1999
	5 WAT	8 WAT	10 WAT	10 WAT	5 WAT††	8 WAT	10 WAT	10 WAT
T-M	0.46 a	1.0 a	0.21 a	0.16 a	12.0 a	8.5 a	11.9 a	4.6 a
T-P	0.51 a	1.0 a	0.19 a	0.05 b	9.2 a	10.7 a	9.9 ab	3.1 b
T	0.38 a	1.1 a	0.19 a	0.06 b	11.7 a	11.1 a	6.7 b	2.8 b
C V††† (%)	30.9	34.5	37.8	61.8	17.2	19.5	32.6	36.4

[a]Mean values followed by the same letter in a column, are not statistically different (Student's *t*-test, 0.05). WAT = Weeks after tomato transplant. †Average of four plants per treatment with readings at 11 and 15 h (1997) and at 11 h, for two consecutive days (1999). ††Average of four plants per treatment with readings every 4 hours over a 24 period. †††C V = Coefficient of variation.

Table 2. Chlorophyll content and starch content in tomato leaves grown intercropped with marigold (T-M) or pigweed (T-P) and non-intercropped (T), for the 1997 and 1999 growing seasons.

Treatment	Chlorophyll†			C-Starch†† (%)
	1997			1999
	5 WAT	8 WAT	10 WAT	10 WAT
T-M	49.5 a	45.6 a	43.0 a	22.7 b
T-P	50.1 a	45.9 a	41.3 b	50.4 a
T	50.5 a	46.9 a	39.4 b	85.7 a
C V††† (%)	7.1	9.7	17.4	49.2

Mean values followed by the same letter in a column, are not statistically different (Student's *t*-test, 0.05). WAT = Weeks after tomato transplant. †Units of SPAD, average of 12 plants per treatment. ††Percent of cuttings showing starch accumulation (potassium iodide and periodic acid–Schiff reactant), average of 600 cuttings from 12 plants per treatment. †††C V = Coefficient of variation.

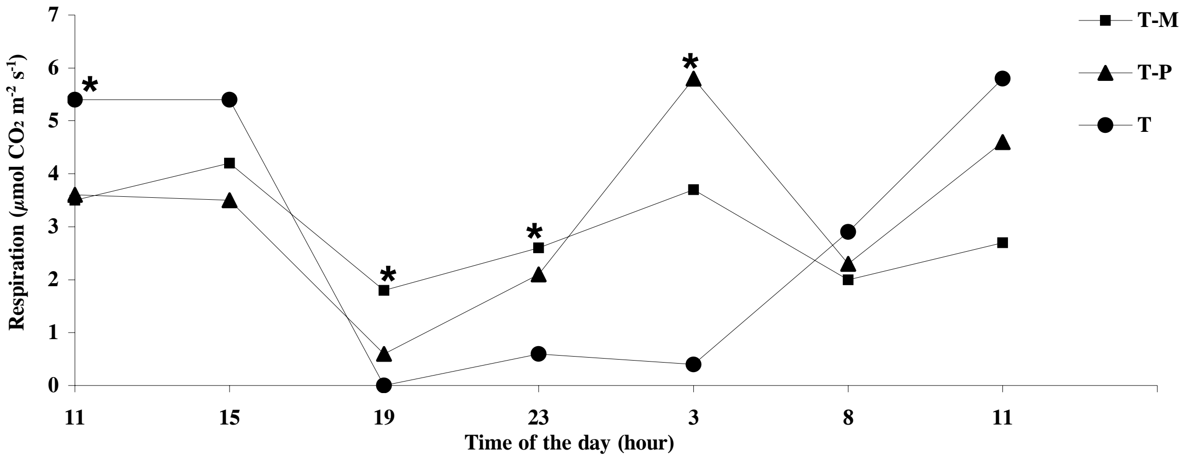

Figure 1. Respiration rate (µmol CO_2 m^{-2} s^{-1}) at 5 weeks after tomato transplant in tomato leaves grown intercropped with marigold (T-M) or pigweed (T-P) and non-intercropped (T). Average of four plants per treatment. * Significant differences among treatments at these hours (Student *t*-test, 0.05), for the 1997 growing season.

T-M was the same than in T-P, althoug lower than in T. Compared to T and T-M treatments, the T-P tomato plants showed a significant decrease in leaf area per plant (63 to 68 %) (Table 5). The specific tomato leaflet area was significantly higher in the intercropped tomato treatments T-P (33 %) than in T during 1997, and in 1999 both T-P and T-M overrated T by 64 and 69 % at 10 WAT, and by 61 and 62 % at 12 WAT. In both years, the thickest leaves were observed in the non-intercropped tomato (Table 5).

Table 3. Plant height in tomato grown intercropped with marigold (T-M) or pigweed (T-P) and non-intercropped (T), for the 1997 growing season.

Treatment	Height (cm) †			
	2 WAT	4 WAT	6 WAT	8 WAT
T-M	11.1 a	18.7 a	27.7 ab	41.8 a
T-P	10.7 a	18.9 a	31.0 a	44.9 a
T	10.7 a	14.2 b	24.4 b	35.6 b
C V†† (%)	26.7	19	14.9	14.2

Mean values followed by the same letter in a column, are not statistically different (Student's *t*-test, 0.05). WAT = Weeks after tomato transplant. †Average of 12 plants per treatment. ††C V = Coefficient of variation.

DISCUSSION

Intercropping with marigold or pigweed induced elongated stems, thinner leaves and larger specific leaf area in tomato plants. These morphological responses are considered typical adaptations in shaded plants (Robson *et al.*, 1996; Taiz and Zeiger, 2002), as it often occurs in intercropped plants (Redfearn *et al.*, 1999; Lin *et al.*, 2001). Even though thinner leaves might facilitate fungal penetration (Agrios, 2005), the leaves from the tomato-marigold association showed the least damage by *A. solani* as indicated by the evaluation carried out in the same experiment and reported elsewhere (Gómez-Rodríguez *et al.*, 2003). Furthermore, when detached leaflets from intercropped tomato plants were inoculated *in vitro*, they showed the same level of infection by *A. solani* than the non-intercropped ones, as it was reported by Gómez-Rodríguez *et al.* (2001). Therefore, tomato leaf damage by *A. solani* is not necessarily correlated with leaf thickness.

Since anatomical adaptations in response to shading frequently caused a reduction in photosynthetic capability as compared to sunlight exposed leaves (Salisbury and Ross, 1994), similar results might be expected in intercropped tomato plants (T-P and T-M). However, the instantaneous net photosynthetic rate and chlorophyll content were higher in tomato intercropped with marigold than in the other two treatments, although this happened only at 10 WAT. This difference among treatments might be attributed to lower leaf damage caused by *A. solani,* due to the allelopathic effect of marigold leaves and to the lesser exposure to high relative humidity, which would promote *A. solani* infection (Gómez-Rodríguez *et al.*, 2003). In tomato and chili pepper (*Capsicum annuum* L.) it has been shown that foliar destruction due to leaf pathogens such as *A. solani,* caused reductions in photosynthetic rate and chlorophyll content (Choulwar and Datar, 1991; Veeramohan *et al.*, 1994).

Both the highest night respiration rate (from 19 to 23 h) and the lowest frequency of leaf sections containing starch granules in tomato intercropped with marigold, compared to monocropped tomato plants, suggest that intercropping promotes a highest production of metabolic energy during

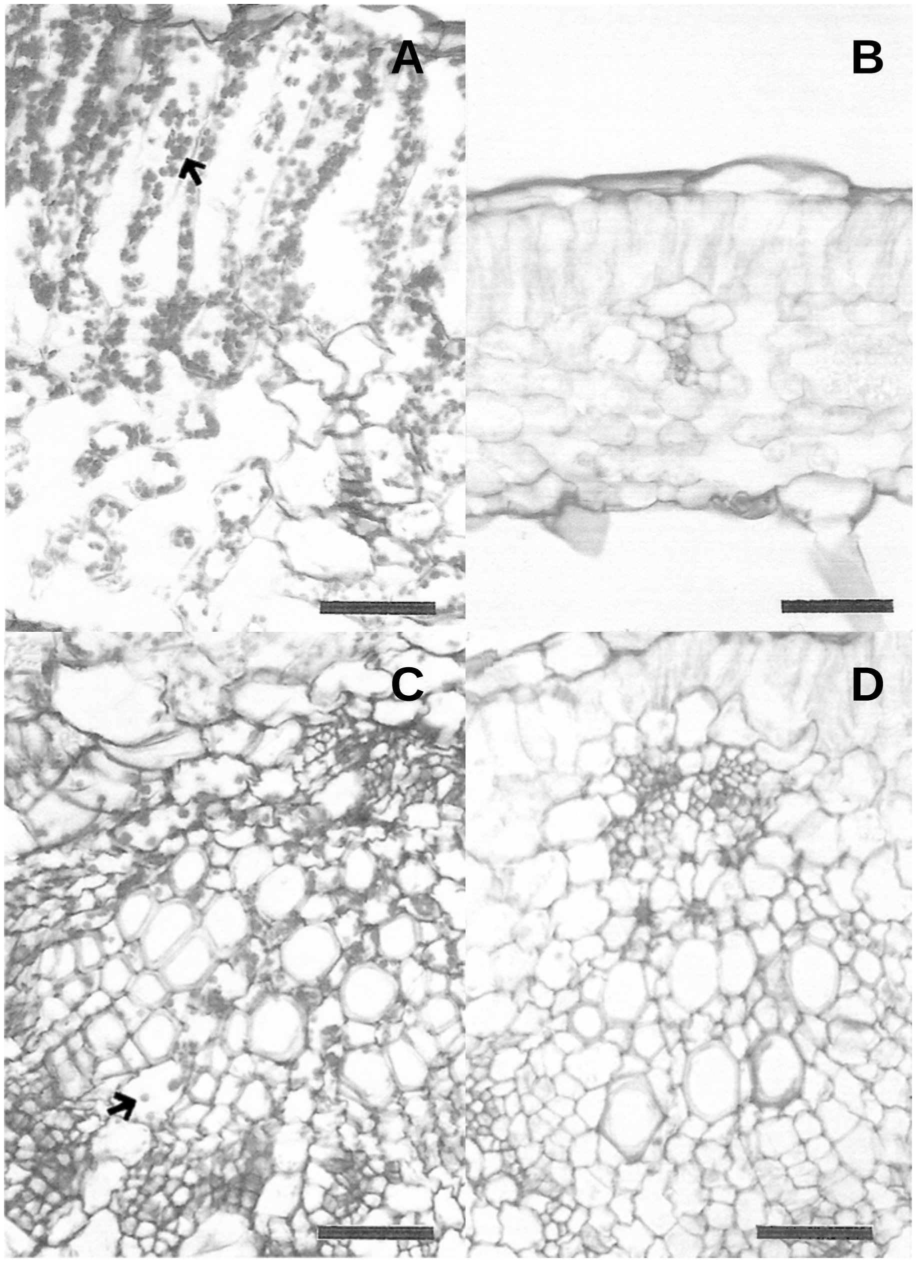

Figure 2. Presence of starch grains in cross sections of tomato leaflets evidenced by stainig by the periodic acid-Schiff reaction. A) Mesophyll in non-intercropped tomato (T), bar = 50 μm. B) Mesophyll in tomato intercropped with marigold (T-M), bar = 50 μm. C) Main vein in non-intercropped tomato (T), bar = 50 μm. D) Main vein in tomato intercropped with marigold (T-M), bar = 50 μm. Arrows point out starch granules in tomato leaflets chloroplasts.

Table 4. Number of inflorescences (NI), number of fruits (NF) and fruit yield (FY) in tomato grown intercropped with marigold (T-M) or pigweed (T-P) and non-intercropped (T), for the 1997 growing season.

Treatment	NI†				NF†		FY††
	2 WAT	4 WAT	6 WAT	8 WAT	6 WAT	8 WAT	15 WAT
T-M	0.6 a	3.4 a	12.9 a	21.3 a	1.2 a	6.2 a	475.0 a
T-P	0.4 a	2.0 b	8.8 b	16.0 b	0.2 b	3.1 b	288.7 b
T	0.5 a	2.2 b	10.3 b	20.5 ab	0.6 ab	2.5 b	334.7 b
C V††† (%)	95.6	51.1	25.7	20.8	165.1	86.8	25.8

Mean values followed by the same letter in a column, are not statistically different (Student's *t*-test, 0.05). WAT = Weeks after tomato transplant. †Average of 12 plants per treatment. ††Fruit yield per plant (g), average of 78 intercropped and 156 non-intercropped tomato plants. †††C V = Coefficient of variation.

Table 5. Leaf area per plant, specific leaf area per leaflet and leaf thickness in leaflets for tomato plants grown intercropped with marigold (T-M) or pigweed (T-P) and non-intercropped (T), for the 1997 and 1999 growing seasons.

Treatment	Leaf area (cm^2) per plant	Specific leaf area (cm^2/g dw) Leaflet			Leaf thickness (μm) [ξ] Leaflet	
	1997[†]	1997[††]	1999[†††]		1997[ξξ]	1999[ξξξ]
	6 WAT	10 WAT	10 WAT	12 WAT	12 WAT	10 WAT
T-M	2985 a	163 ab	286 a	237 a	227 c	202 b
T-P	2034 b	195 a	278 a	235 a	278 b	210 b
T	3193 a	146 b	169 b	146 b	424 a	313 a
C V (%)	5.0	14.3	54.5	34.2	21.2	22.4

Mean values followed by the same letter in a column, are not statistically different (Student's *t*-test, 0.05). WAT = Weeks after tomato transplant. [†]Average of three plants per treatment. [††]Average of four plants per treatment. [†††]Average of 18 plants per treatment. [ξ]Readings from both sides of the central nerve of the terminal leaflet of the fourth leaf from the apex. [ξξ]Average of four plants and a total of 105 cuttings per treatment. [ξξξ]Average of ten plants and a total of 105 cuttings per treatment. C V = Coefficient of variation.

the early night as well as a highest rate in carbohydrate export. On this regard, it has been reported that shaded plants are able to mobilize a higher proportion of carbohydrates in order to maintain leaf and stem growth (Lin *et al.*, 2001), and will thus have less nutritious substrates for pathogen development (Tu, 1985; Lin *et al.*, 2001). However, a high sugar export will not necessarily reduce the amount of starch granules in leaves, since the frequency of tomato leaf sections containing starch granules in parenchyma cells was the same in treatments T-P and T.

Although intercropping is not compatible with modern monoculture agriculture, it is well suited to many farmers who have small land areas because it may render higher yields and yield stability (Altieri, 1999; Gliessman, 2002). In our study, tomato plants intercropped with marigold produced significantly more fruits and inflorescences. An additional advantage of the T-M intercropping is that marigold is a multipurpose crop in México, because of its antagonistic properties against some plant pathogens (Jacobs *et al.*, 1994; Montes and García, 1997; Riga *et al.*, 2005), and for its ceremonial, ornamental, medical and industrial uses (Serrato, 2005).

CONCLUSION

Intercropping with marigold or pigweed induced elongated stems, thinner leaves and larger specific leaf area, higher early night respiration rate and lower frequency of leaf cells containing starch granules in tomato plants, effects which are attributed to shading. However, the higher values of instantaneous net photosynthesis rate and chlorophyll content at 10 WAT in tomato plants intercropped with marigold compared to monocropped tomato or tomato intercropped with pigweed, cannot be attributed to shading but to the specific association with marigold. As a result, tomato plants intercropped with marigold produced significantly more fruits and inflorescences.

ACKNOWLEDGEMENTS

The authors wish to thank the financial support received from the Consejo Nacional de Ciencia y Tecnología (Grant 25863-B).

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