



DETERMINING REGRESSION MODELS FOR PHOTOSYNTHESIS AND STOMATAL RESISTANCE AS AFFECTED BY TEMPERATURE AND LIGHT INTENSITY IN TOMATO (*LYCOPERSICON ESCULENTUM* MILL.) AND EGGPLANT (*SOLANUM MELONGENA* L.) GROWN IN GLASSHOUSES

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Abstract: This study was carried out to examine the relationships between net leaf photosynthesis and temperature and light intensity, between stomatal resistance and temperature and light intensity in tomato and aubergine grown with a range temperature from 10 to 30 °C and different light intensities from 3 to 7 MJm⁻² d⁻¹. The study was carried out in a six-compartment greenhouse (size 4 m * 8 m), the temperature of which can be controlled by air conditioning, on tomato and eggplant plants. Each of the six greenhouse compartments was set to have maximum temperatures of 10, 12, 16, 18, 20 and 24 °C. Commercial varieties named "Counter" for tomato and "Bonica" for eggplant were used. "Fisons M2" commercial compost was used in all growing media and nutrient was applied equally. In the study, different sowing and planting dates were applied to benefit from natural light conditions (between 3 and 7 MJm⁻²d⁻¹). Average temperature in each compartment was recorded using a 'Combine' data logger at 15 minute intervals. A porometer (Delta-T device, MT -3) was used to measure the stomatal resistance of tomato and eggplant leaves. The stomatal resistance measurements of the plants were made at the same time of the day (between 11.00-13.00) at 15-day intervals at the top, middle and lower levels of the crown of four different plants in different environmental conditions. In tomato, leaf photosynthesis increased curvilinearly with temperatures up to about 20.5 °C at low light intensity and declined at higher temperatures. The highest photosynthesis was obtained from the plants grown at a temperature of 22.5 °C and 7 MJm⁻²d⁻¹ light intensity. The lowest photosynthesis was at 10 °C and 3 MJm⁻²d⁻¹. In aubergine, at low light intensities, net photosynthesis increased curvilinearly up to 23 °C while it increased up to 20 °C at high light intensities and declined at higher temperatures. Maximum net leaf photosynthesis was found to be greater in tomato than aubergine.

Keywords: Light intensity, Photosynthesis, Stomatal resistance, Temperature, Tomato

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1. Introduction

Interest in the response of crop photosynthesis to temperature and light is growing in eco-physiological research and practical agriculture (Tuzet et al., 2003; Uzun, 2006). Light limitation on photosynthetic productivity of all crops is of great importance. This phenomenon is especially important for glasshouse crops since the amount of light that plants receive is reduced by 30% or more by the glasshouse structure, and whereas other environmental factors, namely temperature, CO₂ concentration, mineral nutrients and water can be supplemented and controlled at economically optimal levels, supplementary artificial lighting is not commercially worthwhile (Jovanovic and Annandale, 2000).

Photosynthetic light response curves have been studied for tomato over the last twenty years to determine

optimum light requirements of the plants and their adaptability to different environmental conditions (Acock et al., 1978; Cockshull, et al., 1992; Prusinkiewicz, 2004). The net photosynthetic rate of tomato crop canopies under semi-commercial glasshouse is almost directly proportional to light flux density at least up to 200 W m⁻² (Atherton, 1986). For example, in aubergine, after reaching a light saturated value, a decline photosynthesis at higher values was reported to be due to closure of the stomates and also to a reduced CO₂ gradient (Bertin and Heuvelink, 1993; Uzun, 1996).

It has also been reported that the optimum temperature for photosynthesis adapts according to the temperature at which the plant is grown (Dayan, et al., 1993; Heuvelink and Bertin, 1994; Uzun, 1996). In tomato, a decline in photosynthesis at temperatures above 30 °C was reported to be because of higher stomatal resistance



(Seligman, 1990). Furthermore, a linear relationship was found between photosynthesis under saturating CO₂ and irradiance and temperature until the optimum temperature is reached. Temperature during growth also influences the rate of decline of photosynthesis with plant age (Acock, 1991; Uzun, 2006). Stomatal resistance to CO₂ was also reported to decline according to the leaf position on the stem of tomato. Leaf nitrogen content has also been reported to affect leaf net photosynthesis (Acock et al., 1978).

Since environmental preconditioning such as light intensity, temperature and water stress may affect gas exchange in the greenhouse, an attempt was made to study the effect of a wide range of light integral and temperature on adaptation of photosynthesis (Dorais, et al., 1991; Pearson, et al., 1994; Grimstad, 1995). Previous studies have tended to include a rather narrow temperature range for tomatoes, and particularly very little is known regarding photosynthesis and its adaptation to environment in aubergine. The aim of this study was to investigate the net photosynthetic rate in both tomato and aubergine grown with different daily

mean light integral at various temperatures and to find relationships between photosynthesis, stomatal resistance, light intensity and temperature.

2. Materials and Methods

This study was carried out in the spring growing season in Ondokuz Mayıs University Faculty of Agriculture research and application greenhouses in 2005. Actual mean temperature measurements in the growing compartments according to experiment number are presented Table 1. A series of detailed experiments on tomato and aubergine were carried out in a suite of controlled temperature glasshouse compartments (size 4 m* 8 m). Six greenhouse compartments were used to give maximum set temperatures of 10, 12, 16, 18, 20 and 24 °C. The temperature in the compartments was controlled by the air conditioner and it was adjusted to provide automatic heat when the temperature in each compartment fell below the set point, and when the temperature rose 4 °C above the set temperature, the ventilations were operated automatically.

Table 1. Actual mean temperature measurements in the growing compartments according to experiment number.

Experiments		
1	2	3
11.4	15.2	16.1
14.3	15.4	17.1
16.4	17.5	18.0
19.8	21.3	22.1
22.5	22.8	23.1
25.3	26.0	25.8

Seeds of tomato cv. "Counter" and aubergine cv. "Bonica" were sown in modular seed trays containing 228 cells (2 cm x 2 cm) filled with commercial peat based compost (Fison F2). The seed trays were maintained in a glasshouse compartment maintained at a temperature of 22 °C. After the seedlings emerged, the seed trays were placed in a different compartment maintained at 20 °C. Sowing, transplanting and planting dates for each trial were performed in order to obtain natural light conditions (between 3 and 7 MJm⁻²d⁻¹) during experiments.

Three weeks after emergence, plants were pricked out into 15 cm plastic pots containing Fisons M2 commercial compost. After the plants reached the fourth true leaf stage they were planted into Fisons growbags, containing a peat compost, spaced at a distance of 50 cm between the rows and 35 cm in rows. Plants were irrigated on four occasions each day with a standard nutrient feed (Sangral SS 112), diluted to give a concentration of 0.2 g l⁻¹ nitrogen, 0.2 g l⁻¹ phosphorous and 0.4 g l⁻¹ potassium, equivalent to a conductivity of 1600 ms cm⁻² and pH of 6.5, using a trickle irrigation system.

The mean temperature in each compartment was recorded at intervals of 15 minutes using a 'Combine'

data logger (Uzun, 1996). Photosynthetically active radiation (PAR) was recorded using a tube solarimeter (Uzun, 1996). The tube solarimeter was connected to a data logger (Skye, Model 3).

A porometer (Delta-T instrument, MT -3) was employed to measure stomatal resistance of tomato and aubergine leaves. Measurements were taken at 15 day intervals at three different levels of the canopy of four different plants grown under different environmental conditions. Before every measurement, the instrument was calibrated by using a calibration plate. Care was taken to measure stomatal resistance at the same time of day (between 11.00 am and 13.00 pm) for every measurement. The aim of measuring stomatal resistance of both crops was to investigate the changes in stomatal resistance according to different light and temperature environments studied in the present study and consequently to find relationships between stomatal resistance, leaf net photosynthesis, temperature and light for both crops.

Measurements of CO₂ assimilation were carried out using an open system, portable infrared gas analyser system (Analytical Development Co. Ltd, model LCA3). The whole system consists of four units, an Infrared Gas

Analyser (IRGA), a leaf chamber with a lamp unit to supply artificial light, an air supply unit and a data-processor/logger. The air flow rate was adjusted to 400 ml min.⁻¹ for both tomato and aubergine. The air intake was placed outside the glasshouse to minimise disturbances in CO₂ concentrations caused by local factors. The leaf was placed into the leaf chamber with an area of 6.2 cm². Measurements were taken at three different levels of the canopy, namely top, middle and bottom and carried out at three week intervals throughout ontogeny of both crops. After every measurement of leaf, 30 seconds was allowed to elapse between two measurements in order to allow net photosynthesis to reach a new equilibrium. Randomly selected leaves from top, middle and bottom of the plants were used in the measurements for all light levels.

Multiple regression analysis was performed with Microsoft EXCEL following the procedure of Gomez and Gomez (1984). Curve fitting processes were continued until the least sum of squares of residuals was obtained. Fitted planes from multiple regression analysis were shown on 3-D graphs using the 'Slide Write' computer package Version 2.0.

3. Results

In order to determine the overall effect of temperature and light on photosynthesis, multi-regression analysis were carried out by plotting net photosynthesis of tomato and aubergine leaves from different parts of the plant canopy, namely top, middle and bottom, against temperature and light values at which the plants were grown and the following equations were obtained for tomato (equation 1) and aubergine (equation 2).

$$P = -19.2 + 23.68*T + 0.67*L - 0.06*T^2 \quad (1)$$

$$SE (3.79)^{***} (0.44)^{***} (0.16)^{***} (0.01)^{***}$$

$$r^2 = 0.91^{***} \text{ for tomato.}$$

$$P = -42.86 + 3.12*T + 7.26*L - 0.07*T^2 - 0.65*L^2 \quad (2)$$

$$SE (9.25)^{***} (0.87)^{***} (1.31)^{***} (0.02)^{***} (0.13)^{***}$$

$$r^2 = 0.89^{***} \text{ for aubergine.}$$

As seen from the equations above, most of the variation in leaf net photosynthesis, 91 % for tomato and 89 % for aubergine was explained by light integral and temperature. Although there was a positive linear effect of light intensity on net photosynthesis in tomato as well as a curvilinear effect of temperature, both light intensity and temperature had curvilinear effects on photosynthesis in aubergine. Utilising from Equation 1 and 2, the following figures (Figure 1a and b) showing the effect of light intensity and temperature on leaf net photosynthesis of tomato (Figure 1a) and aubergine (Figure 1b) were obtained.

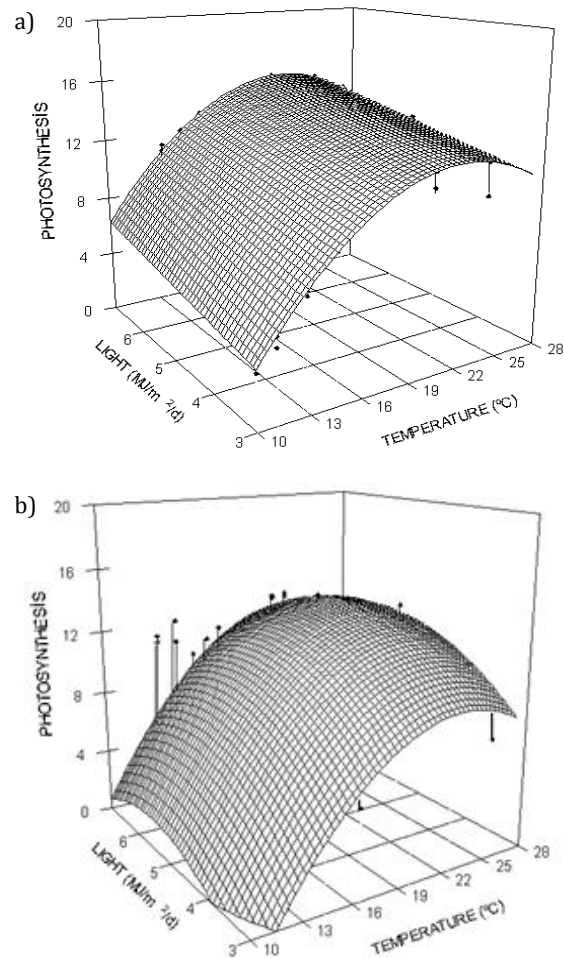


Figure 1. The response of leaf photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$) for (a) tomato and (b) aubergine leaves from different parts of plant canopy (top, middle, and bottom) averaged over growing period of 80 days after planting and grown with different light intensities ($\text{MJ m}^{-2}\text{d}^{-1}$) and temperatures ($^{\circ}\text{C}$).

As seen in Figure 1a and b, in general, the leaf net photosynthesis increased as temperature increased throughout the temperature range investigated at all daily mean light integrals and declined at the highest temperatures for both tomato and aubergine.

In tomato, leaf photosynthesis increased curvilinearly with temperatures up to about 20.5 $^{\circ}\text{C}$ at low light intensity and declined at higher temperatures. Therefore, it can be said that optimum temperatures for photosynthesis increased as light intensity increased (Figure 1a). The highest photosynthesis was obtained from the plants grown at a temperature of 22.5 $^{\circ}\text{C}$ and 7 $\text{MJm}^{-2}\text{d}^{-1}$ light intensity. The lowest photosynthesis was at 10 $^{\circ}\text{C}$ and 3 $\text{MJm}^{-2}\text{d}^{-1}$.

In aubergine, at low light intensities, net photosynthesis increased curvilinearly up to 23 $^{\circ}\text{C}$ while it increased up to 20 $^{\circ}\text{C}$ at high light intensities and declined at higher temperatures. Unlike tomato, optimum temperatures for net photosynthesis increased curvilinearly with light intensity. Maximum net leaf photosynthesis was found to

be greater in tomato than aubergine (Figure 1a and b).

In order to determine the overall effect of temperature and light on stomatal resistance, multi-regression analysis were carried out by plotting stomatal resistance against temperature and light and the following equations were obtained for tomato (equation 3) and aubergine (equation 4).

$$SR = 11.97 - 0.19*T - 0.0029*L2*T \quad (3)$$

SE (0.85)*** (0.057)** (0.00085)**
 $r^2 = 0.81$ *** for tomato.

$$SR = 19.02 - 0.32*T - 0.0042*L2*T \quad (4)$$

SE (1.09)*** (0.057)*** (0.00062)***
 $r^2 = 0.90$ *** for aubergine.

As seen in Equation 3 and 4, most of the variations in stomatal resistance was explained by temperature and light intensity for both tomato ($r^2=0.81$) and aubergine ($r^2=0.90$).

For both crops, increasing light intensities resulted in lower stomatal resistance such as there was a curvilinear decline in stomatal resistance with increasing light intensities (Figure 2a and b). However, the decline in stomatal resistance for both tomato and aubergine leaves was found to be sharper with higher temperatures compared to lower temperatures. Stomatal resistance was reduced by increasing temperatures for both crops. A similar response of stomatal resistance to temperature as to light intensity was found in both crops such as the increase in stomatal resistance with decreasing temperatures was sharper at high light intensities (Figure 2a and b). The highest stomatal resistance was obtained from the plant leaves grown at the lowest light and temperature regimes for both tomato and aubergine. The lowest stomatal resistance was from the plant leaves grown with the highest temperature and light intensities examined in the study.

Figures 3 a and b show the relationship between stomatal resistance and net leaf photosynthesis in both tomato and aubergine respectively. As seen from the figures, there was marked tendency that increasing stomatal resistance resulted in lower net leaf photosynthesis in both tomato and aubergine.

4. Discussion

In this study, net photosynthesis and stomatal resistance of the leaves of tomato and aubergine grown with three different daily mean light integrals and different mean temperatures were investigated and the interrelations of these parameters was examined.

The present study revealed that maximum net leaf photosynthesis declined with time after sowing and more rapidly with increased daily mean light integral for both tomato and aubergine (Figures 3 a and b). This may be due a gradual degradation of all chloroplast number and reduced chlorophyll content which results in declining net photosynthesis with time (Uzun, 1996).

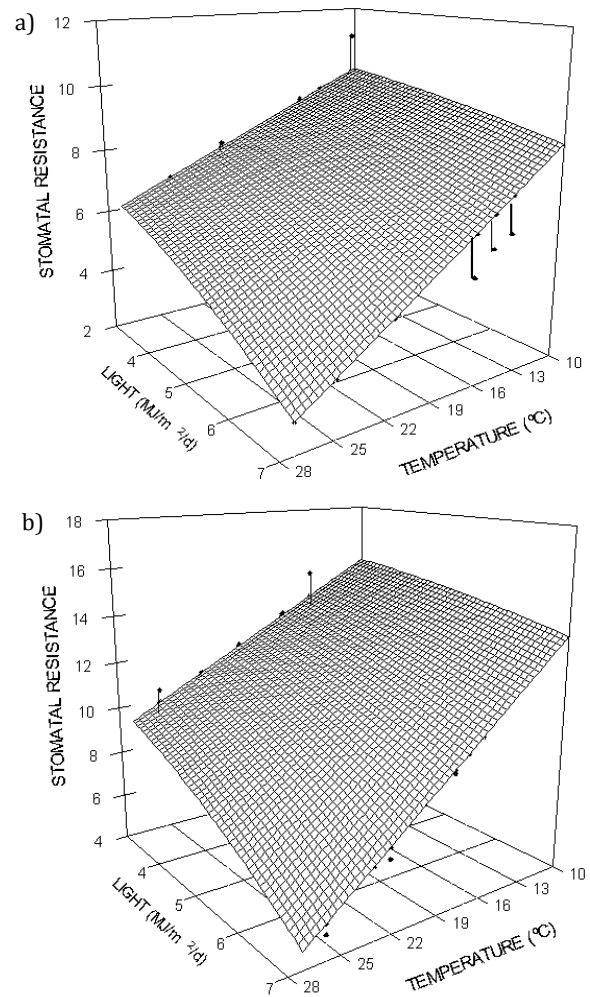


Figure 2. The response of stomatal resistance ($s\ cm^{-1}$) for (a) tomato and (b) aubergine leaves from different parts of plant canopy (top, middle and bottom) averaged over growing period of 80 days after planting and grown with different light intensities ($MJ\ m^{-2}d^{-1}$) and temperatures ($^{\circ}C$).

Long term maximum leaf net photosynthesis increased for both tomato and aubergine grown with higher daily mean light integrals. Many other studies have shown that the leaves of plants grown under high light levels have faster rates of carbon fixation than leaves of plants grown under low light levels (Acock et al. 1978; Özkaraman 2004) also indicated that maximum net photosynthesis per unit leaf from a tomato plant grown at $80\ W\ m^{-2}$ was approximately twice that of a leaf from a plant grown at $20\ W\ m^{-2}$.

Stomatal resistance increased significantly with time at all daily mean light integrals and temperatures. However, the increase in stomatal resistance with time for both tomato and aubergine was less marked as daily mean light integral increased. There was also a significant decline in stomatal resistance with increasing temperature for tomato and aubergine. Bar-Tsur et al. (1985) also reported a decrease in stomatal resistance in tomato up to $25\ ^{\circ}C$ and an increase above $35\ ^{\circ}C$. In this

study, stomatal resistance in the leaves of both tomato and aubergine grown with higher daily mean light integrals was lower than those of the plants grown with lower daily mean light integrals. The effect of light can be explained as an indirect effect via a lowering of the CO₂ concentration in the chloroplast of the leaf by photosynthesis since increased photosynthetic rate through increasing light intensity can cause lower internal CO₂ concentrations in the leaf leading to lower stomatal resistance (Acock et al., 1978).

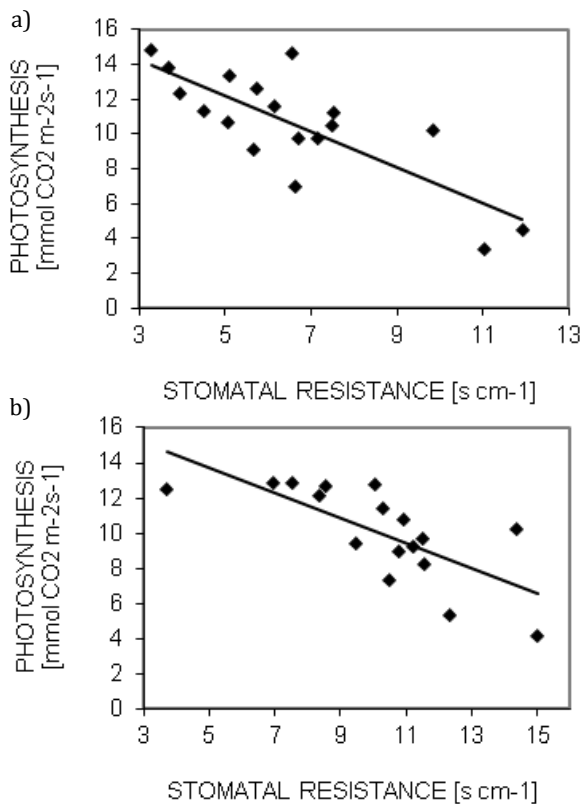


Figure 3. The relationship between mean canopy photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$) and stomatal resistance (s cm^{-1}) of (a) tomato and (b) aubergine grown with different light intensities ($\text{MJ m}^{-2}\text{d}^{-1}$) and temperatures ($^{\circ}\text{C}$).

The effect of temperature on stomatal resistance may be as a result of its influence on leaf water stress, since it would be expected that increasing temperature result in higher stomatal resistance due to the thinner leaves produced under these conditions (Rand and Cooke, 1980). Stomatal resistance also decline from the bottom of the plants to the top for tomato and aubergine. Acock et al. (1978) reported that leaf resistance of tomato leaves from the uppermost leaf layer was smaller than those from the lowest layer which had been exposed to lower light than the upper leaves.

In the present study, it was found that net photosynthesis tented to increase with increasing leaf nitrogen content in both tomato and aubergine. The relationship between leaf nitrogen content and photosynthesis was not implemented since data the present study did not include

different nitrogen levels at constant temperature. It has been reported that there is a strong relationship between the leaf nitrogen content and leaf photosynthesis (Novoa and Loomis, 1981; Evans, 1989). Changes in nitrogen content reflects changes in protein content and about half of the proteins within the leaf tissues are directly associated with photosynthesis and this explains the close relationship that exists between the rate of leaf photosynthesis and nitrogen concentration (Evans,1989). A similar but less clear relationship between net photosynthesis and leaf nitrogen content was shown here. It has also been reported that the photosynthetic capacity of leaves is greatly reduced when plants suffer nitrogen deficiency. In a wide variety of plants, there is a positive correlation between photosynthetic capacity and leaf nitrogen content, expressed either on a dry weight basis or an area basis (Brunetti et al., 2013) since leaf growth is sensitive to nitrogen supply, and leaf expansion rate increases as nitrogen supply increases (Novoa and Loomis, 1981).

Net leaf photosynthesis did however decline very significantly with increasing stomatal resistance in both tomato and aubergine. Many studies have shown that net photosynthesis decline with increasing stomatal resistance (Jones and Sutherland 1991).

The variation in nitrogen in the canopy is proportional to the light transmission. However, irradiance is not the only factor affecting the nitrogen distribution within the leaf canopy, leaf age increases from the top leaves to the bottom and that could also generate a gradient of leaf nitrogen content through the and the relative effects of these two factors, irradiance and age, on the leaf nitrogen distribution is unknown (Poza and Dennett, 1991).

In the present study, analysis on changes in leaf net photosynthesis, stomatal resistance with daily mean light integral temperature showed that there was a negative relationship between stomatal resistance and net leaf photosynthesis in both tomato and aubergine.

Author Contributions

The percentage of the author(s) contributions is presented below. All authors reviewed and approved the final version of the manuscript.

	F.Ö.
C	100
D	100
S	100
DCP	100
DAI	100
L	100
W	100
CR	100
SR	100
PM	100
FA	100

C=Concept, D= design, S= supervision, DCP= data collection and/or processing, DAI= data analysis and/or interpretation, L= literature search, W= writing, CR= critical review, SR= submission and revision, PM= project management, FA= funding acquisition.

Conflict of Interest

The author declared that there is no conflict of interest.

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Ethical Consideration

Ethics committee approval was not required for this study because of there was no study on animals or humans.

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