

Research Article

Simulation of Photosynthetic Capacity of Strawberry Plants at Different Leaf Ages

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Abstract: A mathematical simulation was carried out to study the photosynthetic capacity of strawberry plants (*Fragaria X ananassa* Duch., Benihoppe) at different leaf ages. It also compared the differences in chlorophyll and protein contents in the leaves in order to provide a theoretical basis for the cultivation of high-quality and high-yield strawberry plants. Our results indicated that the chlorophyll content in the functional leaves was 67 and 46% higher than in the new and old leaves and that the soluble protein content in the functional leaves was 21 and 13% higher than in the new and old leaves. Strawberry leaves at different leaf ages had a significantly different maximum photosynthetic rate; the maximum photosynthetic rate of the functional leaves was generally 1.5 times greater than the new leaves and more than 80% greater than the old leaves. The difference in the photosynthetic capacity of the leaves at different leaf ages was consistent with the difference in leaf structure and chlorophyll content. The simulation indicated that the total net photosynthesis of the new and old leaves was approximately 131 mmol/m²/d and 140 mmol/m²/d on clear days, only 62 and 67% the rate of the functional leaves.

Keywords: Apple, diurnal variation, model, stomatal conductance

INTRODUCTION

The fruit of the perennial herb Strawberry (*Fragaria X ananassa* Duch.) goes on sale each year earlier than any other fruits. Protected cultivation can advance strawberry harvest time from November to May, helping ensure year-round strawberry production, improving fruit grower income. Photosynthesis is critical for crop growth and development, because crop yield and quality depend on leaf photosynthetic activity (Massonnet *et al.*, 2008; Gao *et al.*, 2012). Fruit growth and quality are also strongly affected by the “sink-source” relationship and leaves as a source provide carbohydrates to fruits. The presence of carbohydrates can influence the size, color, soluble solid content and hardness of fruits (Green *et al.*, 2001). In order to improve the yield and quality of strawberries, a number of studies have examined the photosynthesis properties of strawberry plants (Cameron *et al.*, 1989; Sharma *et al.*, 2006; Li *et al.*, 2013). However, few studies have simulated the photosynthetic dynamics of protected strawberry. In this study, we constructed a photosynthetic model of “Benihoppe” strawberries under protected conditions to compare the photosynthetic properties of strawberry leaves at different leaf ages, as well as the chlorophyll and protein contents. The results of this study can provide a theoretical basis for protected high-yield and high-quality strawberry cultivation.

MODELS AND METHODS

Experimental design: The experiment was carried out in the training base of Beijing Vocational College of Agriculture. Benihoppe strawberries (*Fragaria X ananassa* Duch.) were planted in a greenhouse for protected cultivation on September 20, 2014 and were fertilized and watered using conventional methods. Out of the planted strawberries, 100 consistently growing strawberry plants were selected and their leaf age was recorded since they were planted. Four treatments were applied based on the leaf age: treatment I for a leaf age of 5-7 d, treatment II for a leaf age of 15-20 d, treatment III for a leaf age of 30-35 d and treatment IV for a leaf age of 60-65 d.

Experimental method: On clear days from November 15 to 18, 2014, a CIRAS-2 portable photosynthesis system manufactured by PP Systems in the United Kingdom was used to determine the photosynthetic parameters and diurnal variations of strawberries with different leaf ages. Fifteen leaves were selected for each treatment and each treatment was replicated three times, giving a total of 180 samples. And the averages were obtained. After that, 15 more leaves were selected for each treatment to determine their soluble protein content and Rubisco activity (Tang, 1999). All photosynthetic model parameters were estimated using the least square method or obtained from previous data (Leuning, 1990; Bernacchi *et al.*, 2003). Acetone

solution was used to extract chlorophyll a and b and a UV-751 spectrophotometer was used to determine the chlorophyll a and b contents and total chlorophyll contents. The soluble sugar content was determined using the anthrone method (Tang, 1999).

Photosynthetic and stomatal models: Strawberries are C₃ plants and Farquhar *et al.* (1980) proposed a biochemical model for simulating C₃ photosynthesis in simple leaves and other scholars (Leuning, 1990; Bernacchi *et al.*, 2003) have constantly improved this model. The improved net photosynthetic model is expressed as:

$$A = \min\{A_c, A_q\} - R_d \quad (1)$$

where,

A_c = The gross rate of photosynthesis limited by Rubisco activity

A_q = The gross rate of ribulose 1, 5-bisphosphate (RuBP) regeneration through electron transport

R_d = The dark respiration of leaves

Stomatal conductance was simulated using the stomatal model improved by Luning (1990):

$$g_{sc} = g_0 + \frac{a_1 A}{(c_s - \Gamma)(1 - D/D_0)} \quad (2)$$

where,

g₀ = The residual stomatal conductance

a₁ and D₀ = Constants

D = The vapor pressure deficit

Γ = The CO₂ compensation point

It was assumed that g_{sc} = g_s/1.56 (Tezara *et al.*, 1999), where g_s is the stomatal conductance for water vapor.

RESULTS

Chlorophyll and protein content in strawberry plants at different leaf ages: Not only can chloroplast pigments absorb and convert light energy during photosynthesis, they can also dynamically regulate the ratio of different chloroplast pigments during environmental changes. This secondary function helps facilitate proper distribution and dissipation of light energy, ensuring normal operation of photosynthetic systems. The chloroplast pigment contents in the functional leaves of the strawberry plants (treatments II and III) were significantly higher than those in the new (treatment I) and old leaves (treatment IV) (Table 1). Further, the total chlorophyll contents in the functional leaves were 67 and 46% higher than those in the new and old leaves, on average. An increase in chlorophyll can improve the maximum photosynthetic rate per unit leaf area. Functional leaves are complete in structure and rich in chlorophyll, allowing for optimal light use efficiency. Most of the proteins found in leaves are related to photosynthetic function and their content has a direct effect on photosynthetic capacity. The protein contents in the strawberry leaves at different leaf ages changed similarly to the chlorophyll contents. They first declined, then increased, then stabilized and began to decline after 50-60 days. The soluble protein contents in the functional leaves were 21% higher than those in the new leaves and 13% higher than in the old leaves. Rubisco activity is one of the key limiting factors of photosynthesis. The Rubisco activity of the functional

Table 1: Chlorophyll contents in strawberry leaves at different leaf ages

	Chlorophyll content (mg/g FW)				Soluble protein content (mg/g FW)	Rubisco activity mol/(mg.min)
	Chla	Chlb	Chla+b	Chla/Chlb		
Treatment I	1.12C	0.34D	1.46D	3.29A	4.97D	1.32D
Treatment II	1.76A	0.62A	2.38A	2.84B	6.12A	2.47A
Treatment III	1.56B	0.55B	2.11B	2.84B	5.88B	2.21B
Treatment IV	1.19C	0.48C	1.67C	2.48C	5.29C	1.72C

a leaf age of 5d for treatment I; a leaf age of 15d for treatment II; a leaf age of 30d for treatment III; a leaf age of 60d for treatment IV, which is the same as below

Table 2: Photosynthetic parameters of strawberry leaves at different leaf ages

Parameter	Treatment I	Treatment II	Treatment III	Treatment IV	Units
c (K _c)	35.79				-
c (K _c)	9.59				-
ΔH _i (K _c)	80.47				kJ/mol
ΔH _i (K _c)	14.51				kJ/mol
c (V _{cmax})	34.56	32.55	33.46	35.83	-
c (J _{max})	41.22	65.02	54.89	42.33	-
ΔHa (J _{max})	78.2	158.2	128.3	80.4	kJ/mol
ΔHa (V _{cmax})	79.01	70.3	75.1	77.6	kJ/mol
ΔHd (J _{max})	0.201	201	201	201	kJ/mol
ΔHd (V _{cmax})	200	200	200	200	kJ/mol
ΔS (J _{max})	0.66	0.66	0.66	0.65	kJ/K/mol
ΔS (V _{cmax})	0.65	0.64	0.65	0.66	kJ/K/mol
α	0.26	0.19	0.22	0.25	mol/mol
g ₀	16				mol/m ² /s
a ₁	15				-
D ₀	3500				Pa

leaves was 77 and 36% greater than that of the new and old leaves, on average. Strawberry plants have developed a specific adaptive mechanism during the long-term process of evolution. New leaves have small sizes and leaf inclination angles, low chlorophyll and protein contents and are exposed to a little light. Old leaves are located below functional leaves, some of their chlorophyll and protein decompose and they are also exposed to a little light. Functional leaves are exposed to the most light and contain the most chlorophyll and protein and the strongest photosynthetic energy, making full use of light energy.

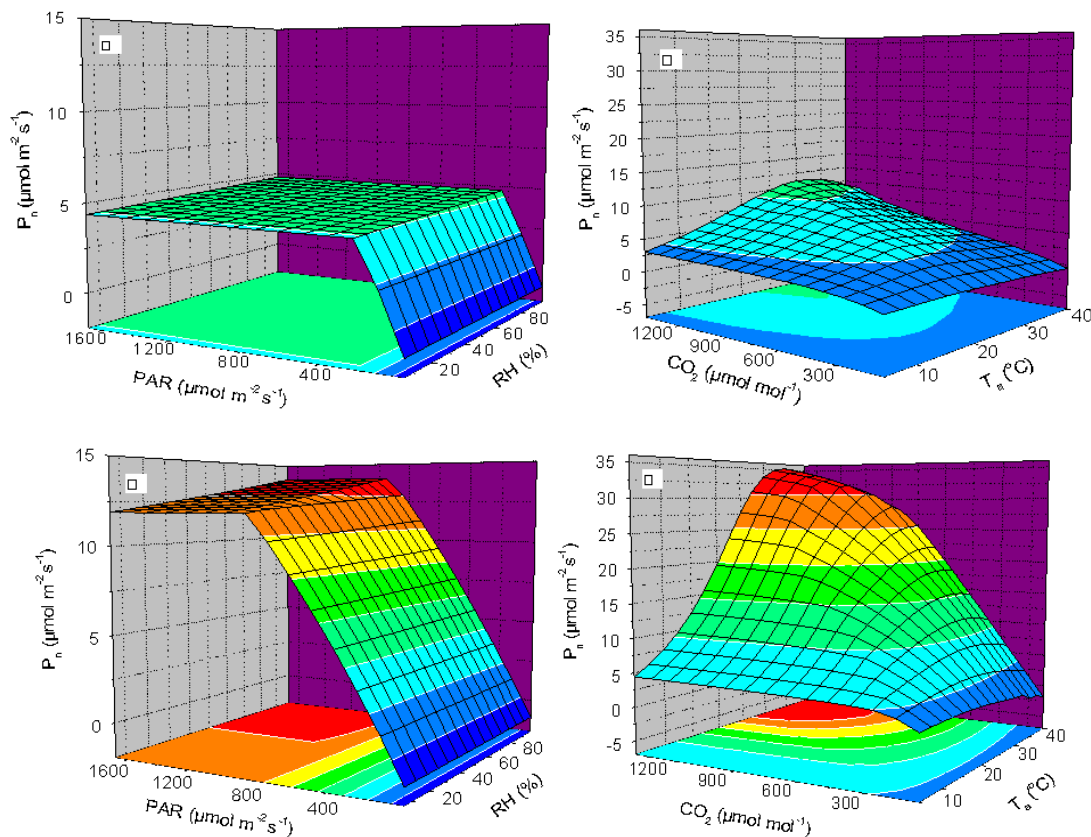
Differential leaf response to microclimatic factors:

The photosynthetic model parameters for the leaves at different leaf ages differed primarily in the maximum photosynthetic rate V_{cmax} and in light quantum efficiency (Table 2). The responses of the leaf photosynthetic rates (P_n) in different parts of the canopy to microclimatic factors are shown in Fig. 1. Differently aged leaves showed similar responses to microclimatic factors. When the Photosynthetically Active Radiation (PAR) was below the light saturation point, P_n increased with PAR until PAR exceeded the light saturation point where it plateaued (Fig. 1). Higher ambient CO_2 concentrations result in great P_n values. In general, once the CO_2 concentration reaches $600 \mu\text{mol/mol}$, P_n gradually begins to saturate.

When temperatures rise, the CO_2 saturation point also increases. The P_n values create a bell curve with increasing temperatures. In general, the optimum P_n temperature is $18-24^\circ\text{C}$ (Fig. 1). Relative humidity did not have a significant effect on P_n , but it did increase slightly with humidity. This slight increase occurred because humidity indirectly affects photosynthesis by altering stoma size. Under sufficient irrigation conditions, stomata have a sufficient opening degree to ensure the flow of CO_2 .

The correlations between measured and simulated values of G_s were shown in Fig. 2. For G_s correlation coefficients of the linear regression equations between measured and simulated values was close to 1. The R values for the regressions were also high. Hence, the models and parameters used in this study were good enough to predict G_s with different microclimatic factors in apple tree canopies. There was a slight underestimation in G_s , which might be caused by light flares and faculae in the canopy.

The maximum photosynthetic rates of the strawberry leaves at different leaf ages differed significantly. The maximum photosynthetic rates of the functional leaves were generally 1-1.5 times greater than the new leaves and 80% greater than the old leaves. The light quantum efficiency of the old leaves was slightly higher than that of the upper leaves, indicating that the lower leaves were more sensitive to



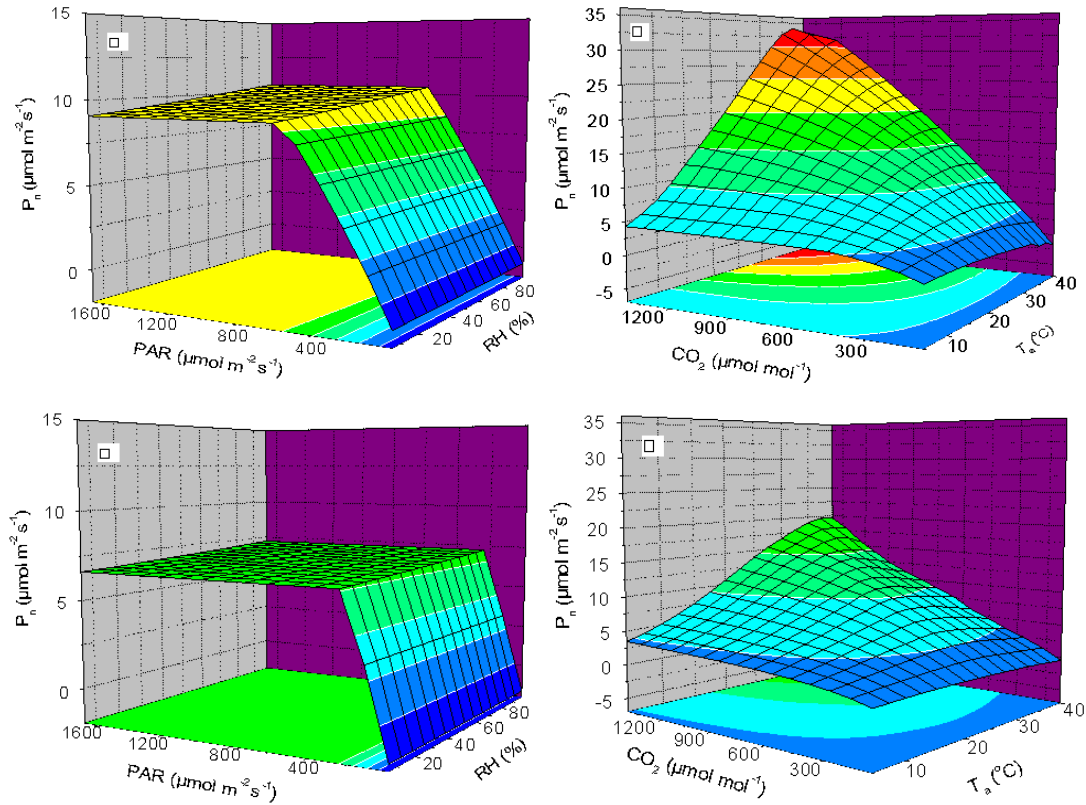


Fig. 1: The response of leaf photosynthesis (P_n) to Photosynthetically Active Radiation (PAR), air Relative Humidity (RH), air temperature (T_a) and CO_2 concentration (CO_2); The range of PAR was from 0 to 1800 $\mu\text{mol/m}^2/\text{s}$, RH from 0 to 100, T_a from 5 to 40 $^{\circ}\text{C}$, CO_2 concentration from 50 to 1500 $\mu\text{mol/mol}$. The standard conditions were PAR = 1500 $\mu\text{mol/m}^2/\text{s}$, RH = 50%, T_a = 25 $^{\circ}\text{C}$, (CO_2) = 360 $\mu\text{mol/mol}$

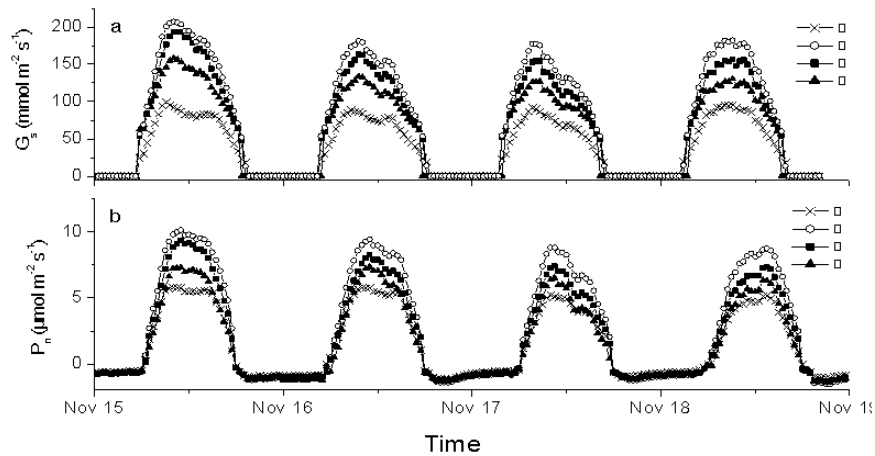


Fig. 2: The diurnal variation of leaf photosynthetic rate (P_n), stomatal conductance (G_s) of different leaf age of strawberry from Nov. 15th to 18th in 2014

light intensity. When the CO_2 concentration increased, the P_n of the functional leaves also increased. However, the new and old leaves were slow to respond to changes in the CO_2 concentration and had no obvious CO_2 saturation point. The strong photosynthetic capacity of the functional leaves was consistent with their thick leaves and high chlorophyll and photosynthetic protein contents. The difference in photosynthetic capacity of

the leaves at different leaf ages was possibly not only related to their development but also was affected by light.

Diurnal variations in photosynthesis of strawberry at different leaf ages: The amount of photosynthetic products has a direct effect on fruit yield and quality and a significant effect on flower bud differentiation

and quality. The P_n of leaves at different leaf ages is not only restricted by photosynthetic capacity, but also by light intensity. New leaves are located in the upper part of plants and are exposed to the greatest irradiation levels, while old leaves are located at the bottom of plants and receive the lowest irradiance levels. Our statistics showed that during the day, the average radiation received by the leaves treatments I-IV were 82, 65, 43 and 18%, respectively of the level received on the upper reference plane of the strawberry plants. The diurnal variations in photosynthesis rates and stomatal activity of the leaves were calculated based on the average radiation received by the leaves and the data from the small meteorological station in the greenhouse (Fig. 2).

The P_n of the functional leaves was significantly greater than that of the new and old leaves (Fig. 2b). On clear days (November 15-18), the maximum P_n value for the new leaves occurred earliest. This is because the new leaves located in the upper part were exposed to sufficient light and were able to quickly reach the light saturation point. The light saturation point of the old leaves in the lower part was lower than that of the functional leaves above. However, they were exposed to insufficient light and therefore the P_n was difficult to saturate, even at noon. The G_s was calculated using Eq. (2) and was found to change consistently with P_n (Fig. 2a). The strong light on the clear days put the new and functional leaves under water and temperature stress and their stomata were partially closed at noon (Fig. 2a), further producing the photosynthetic “noon break” phenomenon.

On clear days, the functional leaves synthesized approximately 210 mmol/m²/d of CO₂ throughout the day, the new leaves synthesized approximately 131 mmol/m²/d of CO₂ throughout the day and the old leaves synthesized approximately 140 mmol/m²/d of CO₂ throughout the day. The total diurnal photosynthesis of the new and old leaves was 62 and 67% of that of the functional leaves. When light was insufficient, the photosynthetic rate of the lower leaves suffered the largest decline, which was related to insufficient light, poor photosynthetic capacity and the big proportion of nighttime respiration. The average stomatal conductance of the old leaves was about 53% of that of the functional leaves and stomatal conductance of the new leaves was about 77% of that of the functional leaves. The strong assimilative capacity of the functional leaves was related to the high chlorophyll and photosynthetic protein contents. This difference is an adaptive mechanism developed by strawberry plants that improves the photosynthetic capacity of the entire plant and helps maximize the utilization efficiency of nutrients, such as nitrogen. The structure and function of the new leaves were not complete, so they had small photosynthetic rates and a smaller output of photosynthetic products. Therefore, at the early growth stage of the strawberry plants in this study, it was inappropriate to reserve too many fruits due to small leaf areas and a great number of new

leaves. However, in order to cause strawberry plants to fruit ahead of time, people sometimes reserve a great number of fruits at the seedling stage, which will not help improve fruit yield and quality. Some of chlorophyll in old leaves has decomposed and their photosynthetic capacity is poor. Therefore, after strawberry plants enter the full bearing stage, it is essential to timely remove the old leaves in order to promote the emergence of new leaves and enhance overall photosynthetic capacity.

DISCUSSION

The simulation of the chlorophyll content and photosynthetic capacity of the strawberry plants at different leaf ages indicated that functional leaves contain the high concentrations of chlorophyll and protein, consistent with their strong photosynthetic capacities. The differences between photosynthetic organs at different leaf ages was primarily caused by the differences in leaf age and light received during growth and development; these differences were further caused by the differences in photosynthetic capacity (Meir *et al.*, 2002; Rodríguez-Calcerrada *et al.*, 2008). The maximum photosynthetic capacity of the functional leaves was two to four times that of the other leaves (Niinemets *et al.*, 2006), which is similar to the results of this study. The total net photosynthesis of the lower old leaves throughout the day was very low, especially on cloudy days with insufficient light. Therefore, during strawberry management, it is necessary to remove old leaves as early as possible in order to minimize the volume of low-light and light-free areas to improve the use of light energy. A large problem with strawberry cultivation is insufficient light availability. Light transmittance becomes increasingly low as the films age in plastic greenhouses. Therefore, more importance should be attached to removing the old leaves of protected strawberry. When the CO₂ concentration in the air increased, the photosynthetic capacity of the strawberry leaves increased significantly (Fig. 1). However, the CO₂ concentration gradually reached the CO₂ saturation point after exceeding 600 μmol/mol, consistent with the results of previous studies (Laforge *et al.*, 1991; Li *et al.*, 2013).

Stomata have been found to be partially closed among many plants and further result in a photosynthetic “noon break”, especially leaves in the upper canopy (Fig. 1). The small Vapor Pressure Deficit (VPD) and high temperature at noon cause serious threats and may be the major causes of stomatal closure (Sellin and Kupper, 2004). This study on the diurnal variation in the photosynthesis of the strawberry leaves also indicated the photosynthetic “noon break” phenomenon and the difference among the leaves at different leaf ages (Fig. 2). In addition, the rise in leaf water potential (Alarcón *et al.*, 2006) is also one of the causes of partial stomatal closure, which failed to be considered in this study. Meanwhile, leaves can accumulate a certain amount of solute in order to

reduce water potential, improve the stress resistance of leaves, maintain the balance of water in leaves and ensure photosynthesis and other normal physiological activities. These substances primarily include proline, soluble sugar and soluble protein.

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