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# Light Harvesting and Photosynthesis by the Canopy

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## 1. Introduction

Photosynthesis is a life-sustaining process driven mostly by green plants to support not only life of plants, but also life on earth in general. The estimated dry matter produced by photosynthesis of land plants reaches as much as  $125 \times 10^9$  per year (Field et al., 1998). About 40% of this material is composed of C, fixed in photosynthesis. Light has long been recognized as a source of energy to convert atmospheric CO<sub>2</sub> into energetic chemical bands which finally appear as sucrose, starch and many other energy containing substances. This conversion will not happen until there is specialized light-harvesting system to capture and transfer light energy to low-energy compounds. Leaves are this specialized system with broad, laminar surface well suited to gather and absorb light. When a large number of leaves are arranged beside each other the canopy will be formed. Organization and spatial arrangement of leaves within the canopy directly affect the amount of light absorbed by this integrated system. Therefore, photosynthetic capacity at canopy level depends not only on factors affecting leaf level photosynthesis but also on factors which influence properties of canopy microclimate, particularly its light distribution profile. Estimating photosynthesis at canopy scale, however can be of great importance as it provides a tool to predict crop yield and help producer to make decision and planning of production. While photosynthesis mechanism in C<sub>4</sub> plants differs virtually from that of C<sub>3</sub> plants, there have been no significant differences in the methods implemented to investigate light harvesting and upscaling photosynthesis from leaf to canopy level, so in this chapter the issues related to the photosynthesis of C<sub>3</sub> plants will be emphasized and addressed.

## 2. Canopy: An integrated foliage structure

There are many factors that determine plant canopy architecture. Some of these factors are genetic and relate to the plant species while some are ecological and relate to the plant-environment interactions. Under the influence of these factors plants develop their canopy so that they reach a compromise between affecting factors and internal physiological requirements. The resultant will be a volume composed of numerous leaves varying in size, thickness, inclination and many other physical and physiological properties distributed in space and time. Naturally, plants attempt to construct their canopy in a way that the highest ambient irradiance could be absorbed. This process is usually done by developing special branching system, efficient leaf arrangement; appropriate canopy dimension and

even sometimes by natural pruning and removing weak and underdeveloped organs. Consequently canopies appear to be a complex, dynamic and ever-changing volumes; being difficult to interpret and understand. The complexity of canopy becomes more apparent when we move from leaf level to pure stand to heterogeneous plant communities, since each level contains elements of the lower levels (Norman & Campbell 1994). In vast plant communities, when diverse plant species mixed together and form a very heterogeneous vegetation stand, description of canopy structure become much more difficult. Therefore canopies composed of single species or integrated of only a few species usually assumed to be homogeneous with uniform monotypic plant stand (Beyshlag & Ryel, 2007).

In order to interpret canopy in detail we may have to consider its components. Canopy structure can be defined in detail by including the size, shape, orientation and positional distribution of various plant organs such as leaves, stems, branches, flowers and fruits. Getting such information for each element in a canopy is not currently feasible, so quantitative description of the canopy by means of mathematical and statistical methods seems to be appropriate. Norman and Campbell (1994) summarized all the methods applied in describing canopy structure to two main groups: direct and indirect methods. They explained that direct methods involve usually much labor in the field and require very simple data reduction when compared to the indirect methods which use simple and rapid field measurements but complex algorithms for the reduction of data. In spite of recent considerable progresses achieved in 3D modeling by computers, this technique still requires a considerable effort to sample all the growing organs of a canopy. Because of this, only a few variables, such as the leaf area density, and the leaf inclination distribution function could be used to describe canopy structure (Weiss et al., 2004). Sound estimation of a crop whole canopy leaf area may be sufficient to predict crop productivity in large scale, but does not give an accurate estimation of vertical gradient of light or spatial distribution of materials applied to the plant canopy. Plant architectural models attempt to fill the gap caused by not considering the influence of plant functioning or environmental variables on the process of morphogenesis through including physiological processes of plant growth and development as well as the physical structure of plants. To do this, more precise and extensive data will be required than usually collected on the dynamics of production of individual organs of plants (Birch et al., 2003).

### **3. Light harvesting**

Light harvesting by plants is influenced by many factors such as, diurnal variation in solar elevation and variation in leaf angle, leaf position in the canopy, sky cloudiness, degree of leaf clumping and amount of sunflecks penetrated through the canopy, and all the factors affecting gas flux properties of individual leaves. Photosynthesis occurs in leaves, the small-sized food factories constituting the majority of the canopy volume. Any disturbances in canopy microclimate such as variations occurred in ambient gas composition, light quantity and quality, temperature and humidity will clearly lead to corresponding changes in C uptake by the leaves. Therefore studying leaves as the primary light harvesting organ within the canopy could merit first priority.

#### **3.1 Light harvesting at the leaf scale**

Before being intercepted by leaves, light travels a long distance between the sun and the earth, passing through the atmosphere according to its composition and physical features, it

experiences some quantitative and qualitative alterations which favor life sustaining processes occurring on the planet. Upon reaching leaf surface light transferred and distributed through the leaf by a phenomenon called **lens effect** created by the planoconvex nature of epidermal cells covering leaf surface. The consequent of this effect is efficient redirecting of incoming radiation to the chloroplasts confined in mesophyll cells. The mesophyll tissue consisted of two distinct cells: palisade and spongy cells. Palisade cells are elongated and cylindrical with the long axis perpendicular to the surface of the leaf, while spongy cells situated below this layer and surrounded by the prominent air spaces (Hopkins & Huner, 2004). Although a large number of chloroplasts occupy the cell volume of palisades, there is still a significant proportion of cell volume that does not contain chloroplast. This chloroplast-free portion of the cell helps to distribute incoming light and maximize absorption by chlorophyll. Consequently, some of the incident light may pass through the first palisade layer without being absorbed, but more likely will be intercepted through successive layers by **the sieve effect**. Additionally, palisade cells help efficient distribution of incoming light by **light-guide effect**, a feature that assists light reaching the cell-air interfaces to be reflected and channeled through these layers to the spongy mesophyll below (Hopkins & Huner, 2004).

A large portion of the light reaching the leaf surface then finally targets the chloroplasts, where photochemical reactions occur. Although the mesophyll layer is the main place hosting chloroplasts, these organelles may be also found in other organs such as; buds, the bark of stems and branches, flowers and fruits. Light interception in chloroplasts is carried out specifically by antenna complex or light harvesting complex (LHC), mainly consisted of chlorophylls (i.e. chlorophyll a and b) and several hundred accessory pigments clustered together in the thylakoid membrane. Carotenoides are one of the most important accessory pigments in green plants which absorb light at wavelength different from that of chlorophyll and so act together to maximize the light harvested. When a pigment molecule absorbed incoming photon energy and excited, it transfers the energy to two special chlorophyll molecules in the photosynthetic reaction center. The reaction center then passes on the energy as a high-energy electron to a chain of electron carriers in the thylakoid membrane. The high energy electrons are then exploited to produce high energy molecules which are eventually used to reduce RuBP by CO<sub>2</sub>.

In response to changes of environmental conditions chloroplast may undergo some modifications in structure and biochemical composition in order to cope with new environment. Some of these environmental factors negatively affect chloroplast activity and therefore directly limit the photosynthetic rate. The consequence of most of these factors, such as high light intensity, UV radiation, air pollutants, herbicides, water and heavy metal stress will usually appear as oxidative stress and often leads to the symptoms of structural damage which emerges as swelling of thylakoids, plastoglobule and starch accumulation, photodestruction of pigments, and inhibition of photosynthesis (Mostowska, 1997). It was shown similarly that chloroplast property changes in accordance with the light gradient within a bifacial leaf (Terashima & Inoue, 1985). That is, near leaf surface facing to ambient light, the chloroplasts have higher rates of electron transport and Rubisco activities per unit of chlorophyll than chloroplasts farther away from the surface. Moreover, in plants acclimated to shade conditions, it was shown that chloroplasts migrate in response to inducing ambient light (lambers et al., 1998).

Plants try to increase their light absorption at leaf level by adjusting leaf weight to plant weight or leaf weight to leaf area. One of the parameters which can be very helpful in giving

good understanding of the plant manner of investment on light harvesting complexes is specific leaf area (SLA). It is defined as projected leaf area per unit leaf dry mass. This parameter relates with the other plant growth parameters as follows:

$$\text{LAR} = \text{LWR} \times \text{SLA} \quad (1)$$

LWR is the ratio of leaf weight to plant weight ( $\text{gg}^{-1}$ ), LAR is the ratio of leaf area to plant weight ( $\text{m}^2\text{g}^{-1}$ ). The equation that links LAR to RGR is:

$$\text{RGR} = \text{NAR} \times \text{LAR} \quad (2)$$

Where RGR is relative growth rate ( $\text{gg}^{-1}\text{d}^{-1}$ ) and NAR denotes net assimilation rate ( $\text{gm}^{-2}\text{d}^{-1}$ ). This relationship implies that transferring a sun-acclimated plant to a shade environment will result in a reduction in RGR caused by a lowering in NAR, reflecting the effect of PAR on photosynthesis. In order to keep RGR unchanged, plant has to increase LAR with the assumption that there is no change in the light dependence of photosynthesis. LAR directly changes with any changes in LWR and/or SLA. It has been revealed that LWR may proportionally change in accordance with plant light regime alterations, having tendency to increase in shade-adapted plants, while showing decline in non-adapted plants in shade (Fitter & Hay, 2002). Studying with many plants indicated that SLA seems to change faster than LWR, playing an important role in acclimation process to varying environmental light regimes. Plants developed under high light usually have thick leaves with a low SLA (Bjorkman, 1981, as cited in Fitter & Hay, 2002). Light-saturated photosynthesis remained unchanged in plants acclimated to shade environment because of doubling SLA (Evans & Poorter, 2001). It can be deduced that SLA is more variable than LWR, or, leaf area is more plastic than leaf weight. Studying with *Cucumis sativa*, a light-demanding species, showed that leaf area changes proportionally with the total ambient light, with a maximum at about  $4.2 \text{ Mj m}^{-2}\text{d}^{-1}$  (Newton, 1963, as cited in Fitter & Hay, 2002). Instantaneous light variations do not exert any immediate changes in SLA, while these changes generally occur in response to total radiation load; this is probably the case for *Impatiens parviflora* which shows an almost threefold increase in SLA when grown in 7% of full daylight (Evans & Hughes, 1961, as cited in Fitter & Hay, 2002). Findings of Evans and Poorter (2001) indicated that increasing SLA is a very important means applied by plants to maximize carbon gain per unit leaf mass under different environmental light conditions.

### 3.2 Light harvesting at the canopy scale

Foliage density distribution and leaves orientation highly impact sunlight attenuation through the canopy. As described before, canopies normally are not solid sheets, but are loosely stacked formation of leaves which help plants to effectively absorb most of the incident light, with leaves near the top of the canopy absorbing near maximum solar radiation and the lower leaves perceiving sunlight of a reduced intensity and also an altered spectral composition. Therefore the amount of photosynthetically active radiation intercepted by a leaf usually depends on its position in the canopy and the angle it faces incoming solar radiation. Leaves within the canopy are generally subject to three types of radiation: light beam, reflected and transmitted radiation. Light beam penetrates through the gaps created in the canopy probably by instantaneous fluttering of leaves caused by wind, or sparse leaf arrangement which naturally forms gaps within the canopy. While passing through the canopy light beam is usually trapped by the lower leaf layers, however,



depending on the canopy architecture some may reach the most lower layers and form “sunflecks”. These packages of high light intensity are not generally stable, but dynamically change their location due to movements of branches, and the changing angle of the sun. Their duration may range from less than a second to minutes. Small-sized sunflecks typically carry lower light energy than direct sunlight because of penumbral effects, but large ones can approach irradiances of direct sunlight (Lambers et al., 1998). Direct beam light predominantly absorbed by the leaves at the top of the canopy, some portion transmitted down with altered spectral quality, due to action of the various leaf pigments. Leaves typically transmit only a few percent of incident PAR in the green band at around 550 nm, and are otherwise efficiently opaque in the visible range. Transmittance of PAR is normally less than 10%, whereas transmittance of far-red light is substantial (Terashima & Hikosala, 1995). This spectral alteration affects the phytochrome photoequilibrium and allows plants to perceive shading by other plants to adjust their photomorphogenesis activities (Lambers et al., 1998). Leaves like to other biological surfaces not only transmit light but reflect a proportion. The amount of reflection depends on morphological and physical properties of leaves such as, leaf shape, thickness and shininess of the cuticle. However, it should be noted that reflected light then may be absorbed or transmitted by the lower leaves similar to the radiation reaching the canopy surface.

Rundel and Gibson (1996) found that leaf angle and orientation are the main factors which control daily integrated radiation, maximum irradiance and diurnal distribution of irradiance. Orientation of leaves at the top of the canopy is usually at oblique (acute or obtuse) to incident light. When leaves in the uppermost layer of the canopy arrange obliquely, they allow a given amount of light to distribute over a greater total leaf area of the plant than when they arrange at right angles to the direction of incoming light. While leaves on the canopy surface are most efficient at utilizing full sunlight when at an oblique angle to the sun’s ray, the leaves located in lower parts do best in lower irradiance if the leaf area is at right angle to the light, intercepting the greatest sunlight per leaf surface. Ontogenetically change from sessile juvenile leaves to petiolate adult leaves is accompanied by a change in leaf orientation from horizontal to vertical (king, 1997). Research by Shelley and Bell (2000) on the heteroblastic species *Eucalyptus globules* Labill. ssp. *Globules* showed that there was no active diurnal orientation between juvenile and adult leaves toward or away from incident radiation. They concluded that greater interception of light by juvenile leaves compared with vertical adult leaves, may be due to their high adaptation capacity to high incident light.

### 3.2.1 Light profile within the canopy

Beer’s law has long been used by many authors to describe light penetration in plant canopy. With the assumption that the gaps are randomly distributed horizontally, the area of direct-beam irradiance penetrating to any depth in the canopy is an exponential function of the cumulative LAI from the top of the canopy (Boote & Loomis, 1991):

$$I=I_0 \exp(-KLAI) \quad (3)$$

$I$  and  $I_0$  are respectively the irradiance beneath and above the canopy ( $\mu\text{molm}^{-2}\text{s}^{-1}$ ),  $K$  is the extinction coefficient and LAI denotes leaf area index. The extinction coefficient is actually the ratio of horizontally projected shadow area per unit ground area per unit leaf area. Both leaf angle and solar elevation angle ( $\beta$ ) affect the shadow projection of leaves. At any point

within the canopy, radiation is composed of contributions from all directions. The angle between leaf surface and incident radiation depend on leaf orientation and the radiation direction. However, for horizontally positioned leaves, the fraction of radiation intercepted by any leaf will be proportional to the leaf area itself, independent of the radiation direction (Marcelis et al., 1998). Consequently, the extinction coefficient is high for horizontally inclined leaves, but low for vertical leaf arrangements. When all leaves distributed randomly in the horizontal plane and are perpendicular to the direct beam with solar elevation of  $90^\circ$ , the value of  $K$  is 1. Solar position changes during the day influence the value of  $K$  by the factor  $1/\sin(\beta)$ . Variations occurred in leaf angle also change  $K$  value dramatically, as vertically oriented leaves intercept less light than horizontal leaves. (Boote & Loomis, 1992). For greenhouse roses trained by arching system  $K$  ranged from 0.58 to 0.66 at different hours of day, with a daily average value of about 0.63 (Gonzalez –Real et al., 2007). Typical values for  $K$  are in the range of 0.5 to 0.8 (Marcelis et al., 1998). A canopy with low extinction coefficient allows more effective light reaches lower leaves. Some crops tend to arrange upper leaves at oblique angles to incident radiation to minimize the probability of photoinhibition and increase light penetration to lower leaves in high light environments, thereby maximizing whole-canopy photosynthesis. (Terashima & Hikosaka, 1995). It should be noted that direct and diffuse light have different extinction profiles in the canopy and due to light saturation of photosynthesis, direct beam should be singled out from the rest of the incoming radiation (Spitters, 1986). For this reason, experimentally determined values for total light extinction would not necessarily be the same as  $K$ . Leaf area index varies with the number and density of leaves within the canopy. In sparsely vegetated communities like deserts or tundra LAI value is less than 1, while for crops it is about 5 to 7 and for dense forests it estimated to range between 5 to 10 (Schulze et al. 1994). About 90% of PAR is absorbed by the canopy when LAI exceeds a value of 3. At leaf level absorption of PAR is approximately 80%-85% (Marcelis et al., 1998).

#### 4. Whole canopy photosynthesis

Photosynthesis is a fundamental process occurring in green plants, algae and photosynthetic bacteria. During the process solar energy is trapped and utilized to drive the synthesis of carbohydrate from carbon dioxide and water. There are two distinct phases in the reactions of photosynthesis: the light reactions and the dark reactions. Light reactions use light energy to synthesize NADPH and ATP, which then transfer the energy to produce carbohydrate from  $\text{CO}_2$  and  $\text{H}_2\text{O}$  during dark reactions. Chloroplast is an organelle in which photosynthesis takes place and has highly permeable outer membrane and an inner membrane that is impermeable to most molecules and ions. Light reactions occur in thylakoids, stacks of flattened chloroplast membranes extended into stroma, the place where the dark reactions are taken place. Two photosystems are involved in light reactions: photosystem I (PSI) and photosystem II (PS II). The difference is that PSI contains chlorophylls which have an absorption peak at 700 nm and so is called P700 but chlorophylls in the reaction center of PSII absorb light mostly at 680 nm and so is referred to as P680. The two photosystems are linked by a chain of electron carriers and when arranged in order of their redox potentials they form so-called Z scheme. Electrons released in PSII flow through Z scheme to reduce  $\text{NADP}^+$  in PSI. Pigments involved in the light harvesting complex (LHC) have already been discussed and here a brief explanation of overall photosynthesis reactions is presented:

Photosynthesis process begins with absorbing light-energy photons and transferring them to the reaction centers of the photosystems where the second process starts. In the thylakoid membrane water splits to release electrons which are then transported along an electron-transport chain to produce NADPH and ATP. All the reactions occurred up to this point are called light reactions of photosynthesis as they depend on light energy to proceed. The produced NADPH and ATP during the light reactions then enter the carbon-reduction cycle (Calvin cycle), in which  $\text{CO}_2$  is assimilated, leading to the synthesis of  $\text{C}_3$  compounds (triose-phosphates). This reaction does not need light to proceed and therefore is referred to as the dark reaction of photosynthesis. In Calvin cycle,  $\text{CO}_2$  molecules are condensed with ribulose 1,5-bisphosphate (a five-carbon molecule) to produce a transient six-carbon intermediate that immediately hydrolyzes to two molecules of 3-phosphoglycerate. This important process will not be complete without the mediation of the key enzyme ribulose biphosphate carboxylase/oxygenase (often called Rubisco). Rubisco is known as a slow enzyme as it only fixes three molecules of its substrate every second and hence plants need a large amount of this enzyme to assimilate enough  $\text{CO}_2$  to sustain plant life. Approximately 50% of chloroplast protein content is Rubisco, probably the most abundant protein on the earth.

#### 4.1 Factors affecting leaf level photosynthesis

The rate of photosynthesis at leaf level varies widely and is influenced not only by leaf internal biochemical and physiological conditions, but also by many environmental variables such as,  $\text{CO}_2$  concentration, light intensity, temperature and humidity fluctuations. Temperature is an essential factor that controls enzymatically catalyzed reactions and membrane processes and in this way it controls photosynthesis (Lambers et al., 1998). Photosynthetic response to temperature varies among species because of the different activation energy required by different reactions processed in various plants. Consequently, temperature-dependent photosynthesis of plants ranges widely from temperatures near freezing to over  $40^\circ\text{C}$ , implying that the specific range depends on species and genotype, plant age, plant origin, and season (Pallardy, 2008). Optimal temperature for any plant is usually defined by the temperature that plant has experienced and adapted to during the entire growing period. High temperatures increase affinity of Rubisco to oxygen than carbon dioxide, consequently leading to enhancing photorespiration. In addition, the solubility of  $\text{CO}_2$  declines with increasing temperature more strongly than does that of  $\text{O}_2$ . At temperatures below about  $15^\circ\text{C}$  the rate of photosynthesis is often reduced in many (sub)tropical plants. For example, after exposing coffee trees to  $4^\circ\text{C}$  at night, the rate of photosynthesis was reduced by more than half (Pallardy, 2008). This kind of damage is called chilling injury and differs from frost damage, a type of damage that only happens below  $0^\circ\text{C}$ . Chilling injury generally results from a precipitous decrease in the activity of metabolic processes, notably respiration, which can be fatal within a few hours or days (Fitter & Hay, 2002). Part of the chilling injury is due to the depression of photosynthetic metabolism caused by: (i) decrease in membrane fluidity, (ii) changes in processes and activities of the enzymes related to the membrane, such as the photosynthetic electron transport, (iii) decline in activity of cold-sensitive enzymes (Lambers et al., 1998). Freezing injury commonly occurs to the woody plants of north temperate, subarctic, and alpine regions. It happens not because of low temperatures *per se*, but due to ice formation within tissues. If ambient temperature falls with intermediate rates ( $10^\circ\text{C}$  to  $100^\circ\text{C min}^{-1}$ ), it will cause intracellular ice formation which disrupts the fine structure of the cells and invariably results in death.



Leaves absorb approximately about 85% to 90% of incident PAR (Nobel, 1999). The rate of absorption depends on leaf morphology and structure, especially on the number of palisade and spongy mesophyll layers (Vogelmann & Martin, 1993). In darkness there is no photosynthesis and leaves continue respiration, releasing  $\text{CO}_2$  to the atmosphere. In accordance with increasing light intensity, the rate of photosynthesis starts to increase until it reaches compensation point where the uptake of  $\text{CO}_2$  in photosynthesis equals releasing of  $\text{CO}_2$  in respiration. At this point there is no  $\text{CO}_2$  exchange between leaves and the atmosphere. When light intensity goes beyond the compensation point the photosynthetic rate starts to increase linearly. The initial slope of this line, located between compensation point and light saturation point, is referred to as quantum efficiency. Quantum efficiency describes the efficiency with which light is converted into fixed carbon. With further increase in light intensity, photosynthesis became saturated and is limited by the carboxylation rate. Increasing irradiance beyond the upper limits may even cause a decline in photosynthesis due to occurrence of photoinhibition, particularly in shade-adapted leaves. Photoinhibition may take place in both shade intolerant and shade tolerant plants. However, shade tolerant species and plants grown under shade are especially prone to photoinhibition (Pallardy, 2008). It was shown when willow leaves that previously developed in the shade were exposed to full sunlight, they showed more photoinhibition than leaves developed in the light (Ogren, 1988). Photoinhibition reduces plant quantum efficiency, therefore negatively influence photosynthetic productivity. Nevertheless, plants develop mechanisms to recover from photoinhibition, and it was indicated that the level of recovery is partly related to the duration of exposure to higher light environment.

Although under normal conditions the probability of photosynthesis reduction caused by decreased levels of enzyme Rubisco is very low, there are nevertheless circumstances under which Rubisco concentration exerts strong control over photosynthetic capacity, for example, in low plants transferred to high light (Lauerer et al., 1993). In addition, it was proven that sufficient amount of Rubisco may effectively regulate other components of photosynthetic apparatus. Antisense plants with greatly reduced levels of Rubisco often suffer imbalances in electron transport and decreased water-use efficiency (Quick et al., 1991).

Availability of carbon dioxide at the carboxylation site within the chloroplast highly affects photosynthesis capacity. This availability is strongly limited by resistances in its diffusion path towards the mesophyll cells. Resistance may be generated by boundary layer of air, cuticle, stomata, and mesophyll air space and liquid diffusion resistance. Regarding predicted atmospheric  $\text{CO}_2$  elevation up to 700-1000  $\mu\text{mol mol}^{-1}$  by the end of the 21<sup>st</sup> century (Houghton et al., 2001), many researches have been conducted over the past decades on the effects of rising atmospheric  $\text{CO}_2$  on the physiological aspects of higher plants. These researches showed that leaf-level photosynthesis was often increased in plants developed under long-term exposure to increased levels of  $\text{CO}_2$  (Curtis, 1996; Gonzalez-Real & Baille, 2000; Tissues et al., 1997). Since Rubisco uses  $\text{CO}_2$  and RuBP as the principal substrate to catalyze the carboxylation reactions, it could be expected that any increase in the environmental  $\text{CO}_2$  concentration may cause increases in the rate of photosynthesis, assuming that there is no other limiting factor. The rate of carboxylation per unit leaf area can be governed by elevated  $\text{CO}_2$  through at least two fundamentally different ways: biochemical mechanisms and leaf morphological modifications (Peterson et al., 1999). The biochemical mechanism consists of three levels, as stated by Peterson et al. (1999):" (i) a

reduction in substrate limitation of Rubisco catalysis (Farquahr, von Caemmerer & Berry, 1980), (ii) competitive reduction of RuBP oxygenation (Farquhar et al., 1980), and (iii) any adjustments in the photosynthetic apparatus (from light capture through starch and sucrose synthesis) that change the RuBP limitation of Rubisco (Sage, Sharkey & Seemann, 1989; Sage, 1990). Modifications in leaf morphology and anatomy are the second way that influences the rate of leaf carboxylation. These alterations appear as changes in mesophyll cell number, carbohydrate concentration and leaf mass per unit area (Lambers et al., 1998).

Photosynthetic capacity at leaf level also depends highly on stomata density per unit leaf area and their gas exchange behavior controlled by environmental factors. Stomatal opening is bordered by a pair of unique guard cells which actively regulate the rate of aperture opening by means of swelling and shrinking mechanism, controlled by proton pump and potassium ion uptake processes. Outer surface of epidermis is coated with CO<sub>2</sub>-impermeable cuticle, therefore nearly all of the CO<sub>2</sub> taken into the leaf for photosynthesis must enter only by diffusion through stomatal pores. The degree of stomata opening determines the rate of gas exchange between the leaf and environment which in turn results in direct influence on the rate of transpiration and CO<sub>2</sub> assimilation. Of the environmental variables affecting stomatal movements, CO<sub>2</sub> and light appear to make a substantial contribution to the rate of opening. Stomatal pores tend to be open when the leaves experience low CO<sub>2</sub> concentration or light, and gradually begin to close when face high CO<sub>2</sub> concentrations (Fig. 1). Although high environmental CO<sub>2</sub> concentration may gradually stimulate closure of stomata, there are a number of studies which show elevated ambient CO<sub>2</sub> enhances plant photosynthesis [Curtis, 1996; Gonzalez-Real & Baille, 2000; Tissues et al., 1997]. Gas concentration gradient between leaf intercellular air spaces and leaf boundary layer, together with the size of aperture determine the rate of gas movement across the stomata, referred to as stomatal conductivity. Water vapor and CO<sub>2</sub> are the two main gases crossing stomata which directly influence the rate of transpiration and photosynthesis respectively. As the concentration gradient across the stomata differs considerably for H<sub>2</sub>O and CO<sub>2</sub>, and since they are not equal in the coefficient of diffusion, rate of gas exchange through the stomata will be different for them. As a result, gas exchange would affect photosynthesis and transpiration almost independently (Fig. 2). It has been recognized that elevating ambient CO<sub>2</sub> increases plant water use efficiency. This term is defined as the ratio of CO<sub>2</sub> molecules assimilated by photosynthesis to the number of water molecules lost *via* transpiration. Efficient water use by crops will result in increased agricultural products per liter of water consumed and therefore it can be highly beneficial to agriculture in arid and semi-arid regions with elevated CO<sub>2</sub>.

Investigations have shown that all the stomata distributed over the entire leaf do not respond homogeneously to environmental factors at least in stressful condition (Pospisilova & Santrucek, 1997). This is called stomata patchiness which occurs when some stomata over the leaf close completely, whereas others are almost open. Meyer and Genty (1999) documented that inhibition of photosynthesis was mainly mediated through stomatal closure, when leaves undergo stress caused by dehydration or ABA treatment.

Water stress is another important factor that controls the rate of leaf photosynthesis. It is carried out partially through regulating the size of stomatal aperture and thus limiting CO<sub>2</sub> diffusion to the leaf air spaces, and partly by means of increasing diffusional resistance to CO<sub>2</sub> movement from intercellular spaces to the chloroplast. Since water stress in drought conditions usually coincide with high solar radiation and higher temperatures, the

mechanism of this down-regulation of photosynthesis in response to water stress is not fully understood (Lambers et al., 1998).

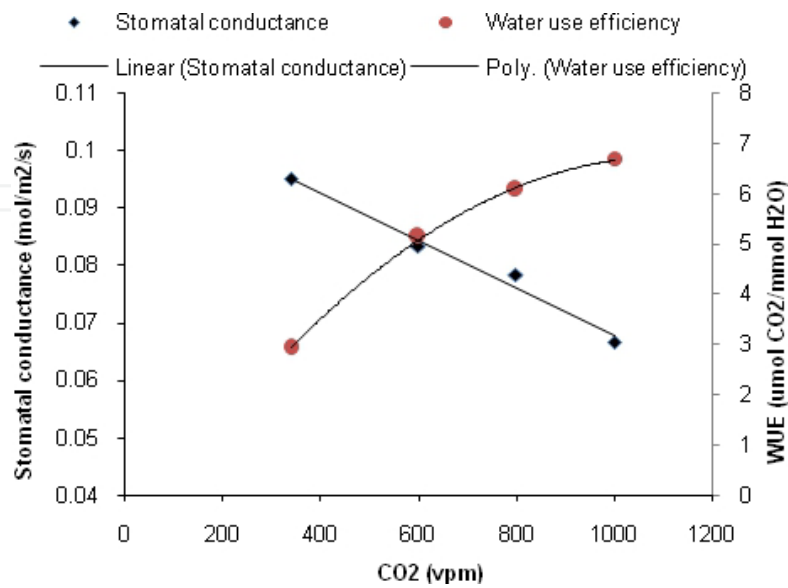


Fig. 1. Effect of CO<sub>2</sub> on stomatal conductance and water use efficiency of *Rosa hybrida* 'Habari'

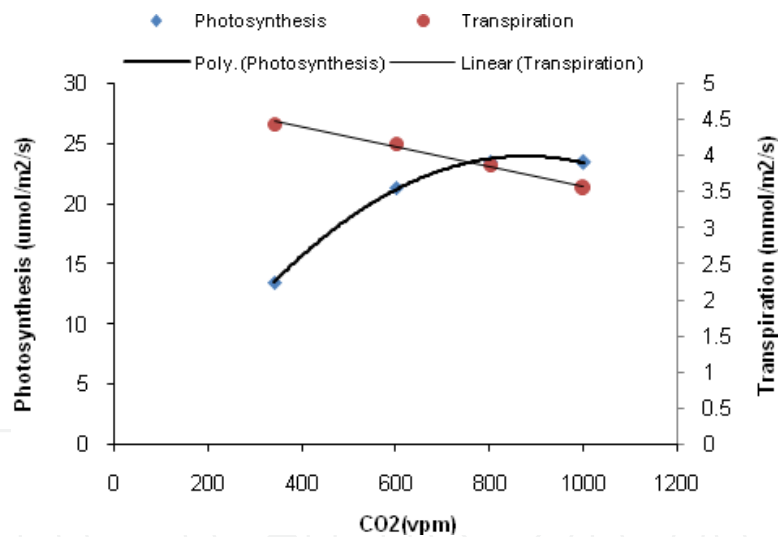


Fig. 2. Effect of CO<sub>2</sub> on the rate of photosynthesis and transpiration of *Rosa hybrida* 'Habari'

4.1.1 Modeling photosynthesis

Models in plant science can be divided into two main groups: mechanistic and empirical. Mechanistic models are descriptive and developed usually based on exhaustive and comprehensive studies which led to globally accepted findings. However, empirical models sometimes referred to as statistical, regression or black-box models are limited to time, location and species on which that model developed and cannot accurately be extrapolated to other conditions and species. Empirical models could be valuable in that they implicitly take into account all unknown effects (Marcelis et al., 1998). In modeling photosynthesis processes both mechanistic and empirical approaches have been considered. Photosynthetic

light response curve was one of the cases that has been noted by many authors to be described by several mathematical functions. Three functions have been used to describe photosynthesis light response curve:

This model was initially proposed by Rabinowitch in 1951, and later reviewed by Johnson and Thornley (1984) in order to describe photosynthesis light response. Non-rectangular hyperbola seems to be one of the best equations in prediction of leaf photosynthetic light response. The function is as follows (Fig. 3):

$$P = \frac{\alpha I + P_{max} - \sqrt{(\alpha I + P_{max})^2 - 4\alpha\theta IP_{max}}}{2\theta} \quad (4)$$

where  $P$  and  $P_{max}$  are respectively the rate of leaf gross photosynthesis ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) and light-saturated photosynthesis ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ ),  $\alpha$  is quantum efficiency ( $\text{mol CO}_2 \text{ mol quanta}^{-1}$ ),  $I$  is irradiance quantity ( $\mu\text{mol quanta m}^{-2}\text{s}^{-1}$ ) and  $\theta$  denotes curvature (convexity) of the light-photosynthesis relationship (dimensionless).

This model have three parameters to be estimated: (i) the quantum efficiency ( $\alpha$ ), the initial slope of the curve which relates the rate of  $\text{CO}_2$  uptake to absorbed or incident light at very low light intensity. Values of this parameter change with the species, leaf history of stress such as; low temperatures, drought and high irradiance and usually range between 0.040 to 0.075  $\text{mol CO}_2 \text{ mol quanta}^{-1}$  at ambient  $\text{CO}_2$  concentrations (Cannell & Thornley, 1998), (ii) the light -saturated photosynthetic rate ( $P_{max}$ ), which varies extremely among species and is affected by the temperature and life history of leaves which influence leaf morphological and physiological properties like N content and leaf thickness, (iii) and the curvature factor ( $\theta$ ), which indicates how quickly the transition of the curve is made from Rubisco-limited region to RuBP-regeneration-limited region. There are many studies, indicating that non-rectangular hyperbola usually best fitted with  $\theta$  ranging from 0.7 to 0.9 (Matloobi, 2007; Marshall & Biscoe, 1980; Cannel & Thornley, 1998; Kim et al., 2004).

In non-rectangular hyperbola when  $\theta$  closes zero, the equation appears to be a rectangular hyperbola (Fig. 4):

$$P = \frac{\alpha IP_{max}}{\alpha I + P_{max}} \quad (5)$$

This equation recalls the famous Michaelis-Menten equation. With  $\theta=1$  the equation will be Blackman response with two intersecting straight lines.

Another equation that is used to model photosynthesis light response is asymptotic exponential equation (Fig. 5):

$$P = P_{max}(1 - e^{(-\alpha I/P_{max})}) \quad (6)$$

In an experiment we measured leaf gas exchange parameters in a rose crop (*Rosa hybrid* "Habari") by a portable photosynthesis measurement system (Matloobi, 2008). Obtained data then were used to estimate the models parameters by non-linear least squares regression method. A linear regression was fitted to the data obtained by direct measurement and those estimated by the models. Results showed that all the models had the potential to present good estimations of the leaf photosynthetic light response with roughly high  $R^2$  (coefficient of determination), but the non-rectangular hyperbola with the highest  $R^2$  ( $R^2=0.968$ ) was the best as it predicted values more closer to the observed ones

(Fig. 3). Non-rectangular hyperbola has been frequently used to describe observed leaf photosynthetic responses to environmental variables (e.g. Pasian, 1989; kim et al., 2004; Cannel & Thornley, 1998)

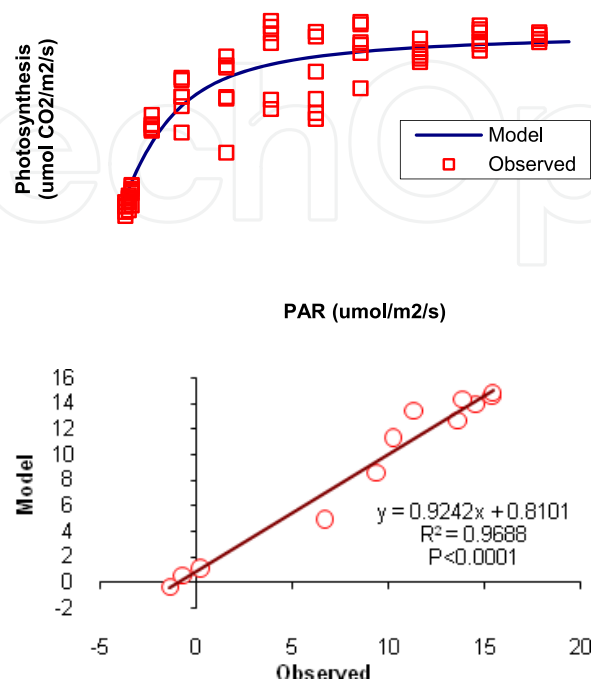


Fig. 3. Photosynthetic light response of *Rosa hybrida* 'Habari', non-rectangular hyperbola model was fitted to the observed data (top), regression between the model and observed data estimates model efficiency (bottom)

The model proposed by Farquahr et al. in 1980 for leaf photosynthesis of  $C_3$  plants is the only mechanistic model which is accepted and widely used for determination of the leaf  $CO_2$  assimilation capacity. This model developed based on the amount and kinetic properties of Rubisco and the ratio of RuBP to enzyme (Rubisco) active site (Harley & Tenhunen, 1991). In this model two limiting factors were assumed to control the leaf photosynthetic capacity:

$$A_n = \min\{A_v, A_j\} - R_d \quad (7)$$

where  $A_v$  and  $A_j$  are the rate of gross photosynthesis limited by Rubisco activity and the rate of RuBP regeneration through electron transport, respectively, and  $R_d$  is the rate of mitochondrial respiration. Rubisco limited photosynthesis is given by:

$$A_v = V_{cmax} \frac{C_i - \Gamma^*}{C_i + K_c ((1 + O / K_o))} \quad (8)$$

where  $V_{cmax}$  is the maximum carboxylation rate, with  $K_c$  and  $K_o$  the Michaelis constants for carboxylation and oxygenation, respectively, and  $C_i$  and  $O$  are the partial pressure of  $CO_2$  and  $O_2$  in the intercellular air spaces, and  $\Gamma^*$  is the  $CO_2$  compensation point in the absence of mitochondrial respiration. The rate of photosynthesis limited by RuBP regeneration is given by:



$$A_j = \left(\frac{J}{4}\right) \times \frac{(C_i - \Gamma^*)}{(C_i + 2\Gamma^*)} \quad (9)$$

where  $J$  is the rate of electron transport,  $J$  is related to irradiance usefully absorbed by photosystem II,  $I_2$  by:

$$J^2 - (I_2 + J_{max})J + I_2J_{max} = 0 \quad (10)$$

where  $J_{max}$  is the potential rate of electron transport,  $I_2$  is related to the incident PAR,  $I_o$  by the following equation:

$$I_2 = I_o(1-f)(1-r)/2 \quad (11)$$

where  $f$  is spectral correction factor ( $\sim 0.15$ ) and  $r$  is the reflectance plus any small transmittance of the leaf to PAR ( $\sim 0.12$ ).

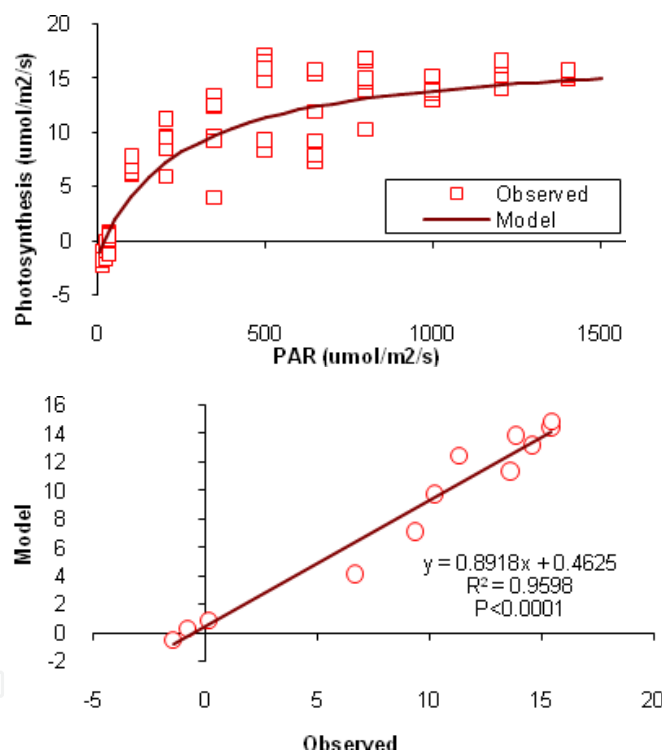


Fig. 4. Photosynthetic light response of *Rosa hybrida* 'Habari', rectangular hyperbola model was fitted to the observed data (top), regression between the model and observed data estimates model efficiency (bottom)

The two key parameters in this model which vary among species are  $V_{cmax}$  and  $J_{max}$ . The potential rate of electron transport,  $J_{max}$ , is a property of the thylakoids that varies depending on growth conditions (Farquhar & Evans, 1991). Factors affecting the chlorophyll content per unit leaf area determine the rate of  $J_{max}$ . There are many studies showing that the chlorophyll content of leaves dynamically change according to the environmental light availability [Kitajamia & Hogan, 2003; Matloobi et al., 2009; Walters, 2005). Plants acclimated to low irradiance are enriched in the light-harvesting chlorophyll a/b protein complex and

deplete in the photosystem II reaction-center complexes, therefore the electron-transport capacity per unit of chlorophyll is less in leaves acclimated to low irradiance (Farquhar & Evans, 1991).

It was found that there is a good correlation between the leaf N content and the photosynthetic maximum carboxylation rate,  $V_{\text{cmax}}$ . Gonzalez-Real and Baille (2000) documented that in rose crop there is a gradient in the leaf photosynthetic N concentration from the top of canopy down to the bottom layers according to the amount of light absorbed. The value of  $V_{\text{cmax}}$  decreased from  $66 \mu\text{molm}^{-2}\text{s}^{-1}$  for leaves situated at the top of the canopy to  $44 \mu\text{molm}^{-2}\text{s}^{-1}$  for leaves located at the bottom layers. The ratio of  $J_{\text{max}}/V_{\text{cmax}}$  for all leaf layers within the canopy was almost constant and resulted 2.3. It should be noted that photosynthetic key parameters ( $J_{\text{max}}$  and  $V_{\text{cmax}}$ ) change proportionally with seasonal variations in soil water content, air temperature and VPD (Xu & Baldocchi, 2003). Parameterization of the photosynthetic models for several plants have been previously done (Gonzalez-Real & Baille, 2000; Kim & Lieth, 2002; Kim & Lieth, 2003; Matloobi, 2007) and still it is noted and under research by many authors around the world.

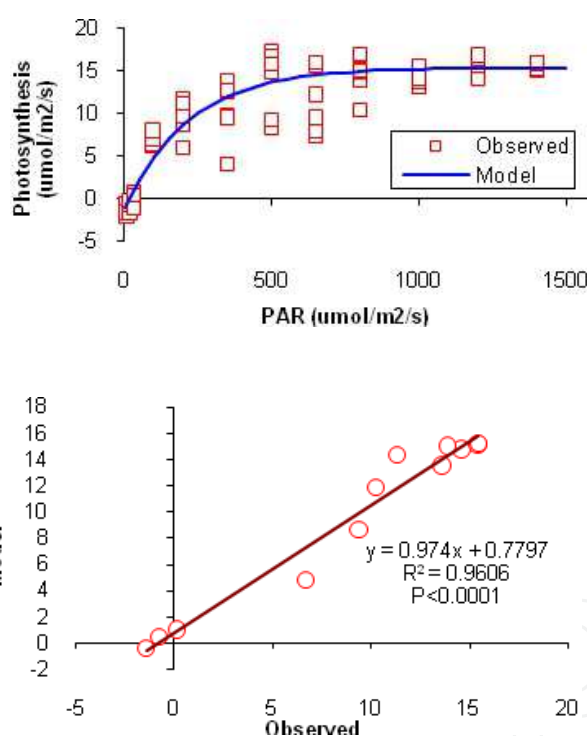


Fig. 5. Photosynthetic light response of *Rosa hybrida* 'Habari', asymptotic exponential model was fitted to the observed data (top), regression between the model and observed data estimates model efficiency (bottom)

#### 4.2 Photosynthesis at canopy level

Canopy photosynthesis at the first step highly depends on the rate of photosynthesis at leaf level which is controlled by interaction of many internal and some external factors, outlined earlier. Therefore in order to obtain an estimation of the plant whole-canopy photosynthesis one must first consider the factors affecting leaf level  $\text{CO}_2$  assimilation and then accurately

incorporate them to upscale photosynthesis from individual leaves to the canopy. To achieve this, the first challenge will be calculating the amount of radiation absorbed by individual leaves and finally by the plant whole canopy.

Beer's law (equation 3) has been used as a basis to develop more precise models in order to get a clear profile of light distribution within the canopy. Three approaches have been considered in modeling light absorption by the canopy: (i) big leaf model (ii) multi-layer model (iii) sun and shade model.

Big leaf model tries to simplify rather than increase canopy structural complexity (Beyschlag & Rye, 2007). The concept comes from the findings of Farquhar (Farquhar, 1989, as cited in Evans & Farquhar, 1991) who demonstrated that the equation for whole-leaf photosynthesis would be the same form as for individual chloroplast provided that chloroplast photosynthetic capacity distributes in proportion to the profile of absorbed irradiance and that in all layers the shape of the response to irradiance become identical. This approach applies to predict canopy light absorption by reduction of properties of all leaves within the canopy to a single leaf. However, this prediction will not be accurate enough to ignore developing alternative models. While Beer's law describes time-averaged profile of absorbed irradiance and the spatially averaged instantaneous profiles in a canopy, it doesn't describe the actual instantaneous distribution of absorbed irradiance. In fact, some leaves located deep in the canopy receive much higher radiation than the amount that Beer's law would predict when they are subject to sunflecks. Generally Beer's law does not represent the instantaneous profiles of absorbed irradiance in canopies because of errors created by both sunflecks and leaf angles (De Pury & Farquhar, 1997).

Multi layer model of light penetration through the canopies was proposed by Goudriaan (Goudriaan, 1977, as cited in De Pury & Farquhar, 1997). In this model the plant canopy is divided into multiple leaf layers (increments in  $L$  of 0.1) distributed horizontally and assumed to be homogeneous with respect to leaf angles. Two groups of leaves are identified in each layer: shade and sunlit leaves, and sunlit section is divided into nine leaf angle classes. Irradiance absorption by each leaf group (sunlit and shade leaves) and also by each angle class of sunlit leaves is then calculated separately and integrated to give the whole canopy light absorption profile.

Sun-shade model initially introduced by Sinclair et al. (Sinclair et al., 1976, as cited in De Pury & Farquhar, 1997) and then applied by Norman (Norman, 1980, as cited in De Pury & Farquhar, 1997), recently improved by De Pury and Farquhar (1997). This model gives predictions of canopy photosynthesis that closely match estimations of multi layer model with far fewer calculations. Sun-shade model divides canopy into large foliage groups: sunlit foliage which receives direct beam, and shade foliage which is subject to diffuse and/or transmitted irradiation. Amount of irradiance absorbed by each of these parts is calculated as an integral of absorbed light and the corresponding leaf area fraction.

Regardless of the way one calculates the rate of irradiance absorbed by the canopy, the next step in prediction of canopy photosynthesis will be estimation of the rate of photosynthesis undertaken by each group of leaves. In big leaf model an averaged value of light intercepted by the whole canopy enters photosynthesis model to calculate entire plant  $\text{CO}_2$  assimilation rate. The method may be quite complex with multi layer model and somehow with sun-shade model as in these cases the calculations should be done in detail and more accurately for each leaf class. The performance of big leaf model in estimation of canopy photosynthesis depends in part on the accuracy by which the nitrogen distribution was

predicted in proportion to the daily irradiance. While sun-shade model gives predictions of canopy photosynthesis with best approximation to those predicted by multi layer model, the big leaf model usually shows deviations ranged from 10% to 45% (De Pury & Farquhar, 1997). Each model accompanies advantages and disadvantages, differing in the rate of accuracy and degree of complexity in calculations. Presently, computer software makes it so feasible to integrate many mathematical formulas into one distinctive program, facilitating calculations of even more complex equations.

## 5. Training systems and canopy photosynthesis

Pruning and training techniques are professional horticultural practices developed not only to control plant growth in some circumstances but also to modify plant canopy in such a way that increases the amount of light absorption. Fruit trees commonly are subject to training systems during their juvenile period when the plant canopy is being formed. Depend on the type of buds (vegetative or reproductive), abundance and method of distribution within tree crown, pruning and training practices are carefully adopted so that it ensures maximum light penetration through the canopy, and provides plants the highest growth and productivity. In an experiment with two cultivars of apple trees Mierowska et al. (2002) indicated that summer pruning enhances photosynthetic acclimation of spur leaves, previously developed under shade, by rapid increasing of the chlorophyll a/b ratio. Similarly, in *phalaenopsis*, it was shown that providing the lower shade-developed leaves with higher rates of light intensities caused increased rate of photosynthesis (Lin & Hsu, 2004). Pruning resulted in changes in light harvesting complexes of rose plants, showing that rose leaves are very plastic and acclimate rapidly to any changes in light intensity (Calatayud, et al., 2007).

Training systems alter canopies light harvesting behaviour through changing the foliage density, spatial form; the ratio of sun/shade leaves, leaf angles and finally the canopy leaf distribution pattern. There are several training systems developed for fruit trees based on the tree reproductive biology such as, central leader and modified leader particularly appropriate for pome fruits (apple, pear and quince trees) and open center specifically developed for prunes (peach, plum, and cherry trees). Recently, most greenhouse cut rose producers apply a type of training system, called arching technique recognized as an effective method to improve marketable qualities of cut flowers (Lieth & Kim, 2001; Sarkka & Rita, 1999). In this system most weak and blind shoots (shoots without flower bud) are bent toward the aisle instead of being pruned, a common practice traditionally performed before introducing bending method. This training system divides the rose canopy into two different parts: upright shoots which comprise the crop harvesting stems and bent stems which consisted of unmarketable shoots devoted to extend plant leaf area facing high solar radiation and to act as a pool to store and reserve assimilates in order to be used in future production of high quality flower shoots. It was found that  $K$  value (equation 3) for bent layer of the rose canopy is higher than the value determined for upright canopy (Gonzalez-Real, et al. 2007). Additionally, bent layer showed lower rate of photosynthesis than upright shoots (Kim et al., 2004; Gonzalez-Real et al., 2007).

In an experiment we examined effects of 5 training systems on the rate of canopy light absorption and photosynthesis of *Rosa hybrida* 'Habari' (Matloobi et al., 2009). Treatments were combinations of bending height on the mother stem and height of harvesting on the successive flower shoots: (i) T.S. 1-1: bending at the base of the primary shoot and harvesting all flowering shoots above the first bud, (ii) T.S. 3-3: bending above the third bud,

and harvesting above third bud for the first-order flowering shoot and above first bud for the following flowering shoots, (iii) T.S. 3-3-2: after bending primary shoot above third bud, the first-order flower shoot was harvested above the third bud and the second-order one above the second bud, (iv) T.S. 5-1: primary shoot was bent above fifth bud and the bearing flower shoot was harvested above first bud, (v): T.S. 5-3: primary shoot was bent above fifth bud and the bearing shoot was harvested above third bud. Leaf photosynthetic measurements have been performed for three layers of upright shoots (top, middle and bottom layer), and bent layer. Results exhibited that training system did not affect whole canopy light absorption significantly, but affected photosynthetic rate at canopy level (Table 1). This implies that photosynthetic rate at canopy level was influenced particularly by the interaction between light distribution profile through the canopy and canopy leaf area distribution rather than the

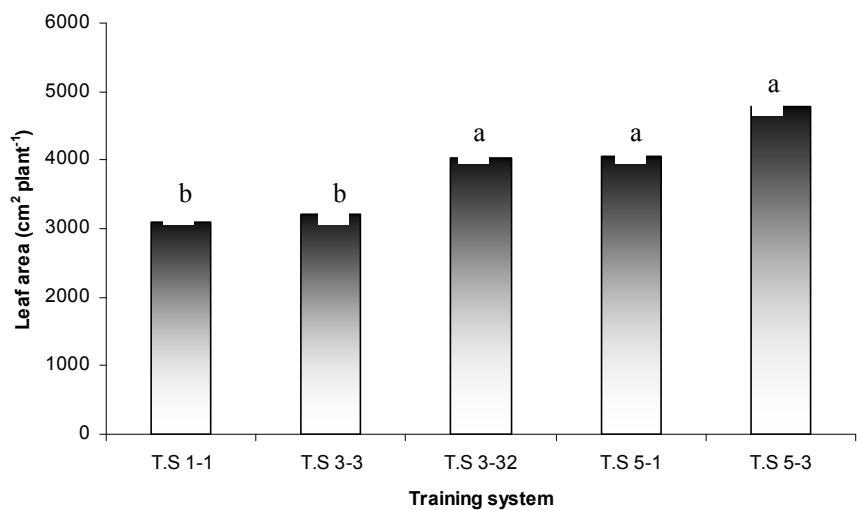


Fig. 6. Effect of different types of training system on the leaf area of *Rosa hybrida* ‘Habari’. Different letters above columns indicate significantly difference according to the Duncan’s multiple range test ( $p<0.05$ ).

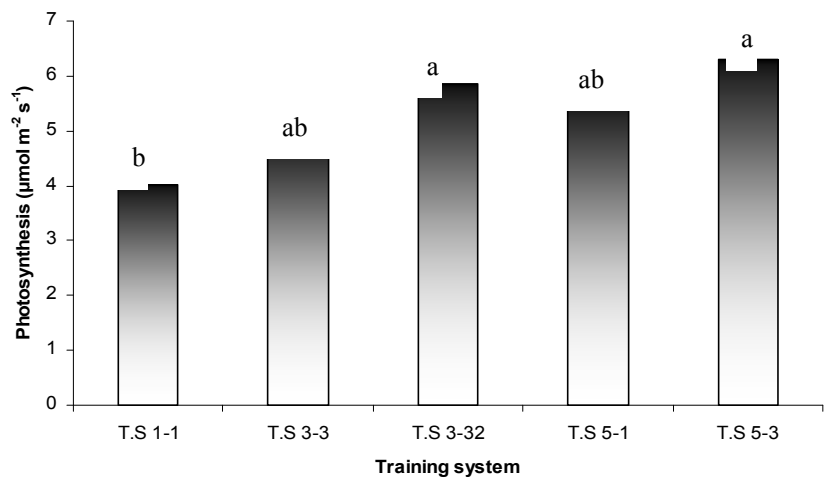


Fig. 7. Effect of different types of training system on the whole photosynthetic rate of *Rosa hybrida* ‘Habari’. Different letters above columns indicate significantly difference according to the Duncan’s multiple range test ( $p<0.05$ ).



amount of light incident on the canopy. In other words, interaction between light intensity, light quality, leaf age, leaf area and many other intrinsic factors related to the leaf photosynthetic capacity have determined the canopy entire photosynthetic rate (Fig. 6 & Fig. 7). However, it was clearly deduced that canopy training system affected plant leaf area distribution between different leaf layers and accordingly impacted the rate of photosynthesis in each leaf layer. Plants developed by T.S. 1-1 method showed the lowest rate of canopy photosynthesis because they produced much less leaf area among the other training systems (Fig. 6). Although photosynthetic rate of the bent-shoots layer per unit leaf area was lower owing to the lower incident PAR, this layer accounted for about 40% of the whole plant photosynthetic capacity as a result of increased leaf area. Increasing leaf area does not enhance canopy assimilation rate unlimitedly due to leaves mutual shading caused by clumping effect. Lower layer of the bent shoots contributes negatively to the total canopy carbohydrate balance if its leaf area exceeds an optimal range (Pien et al., 2001). As a consequence, before adopting any type of training system or pruning strategy one should consider the results of *in situ* researches and try to optimize the canopy architecture and morphology based on environmental conditions and plant physiological and phenological characteristics.

Leaf layers	Incident PAR	Photosynthesis		Leaf area
	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	$\mu\text{mol m}^{-2}\text{leaf s}^{-1}$	$\mu\text{mol m}^{-2}\text{layer s}^{-1}$	$\text{cm}^2$
Top layer	630.1 a	18.25 a	0.979 c	534.8 c
Middle layer	502.6 b	16.91 a	1.495 b	874.4 b
Bottom layer	343.6 d	10.78 b	0.747 c	664.6 c
Bent layer	411.1 c	11.90 b	2.102 a	1769.5 a

Table 1. Means comparison of the measured properties within different leaf layers of *Rosa hybrida* ‘Habari’

Training systems or pruning methods may influence canopy photosynthetic rate by altering source-sink relationship. This alteration may lead to negative feedback control of leaf photosynthesis capacity. In *citrus unshiu*, girdling and defruiting induced leaf starch accumulation and reduced photosynthesis, whereas partial defoliation induced the opposite effect (Iglesias et al., 2002). Partial defoliated apple trees have shown similar results (Zhou & Quebedeaux, 2003). Matloobi et al. (2008) indicated that in cut roses the leaf attached to the bud immediately below the harvesting place, actively contributes in assimilate supply to the new growing shoot. Photosynthetic rate of the leaf attached to the bud, above which the shoot was pruned, was more or less constant from time of harvest until the growth of axillary bud. After the bud started to grow, the photosynthetic rate began to decline sharply, showing that the leaf had been degrading photosynthesis-related enzymes and other chloroplast proteins in order to support the growing young shoot (strong sink). This reduction in carbon fixation may arise from N depletion due to remobilization of N towards the growing point. Surprisingly, removing flower bud (another strong sink) did not significantly affect carbon assimilation rate of the leaf nearest to the flower bud over one week of gas exchange measurements. This implies that sink removal might have contrasting responses regarding plant species, type of the sink organ to be removed and its spatial position in relation to the sources.

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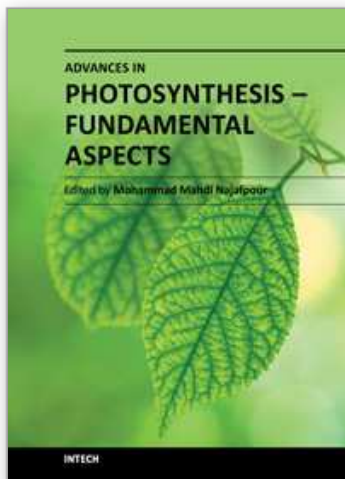
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Photosynthesis is one of the most important reactions on Earth. It is a scientific field that is the topic of many research groups. This book is aimed at providing the fundamental aspects of photosynthesis, and the results collected from different research groups. There are three sections in this book: light and photosynthesis, the path of carbon in photosynthesis, and special topics in photosynthesis. In each section important topics in the subject are discussed and (or) reviewed by experts in each book chapter.

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