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Leaf age and light intensity affect gas exchange parameters and photosynthesis within the developing canopy of field net-house-grown papaya trees

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ABSTRACT

Leaf age and light intensity dramatically affect the leaf photosynthetic capacity of the developing canopy of erect herbaceous plants. However, little is known regarding this response in papaya trees. The objective of this study was to determine how leaf age and light intensity affect the gas exchange characteristics within a developing papaya canopy by examining the distribution of maximum net CO_2 assimilation in saturated light (A_{CO_2}) and photosynthetic photo flux density (PPFD) of papaya trees cultivated in a field net-house. To measure changes in relative gas exchange capacity with leaf age, a comparison of the gas exchange parameters of individual tagged leaves and the leaf position with maximum A_{CO_2} within the developing canopy was carried out at a leaf age between 14 and 98 days in two cropping seasons (2008–2009 and 2009–2010). At or before the time of full leaf expansion (leaf age 26–36 days), the total chlorophyll concentration, relative A_{CO_2}, transpiration rate (E), stomatal conductance (g_s) and PPFD reached maximum levels. In leaves aged 26–62 days, the relative A_{CO_2} remained at above 90% of the maximum A_{CO_2} and above 60% of PPFD. As the leaves aged and gradually became over-shaded within the canopy, the relative A_{CO_2} gradually declined to 45–55% of the maximum. The degree of decline in g_s was larger than that in A_{CO_2} and E, but no significant differences were observed in C_i among the various leaf ages. Therefore, our results imply that A_{CO_2} was limited by coordinated changes in both stomatal and nonstomatal factors. To access the photosynthetic capacity and light intensity profile in the papaya canopy, we investigated the A_{CO_2} and PPFD at each leaf position within the canopy near time of harvest. The observed high extinction coefficient value (1.68) for field net-house-grown papaya at a high solar elevation indicated that the mature leaves in the top layer did not cover each other in the upper strata but effectively shaded leaves in the lower strata. The mature leaves in the upper layer of the canopy with a LAI of 0.3–1.4 $m^2\,m^{-2}$ (46% of the total leaf area of the canopy) were able to maintain high PPFD and A_{CO_2}. The study suggests that an ideal papaya canopy should be exposed to a LAI of 0.3–1.4 $m^2\,m^{-2}$ (approximately the 11th–29th leaf position) to acquire the maximum amount of PPFD and maintain photosynthetic capacity during mid-day measurements near harvest.

1. Introduction

In erect herbaceous plants, stems and new leaves are continuously formed during most of the plant's lifespan such that the lower canopy leaves, which are formed first under high photosynthetic photon flux density (PPFD), are shaded by younger leaves above, resulting in simultaneous gradients in leaf age and PPFD that generated strong interactions between age and PPFD within the canopy (Niinemets, 2007). In general, the maximum net photosynthetic rate (A_{CO_2}), transpiration rate (E) and stomata conductance (g_s) under saturated light conditions for herbaceous plants appear at or shortly before maximal leaf expansion and then decline along with leaf age (Constable and Rawson, 1980; Thomas and Turner, 1998; Xu et al., 1997). The intrinsic photosynthetic properties of individual leaves are dynamic during and after leaf development because of changes in light intensity, nutrition and leaf aging (Hikosaka, 1996; Niinemets, 2007; SassenrathCole et al., 1996; Trouwborst

Abbreviations: A_{CO_2}, maximum net CO_2 assimilation in saturated light; E, transpiration; g_s, stomatal conductance; C_i, internal CO_2 concentration; VPD, vapor pressure deficit; PPFD, photosynthetic photo flux density; LAI, leaf area index; k, extinction coefficient.

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et al., 2011). However, most studies examining photosynthesis during leaf aging have not considered the light environment for the leaves (Hikosaka et al., 1994).

Total dry matter production and, in many cases, crop yield are determined by processes integrated over the canopy, primarily those involved in light interception (Lawlor, 1995). The efficiency in transforming intercepted photosynthetic energy into biomass depends on leaf photosynthetic ability and leaf area. Leaf area index (LAI) is applied in the study of light interception and transpiration measurement to establish the basis of canopy efficiency (Faust, 1989). Therefore, understanding the LAI interaction of crops with light environmental factors is necessary to maximize yield and identify quality limiting effects on the photosynthetic capacity.

Papaya (*Carica papaya* L.) is a fast-growing herbaceous plant with a single main stem and a canopy of large palmately lobed leaves that is capable of producing two to three new leaves per week at the apex (and continual fruiting) while old leaves senesce and fall during the growing season (Paull and Duarte, 2011). Therefore, new leaves in the upper canopy cause a self-shading effect on the old leaves beneath them. The maximum A_{CO_2} in saturated light is 25–30 μmol m^{-2} s^{-1} in papaya leaves in appropriate field conditions (Campostrini and Glenn, 2007). A_{CO_2} in papaya also decreases with leaf age (Chutteang et al., 2007; Lin and Ehleringer, 1982). To the best of our knowledge, no attempt has been made to determine the interaction between the leaf age and light environment within the developing canopy of papaya trees.

In Taiwan, papaya is commercially planted in field net-houses to protect plants from aphids, the vector of the papaya ringspot virus (Sheen et al., 1998). Papaya planted in field net-houses experience approximately 20% lower light intensity and higher temperatures during the day than those in the open field (R. H. Wang, unpublished data). The high density planting system (1800–2400 plants ha^{-1}) causes most of the light to be captured in the upper strata of the canopy. The impact of the field net-house environment on leaf photosynthetic capacity needs to be accounted for but the characteristics of canopy's photosynthetic profiles still remain poorly understood.

The aim of this study was to develop an integrated model of whole-plant photosynthetic capacity responding to light intensity within the developing canopy of individual papaya trees. In these field net-house experiments, we documented the effects of leaf age and canopy light environment on the developing canopy and on the major gas exchange characteristics of papaya 'Tainung No. 2' grown in a field net-house. To measure changes in the relative gas exchange capacity that occurs with leaf age before leaf senescence, a comparison of the gas exchange parameters of individual tagged leaves at various leaf positions with a maximum A_{CO_2} within the canopy was carried out from a leaf age of 14–98 days in two cropping seasons (2008–2009 and 2009–2010). To create a profile of photosynthetic capacity and light intensity, we investigated the relationship between the cumulative LAI above each mature leaf and the A_{CO_2} and PPFD at each leaf position within the canopy.

2. Materials and methods

2.1. Plant material and experimental conditions

Experiments were conducted with 'Tainung No. 2' papaya at Kaohsiung District Agricultural Research and Extension Station in Changjhih, Pingtung (latitude 22°70′N, 120°52′E) in southern Taiwan over two cropping seasons (2008–2009 and 2009–2010). In 2008–2009 cropping season, only the trends in gas exchange characteristics with leaf age was studied. The completed investigations were evaluated in 2009–2010 cropping season. Five weeks after germination, and after the appearance of the sixth true leaf, the seedlings were transplanted to the net-house on September 30, 2008 and September 15, 2009, respectively. Originally, three seedlings were planted per plant spacing, but only one seedling was kept in the space after hermaphroditic plant was selected. The tree spacing was 2.7 m between rows and 2.0 m between plants with a north-south orientation, totaling 1850 plants ha^{-1}. Drip fertigation was applied for all plants using an installed soil water-based irrigation set. Soil water potential was maintained using tensionmeters (Model R, Irrometer Company Inc., Riverside, CA, USA) positioned at a soil depth of 30 cm with readings kept between 30 and 50 kPa. The fertilizer application rate in the experimental orchard was 14 kg ha^{-1} N (NH_4NO_3), 22.9 kg ha^{-1} P_2O_5 ($(NH_4)_3PO_4$) and 12.4 kg ha^{-1} K_2O (KNO_3) every two weeks for plants 7 months and older, at 1/3 rate for plants 1–3 months old and 1/2 rate for plants 4–6 months old. Pesticides were applied as needed to control mites and maintain good leaf health.

2.2. The changes in gas exchange characteristics and PPFD with leaf age

Eight uniform trees, approximately 4 months old, with 17 ± 2 fully mature leaves in the developing canopy were randomly selected from the experimental orchard. The first young leaf of each tree was tagged on February 7, 2009 and January 14, 2010, respectively. The tagged leaves with approximately 1–2 cm midrib, were defined as day 0 and the first leaf position. In 2009, only the leaf gas exchange of the tagged leaves were examined weekly for leaves aged 20–96 days between February 27 and May 14, 2009. The leaf gas exchange, mid-day PPFD, leaf area and the total chlorophyll concentration of the tagged leaves from each plant were measured weekly for leaves aged 14–98 days between January 28 and April 22, 2010. Measurements began 14 days after tagging, when the leaves were large enough to fit into in a 2 cm × 3 cm leaf chamber for a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, Nebraska, USA).

2.3. The distribution of A_{CO_2} and PPFD in the papaya canopy

Five plants were randomly selected to measure the A_{CO_2}, mid-day PPFD and cumulative LAI at each leaf position between the 6th and 45th position (from the youngest one) in the canopy from April 23 to April 25, 2010.

2.4. Measurements

Gas exchange measurements were taken between 08:00 and 11:00 am for the tagged leaves of each tree using a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, Nebraska, USA) with an internal red/blue LED light source (LI-6400-02B, Li-Cor, Lincoln, Nebraska, USA) set at 1400 μmol m^{-2} s^{-1}, which is above the light saturation point for papaya leaves (Marler and Mickelbart, 1998). The ambient CO_2 concentration in the cuvette was controlled at 380 μmol mol^{-1} using the LI-6400 CO_2 injection system and cylinders. The A_{CO_2} measured under these conditions represented the photosynthetic capacity at the specific leaf age or position of each leaf. Air relative humidity and temperature in the cuvette were monitored by LI-6400 devices A_{CO_2}, E, g_s and internal CO_2 concentration (C_i) were recorded. In most experiments we measured the leaf in its natural illuminated position on the plant and the mean values from the two measured areas were recorded. During the measurement period, the average air temperature inside the net-house and the vapor pressure deficit (VPD) were 26.5 ± 3.2 °C and 0.6–1.6 kPa in 2009, 25.4 ± 3.6 °C and 0.6–1.5 kPa in 2010, respectively. By simultaneously measuring the gas exchange capacity of the tagged leaf and the maximum A_{CO_2} of the fully expanded and well exposed leaf at the 13th–15th leaf position in the canopy,