Physiological Basis for Light Use Efficiency Models

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Abstract

Modeling whole canopy photosynthesis is a fundamental step in orchard modeling. Simplification of this step is desirable in order to obtain practical and effective models. Light use efficiency models are very simple models of crop productivity, which are based on the proportionality between net primary productivity (NPP) and absorbed photosynthetically active radiation (APAR). Physiological bases for this relationship have been theorized. However, in real canopies, with the varying light conditions of the field, the existance of a linear relationship between photosynthesis and intercepted light of single leaves has not been tested. In the present study the daily leaf photosynthesis was estimated from measured (i.e. not modeled) leaf photosynthetic properties and from measured leaf intercepted irradiance on both peach trees and eggplant plants, grown with either abundant or scarce nitrogen fertilization. Daily leaf photosynthesis was linearly related to daily leaf intercepted irradiance (which implies constant light use efficiency), and the slope of this relationship increased with N fertilization. This slope did not change under either sunny or overcast weather. This slope (i.e. the light use efficiency) could be calculated with good approximation from the photosynthetic properties (i.e. the photosynthetic light response curve) of top-canopy leaves and from incoming PAR, which can be obtained from weather stations. Thus, canopy photosynthesis can be estimated from canopy intercepted radiation and from the crop's light use efficiency, the latter being estimated simply from the light response curve of upper canopy leaves.

INTRODUCTION

Modeling whole canopy photosynthesis and productivity is a fundamental step in orchard modeling. Simplification of this step is desirable in order to obtain practical and effective models. A very simple model of canopy productivity is the light use efficiency model which is based on Monteith's (1972; 1977) observation that proportionality exists between net primary productivity (NPP) and intercepted solar radiation. This relationship holds for forests and natural ecosystems, but especially for crops where growth is not limited by water or nutrient shortage or by adverse climatic conditions which may decrease the light use efficiency (Monteith, 1977; Ruimy et al., 1995). Thus, for cultivated crops, canopy photosynthesis can be modeled as a linear function of absorbed photosynthetically active radiation (APAR) and the resulting slope of this relationship represents the light use efficiency (LUE or ε). The physiological bases for this linear relationship are not well understood and it seems counter-intuitive that canopy photosynthesis and APAR should be linearly related since leaf photosynthesis is curvilinearly related to light and tends to saturate. An explanation for this apparent contradiction was supplied by Haxeltine and Prentice (1996), Dewar (1996) and Dewar et al. (1998) who showed that, if leaf nitrogen content (and thus leaf photosynthetic properties) in a canopy is distributed along the light gradient in order to optimize canopy photosynthesis, then a linear relationship between photosynthesis and APAR results. This implies that all leaves in a canopy have similar LUE independent of the radiation they intercept. This explanation was derived from theoretical studies, assuming optimal nitrogen allocation in the canopy and estimating leaf irradiance based on a modeling approach which implies averaging of light in space and/or time. Real leaves, however, are never exposed to average irradiance and the radiation received by the leaves changes on a time scale, which is too rapid for the adaptation of leaf photosynthetic capacity (de Pury and Farquhar, 1999). Further, averaging of leaf light, either in space or in time, leads to overestimation of photosynthesis (Sinclair, 1976; Spitters 1986). Thus, the use of modeled (i.e. average) light and of optimal nitrogen distribution based on average light, represent simplifications that may or may not lead to correct understanding. The existance of similar LUE through canopies and thus a linear relationship between daily leaf photosynthesis and intercepted light, in real canopies with the varying light conditions of the field, has not been demonstrated.

In the present study, the daily leaf photosynthesis was estimated from measured (i.e. not modeled) leaf photosynthetic properties and from measured leaf intercepted irradiance on both peach trees and eggplant plants. The daily leaf photosynthesis was then plotted against daily leaf intercepted irradiance in order to test whether a linear relationship (which implies constant LUE) would result. In order to investigate the effect of nitrogen availability on LUE, the experiment was carried out with either abundant or scarce nitrogen fertilization. Further, the possibility of assessing LUE without the need of measuring several single leaf light interception and photosynthetic properties was also investigated.

MATERIALS AND METHODS

Peach Trees

1. Plant Material Four year old nectarine trees (*Prunus persica* cv. Fantasia) were used. The orchard was situated at the Pomology Department experimental field of the University of California, Davis, California. Trees were trained to a perpendicular V configuration (DeJong et al., 1994) and received routine horticultural care suitable for commercial fruit production including pruning, fruit thinning, harvesting, irrigation, pest control, etc. In 1994 the orchard was divided in 4 nitrogen treatments with 4 randomly distributed replications. For the present experiment 2 trees of the zero nitrogen and 2 of the 300 kg of N ha⁻¹ treatments were chosen. The zero N trees were reduced in size and had pale foliage compared to other trees but were functional and produced regularly. There were no other apparent symptoms of N deficiency.

2. Light Measurements The daily course of photosynthetically active radiation (PAR) was monitored on single leaves throughout the canopy of the two trees of each treatment with GaAsP photosensors (Hamamatsu) previously calibrated with a quantum sensor (LI-190, LI-COR Inc., Lincoln, NE, USA), monitored with a battery operated datalogger (CR21 Micrologger, Campbell Scientific Inc., Logan, Utah, USA). Data were logged every 30 seconds from 6.00 to 20.00 hour during several clear days in July 1997. All data were used without averaging. The sensors were placed on the leaf adaxial surface so they were parallel to the leaf lamina and were kept in place by the electrical wires. On each measurement day, one sensor was placed horizontally above the canopy to measure incoming PAR.

3. Gas Exchange Measurements and Leaf Parameters Gas exchange measurements were made with a portable computerized open-system IRGA (LI-6400, LI-COR. Inc., Lincoln, Nebraska., USA). A cool light source (6400-02 LED) under software control was mounted on the leaf chamber as the source of variable light. All measurements were taken setting cuvette temperature at 27° C and relative humidity at 50 %.

Light saturated net photosynthesis (A_{max}) was measured on all sampled leaves the day after light measurements. In addition, photosynthetic light response curves were measured on 8 leaves (4 on each tree) ranging from inner canopy to outer canopy leaves on each of the 2 N treatments. From these 16 curves, a linear regression between dark respiration (R_d) and A_{max} was calculated as well as the values for the curvature factor and

the apparent quantum yield that best fitted all curves (non-rectangular hyperbolas: Thornley, 1976). With this information, all parameters for the light response curve were estimated from the measured A_{max} of each leaf. Thus the estimated light curve of each leaf was obtained and used with the daily light data of the correspondent leaf to estimate the daily leaf carbon gain. No averaging of light data, either in space or in time, was done, but each single value of light was used to estimate the correspondent photosynthesis.

Eggplant

Eggplants (*Solanum melongena* L. cv. Cima di Viola) were grown at the experimental field of the Research Institute for Vegetable Crops, Pontecagnano (SA) Italy, at two different rates of N fertilization corresponding to a total of 50 (N50) and 355 (N355) kg of N ha⁻¹ in a randomized complete block with three replicates (140 plants per replicate). Other than for N fertilization, plant were grown as in a commercial crop.

Leaf light and gas exchange measurement were carried out as for peach trees with the following differences. Light data were logged every 60 seconds. The light measurements were taken during the end of July and August, 1997 (ten sampled days, including clear, partially cloudy and cloudy days). Light curve parameters were obtained from 12 measured light curves. Gas exchange was measured with the LI-COR LI-6200 using sun light and neutral shade cloth for the light curves.

RESULTS

Daily leaf photosynthesis was linearly related to daily leaf light interception (Fig. 1). The slope of this relationship (i.e. the LUE) increased with N fertilization in both crops and was higher for eggplant compared to peach trees.

When daily photosynthesis was calculated from the daily average light rather than form the minute by minute light data, the slope of the regressions increased by about 20-25% (data not shown).

Figure 2 shows the regression between daily leaf photosynthesis and daily leaf light interception calculated for 11 leaves on a cloudy day and a subsequent clear day (the light sensors were left for the 2 subsequent days on the same leaves). The slope of the regression was similar between the two days, indicating that light use efficiency was constant under either clear or overcast conditions.

To investigate the possibility of calculating the slope of the relationship between daily leaf photosynthesis and daily leaf light interception (i.e. LUE) without the need of measuring many single leaf light interception and photosynthetic light response curves, LUE was estimated from minute by minute incoming PAR above the canopy (instead of measured leaf light interception) using the light response curve of the leaf with the highest A_{max} for each data set (i.e. high N and low N) of eggplant data. The incoming PAR from the two (low N) and three (high N) days with the highest daily incoming light was used. The linear regression thus obtained (Fig. 3), imposing a zero intercept, was virtually identical to that obtained from single leaf data, suggesting that LUE could be calculated from incoming PAR and the photosynthetic properties of top canopy leaves.

DISCUSSION

The linear relationship found between daily leaf net photosynthesis and intercepted irradiance, both in peach trees and in eggplant (Fig. 1), supports previous findings showing that, especially in cultivated crops where water and nutrient supply does not limit growth, light use efficiency tends to be constant. This provides the basis for the application of the light use efficiency model in such crops. While Ruimy et al. (1994) found that LUE is variable between natural vegetation types, Monteith (1977) showed that LUE is constant over a wide range of crops and climatic conditions in Britain. In the present data the slope of the linear relationship between daily leaf net photosynthesis and intercepted irradiance increased by about 35% from peach trees to eggplant suggesting that there is large variability in LUE between crops. Thus, in order to use LUE models, the LUE of single crops needs to be assessed.

The slope of the linear relationship between daily leaf net photosynthesis and intercepted irradiance also increased with N fertilization on both species as predicted from Ruimy et al. (1995). Dewar (1996, 1998) speculated that limiting N supply decreases canopy photosynthesis mainly through limiting leaf area (and thus light interception) rather than by diminishing LUE. The present data suggest that limiting N supply may also reduce LUE and thus LUE models may need to model changes in LUE with N nutrition.

The linear relationship found between daily leaf net photosynthesis and intercepted irradiance, using actual field data of leaf light interception and photosynthetic properties, appears to agree with the Dewar (1996, 1998) and Haxeltine and Prentice (1996) explanation for the linear relationship between canopy photosynthesis and canopy intercepted light. However, their interpretation is based on the assumption that leaves are exposed to an average (in space and/or time) light level and assuming optimal N allocation in the canopy based on this average light. This explanation implies that in the short term, before any reallocation of N (thus photosynthetic properties) may occur, LUE should be greater at lower irradiance, reflecting the curvature of the single leaf photosynthetic response curve. The present data do not support this interpretation since the slope of the regression between daily leaf net photosynthesis and intercepted irradiance was similar for both a clear-sky and an overcast day (Fig. 2). This contrast is probably related to the fact that real leaves are never exposed to average irradiance and the radiation received by the leaves changes on a time scale, which is too rapid for the adaptation of leaf photosynthetic capacity (de Pury and Farquhar, 1999). Thus, a better understanding of the linearity between photosynthesis and intercepted light may derive from studying the actual dynamics of light interception on single leaves of field canopies.

Another limitation of modeling approaches based on averaging irradiance is the overestimation of canopy photosynthesis (Sinclair, 1976; Spitters 1986). In the present data, using average daily light overestimated the slope of the regression between daily leaf net photosynthesis and intercepted irradiance by about 20-25%. This might also limit the understanding that can derive from modeling approaches based on the assumption of average irradiance.

Using the incoming PAR of the sunniest days and the photosynthetic light response curve of a top canopy leaf, and assuming a zero intercept, allowed calculating of a regression between daily leaf net photosynthesis and intercepted irradiance which was nearly identical to that calculated using all data (Fig. 3). This can be explained considering that if all leaves in a canopy (i.e. from bottom-canopy to top-canopy) have the same LUE (linear relationship between daily leaf net photosynthesis with approximately zero intercept), also an hypothetical leaf, placed at the very top of the canopy and exposed to incoming PAR, should have similar LUE. This assumption allowed to calculate the LUE from incoming PAR and from the photosynthetic properties of a single top-canopy leaf. Since incoming PAR can be obtained from weather stations, this allows to calculate LUE of a given crop from the photosynthetic properties of well exposed leaves, without the need to measure actual leaf light interception. Further, if the light intercepted by the crop can be obtained from remote sensing, then the whole canopy photosynthesis could be calculated with a LUE model based on the photosynthetic properties of leaves from the top of the canopy.

CONCLUSIONS

The present data suggest that linearity between daily leaf photosynthesis and daily leaf intercepted light actually occurs in field conditions as predicted by modeling. This provides the basis for the use of the LUE models. However, our results show that models need to account for the changes in the LUE with both crop and N availability. Further, due to the limitations in some of the assumptions of most models (i.e. averaging light in space and/or time, and assuming optimal canopy N distribution based on average light) it appears that a better understanding of the physiological bases for the constancy of LUE within canopies may need to be achieved by studying actual dynamics of light interception under field conditions.

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Figures



Fig. 1. Relationship between daily leaf net photosynthesis (Daily A_n) and daily leaf light interception (Daily PAR) on eggplant and peach trees grown with high (solid line) or low (broken line) N fertilization.



Figure 2. Relationship between daily leaf net photosynthesis (Daily A_n) and daily leaf light interception (Daily PAR) on eggplant for a cloudy and a following clear day.



Figure 3. Relationship between daily leaf net photosynthesis (Daily A_n) and daily leaf light interception (Daily PAR), calculated either on all data (closed circles and solid lines) or using the photosynthetic response curve of a top canopy leaf and the incoming PAR of very sunny days (open circles and dotted lines), for eggplants grown with either low or high nitrogen fertilization. The equations on the left of each panel refer to the fit for all data; equations on the right refer to the fit obtained with one leaf and incoming PAR.