Vertical profile of photosynthetic CO$_2$ response within rice canopy

Y.P. LV$^+$ and Y. PAN

College of Hydraulic Science and Engineering, Yangzhou University, 225009 Yangzhou, Jiangsu, China

Abstract

Leaf-specific Farquhar–von Caemmerer–Berry (FvCB) model was fitted to characterize the vertical profile of photosynthetic CO$_2$ response within rice canopy. Leaf-position-specific and canopy average FvCB models were fitted to study a suitable leaf representing photosynthetic parameters at the canopy scale. The results showed that leaf photosynthesis was limited by Rubisco activity or ribulose-1,5-bisphosphate regeneration under field conditions. The maximum rate of carboxylation, maximum rate of electron transport, rate of triose phosphates utilization, and light respiration rate in the FvCB model reached the highest values for the top second leaf and then decreased, while the mesophyll diffusion conductance kept decreased in downward leaves. The integrated photosynthetic CO$_2$-response curves for the top fourth and fifth leaves were appropriate for estimating parameters in the FvCB model at the canopy scale.

Keywords: critical CO$_2$ concentration; leaf position; parameters in FvCB model.

Introduction

The Farquhar–von Caemmerer–Berry (FvCB) biochemical photosynthetic model has been the heart of estimating crop CO$_2$ assimilation (Alagarswamy et al. 2006, Kattge and Knorr 2007, Zhang et al. 2012, Busch et al. 2018). Determining the parameters in the FvCB model, namely the maximum rate of carboxylation $V_{\text{cmax}}$, maximum rate of electron transport $J_{\text{max}}$, rate of triose phosphates utilization $V_{\text{p}}$, and light respiration rate $R_l$, is essential to depict the photosynthesis trait by some ecosystem models (Chen et al. 1999, Sharkey et al. 2007, Patrick et al. 2009, Walker et al. 2014). Other than reverse calculation (Zhang et al. 2014, 2018), fitting leaf photosynthetic CO$_2$-response ($P_N/C_i$) curves based on the FvCB model is frequently used to estimate parameters in the FvCB model, which offers a mechanistic way for simulating the photosynthesis from cellular to global scale.

Highlights

- The $V_{\text{cmax}}, J_{\text{max}}, V_{\text{p}}$, and $R_l$ reached the highest values for the top second leaf
- The $g_m$ kept decreased in downward leaves
- Top-4th or Top-5th was appropriate for estimating canopy FvCB parameters

Abbreviations: $C_a$ – ambient CO$_2$ concentration; $C_i$ – critical ambient CO$_2$ concentration for photosynthetic CO$_2$-response curve at which the transition between Rubisco- and RuBP-limited photosynthesis occurs; $C_{i1}$ – critical ambient CO$_2$ concentration for photosynthetic CO$_2$-response curve at which the transition between RuBP- and TPU-limited photosynthesis occurs; $C_{i2}$ – critical intercellular CO$_2$ concentration for photosynthetic CO$_2$-response curve at which the transition between Rubisco- and RuBP-limited photosynthesis occurs; $C_{i1}$ – critical intercellular CO$_2$ concentration for photosynthetic CO$_2$-response curve at which the transition between RuBP- and TPU-limited photosynthesis occurs; $F_{\text{vCB}}$ – Farquhar–von Caemmerer–Berry; $g_m$ – mesophyll diffusion conductance; $J_{\text{max}}$ – maximum rate of electron transport; $P_i$ – net photosynthetic rates limited by Rubisco activity; $P_j$ – net photosynthetic rates limited by RuBP regeneration; $P_N$ – net photosynthetic rates; $P_{N1}$ – critical net photosynthetic rate for photosynthetic CO$_2$-response curve at which the transition between Rubisco- and RuBP-limited photosynthesis occurs; $P_{N2}$ – critical net photosynthetic rate for photosynthetic CO$_2$-response curve at which the transition between RuBP- and TPU-limited photosynthesis occurs; $P_{N/C_i}$ – photosynthetic CO$_2$ response; $P_{\text{p}}$ – net photosynthetic rates limited by triose phosphates utilization; $R_l$ – light respiration rate; RuBP – ribulose-1,5-bisphosphate; Top-1st, Top-2nd, Top-3rd, Top-4th, Top-5th, Top-6th, and Top-7th – the top first, second, third, fourth, fifth, sixth, seventh leaf; TPU – triose phosphates utilization; $V_{\text{cmax}}$ – the maximum rate of carboxylation; $V_{\text{p}}$ – rate of triose phosphates utilization.

Conflict of interest: The authors declare that they have no conflict of interest.
levels (de Pury and Faroughar 1997, Bernacchi et al. 2013, Wu et al. 2016, Ren et al. 2017). Leaf photosynthesis is influenced by various leaf attributes, such as leaf chemical elements, specific leaf mass, leaf age, and so on (Peterson et al. 2010, Peri et al. 2011, Wang et al. 2020). Consequently, the photosynthetic CO2 response, as well as parameters in the FvCB model, varies greatly among leaves, which has been reported for different crops in different regions (Zhou et al. 2007, Yin et al. 2009, Qian et al. 2012). Moreover, leaf position affects considerably leaf photosynthesis, as the leaves differ in leaf ages and light acclimation within crop canopy (Suzuki et al. 2009, Niinemets 2016, Townsend et al. 2018). For example, the measured leaf net photosynthetic rates (Pn) at a certain light intensity for wheat decreased significantly in a sequence of the top first, second, third leaf (Li et al. 2013). The light-saturated leaf Pn for rice increased to the maximum when a leaf was fully expanded, and then decreased during leaf ontogeny (the upper leaves are physiologically younger than the lower ones), or declined in downward leaves within the canopy (Yin et al. 2004, Xu et al. 2019, Li et al. 2020). No results were discussing the difference in Pn/C curves and parameters in the FvCB model among leaves at different positions and among different crops. All models trusted parameters in FvCB model homogeneously for all rice leaves, that assumed the variation in the Pn was determined by the distribution of incident irradiance and leaf nitrogen within the crop canopy (Kim and Lieth 2003, Greer and Weedon 2013, Wang et al. 2021). Insight into the vertical profile of leaf photosynthesis is necessary as well as the parameters in the FvCB model, within the canopy, is critical to understand the vertical characteristic of leaf photosynthesis within crop canopy, which provide basic information to either determine the optimal leaf representing canopy photosynthetic parameters, or upscale photosynthesis or photosynthetic parameter from leaf to canopy by considering detailed three-dimensional canopy structure model (Wang et al. 2006, Kim et al. 2016, Retzke et al. 2018).

In the current research, each measured photosynthetic CO2 response for leaves at different positions was fitted to reveal the vertical profiles of critical CO2 concentration (at which limited factors of leaf photosynthesis shifted) and parameters in the FvCB model within the rice canopy. Subsequently, leaf-position-specific and canopy average FvCB models were fitted respectively based on measured Pn/C curves at each specific position and all Pn/C curves within the rice canopy. Finally, the suitable leaf position, at which all the parameters in the FvCB model of rice canopy, was determined by both analyzing the relationship between parameters of leaf-position-specific and canopy average FvCB models and evaluating the performance of canopy average FvCB model in estimating Pn/C curves for leaves at different positions.

Materials and methods

Field measurement: The rice (variety of Japonica rice N1646) was transplanted (13 + 25 cm hill spacing) on 1 July, and harvested on 26 October in 2017 at Kunshan, Jiangsu, East China (31°15′15′′N, 120°57′43′′E). Primary shoots (30 days after emergence of the top first leaf) and then decreased during leaf ontogeny (the top first, second, third, fourth, fifth, sixth, seventh leaf, namely, Top-1st, Top-2nd, Top-3rd, Top-4th, Top-5th, Top-6th, and Top-7th) was measured at 14 ambient CO2 concentrations (C) in the order of 400, 300, 200, 100, 50, 400, 500, 600, 800, 1000; 1300; 1500; and 1800 μmol mol−1, by a portable photosynthesis system (LI-6000 LI-COR, Lincoln, NE, USA) at booting stage. In total, six Pn/C curves were measured for leaves at each specific position. For each Pn/C curve, photosynthetic photon flux density (PPFD), chamber temperature, and relative humidity were set at 1,600 μmol m−2 s−1, 30°C, and 70%, respectively, and such conditions were maintained for 15 min at C0 of 400 μmol mol−1 for acclimation and stabilization of leaf photosynthesis before measurements were logged; then leaf Pn was logged automatically at 120-s intervals at each C0 concentration.

FvCB model: The Pn can be estimated according to the steady-state photosynthesis model (Faroughar et al. 1980):

\[ P_n = \min \left( P_{n, max}, \frac{P_{a}}{C_i + K_c} \right) \times R \]  

where \( P_{n, max} \) is the maximum羧基化 activity of Rubisco, \( R \) [μmol m−2 s−1] is the photosynthetic rate at any given chloroplastic CO2 concentration \( C_c \) [μmol mol−1]; \( P_{n, max} \) and \( P_{a} \) [μmol m−2 s−1] are the Pn limited by Rubisco activity, ribulose-1,5-bisphosphate (RuBP) regeneration, and triose-phosphates utilization respectively. \( C_c \) and \( C_i \) [μmol mol−1] represent a scaling constant and activation energy, respectively.

\[ \Gamma = \frac{C_i}{C_c + 1} \times \frac{O}{K_o} \]  

where \( C_i \) [μmol mol−1] is the hypotetical CO2-compensation point of photosynthesis in the absence of RuBP and \( K_o \) [μmol mol−1] is the Michaelis–Menten constant for CO2 and oxygen.

The parameters of \( K_c, K_o, L, \) and \( R \) at a chamber temperature of 30°C were determined by analyzing the relationship between parameters of leaf-position-specific and canopy average FvCB model, namely \( P_{n, max}, \Gamma, \) and \( \Gamma \). which was used to reveal vertical profiles of these parameters within the rice canopy. Moreover as well as \( \Gamma \), an intercellular CO2 concentration and \( C_c \) was determined to reveal the factors that limited photosynthesis for leaves at different positions under various CO2 concentrations. Forth, all leaves on the primary shoot and on the first leaf represented the parameters in the FvCB model at which limited factors of leaf photosynthesis shifted, and parameters in the FvCB model, as well as \( \Gamma \) and \( \Gamma \), were fitted respectively based on six measured Pn/C curves at each specific position and all Pn/C curves within rice canopy. Finally, the photosynthetic electron transport was calculated using the relationship among parameters in leaf-position-specific and canopy average FvCB model and evaluating the performance of canopy average FvCB model in estimating Pn/C curves for leaves at different positions.

Statistical analysis: The one-way analysis of variance (ANOVA) and least significant difference multiple comparison tests were used to reveal the differences in \( C_c, C_i \) and \( P_{n, max} \) between leaves at different positions. The performance of leaf-specific, leaf-position-specific, and canopy average FvCB models was evaluated by average absolute error AE and the root mean square error RMSE (Eq. 9, 9):

\[ AE = \frac{1}{n} \sum_{i=1}^{n} \left| P_{n, est} - P_{n, obs} \right| \]  

\[ RMSE = \sqrt{ \frac{1}{n} \sum_{i=1}^{n} \left( P_{n, est} - P_{n, obs} \right)^2} \]  

where \( P_{n, est} \) and \( P_{n, obs} \) are the Pn estimated by the FvCB model and the corresponding measured value. \( n \) is the total number of Pn data.

Results

Measured photosynthetic response to intercellular CO2 concentration: These Pn/C curves were similar among leaves at different positions and could be described as three phases (Fig. 2). As the \( C_c \) increased from its minimum concentration, the \( dP_{n}/dC_c \) was high and constant (Rubisco-limited stage), then there was an inflection to a lower \( dP_{n}/dC_c \), that gradually approached zero (RubBP-limited stage). Finally, a further increase in \( C_c \) resulted in another transition to a plateau (TPU-limited stage). Furthermore, leaf Pn/C curves were quite different from each other between leaves at various positions. Generally, the difference in \( P_{n, max} \) at low \( C_c \) was considerably higher than that of the Top-1st leaf, however, it decreased with a lowering leaf position, and the standard deviation of mean \( P_{n, max} \) for Top-1st and Top-7th was considerably higher than that for leaves at the other positions. Especially, the maximum \( P_{n, max} \) of the Top-2nd was 36.78 μmol m−2 s−1, which was 2.76 times the maximum \( P_{n, max} \) of the Top-7th leaf.

Fig. 1. Fitted response of net photosynthetic rate \( P_n \) for rice leaves to intercellular CO2 concentration \( C_c \) based on the FvCB model. The \( C_c, \Gamma, \) and \( \Gamma \) were respectively the critical \( C_c \) and \( \Gamma \), at which the transition from Rubisco- to RubBP-limited and from RubBP- to TPU-limited photosynthesis occurred.
Critical ambient and intercellular CO₂ concentration: The Cᵣ was related linearly with the Cᵣ for leaves at each specific position and the ratio of Cᵣ: Cᵣ(i) decreased to the minimum of 0.624 for the Top-3rd leaf and then increased to the maximum of 0.849 for the Top-7th leaf with downward leaf (Table 1). The three phases of each P/Vc curve were fitted respectively based on Eq. 2, Eq. 4, and Eq. 6 in the FvCB model. The model performed well in describing P/Vc curves, with high R² (range from 0.989 to 1.000) and low errors (RMSE and AE) ranged from 0.060 to 1.180 μmol m⁻² s⁻¹ and from 0.041 to 0.781 μmol m⁻² s⁻¹, respectively. There were differences in Cᵣ, Cᵣ(i), Pᵣ, and Cᵣ(i), Pᵣ between leaves at various positions (Table 1). The Cᵣ for leaves from the Top-2nd to the Top-6th differed slightly (ranging from 345.9 to 399.8 μmol m⁻²) and were significantly higher than the Top-1st and Top-7th leaves (270.8 and 264.8 μmol m⁻², respectively). The Cᵣ and Pᵣ reached the maximum for the Top-3rd and Top-2nd leaf (610.8 μmol m⁻² and 25.9 μmol m⁻² s⁻¹), respectively, and then decreased to the minimum for the Top-1st leaf (311.3 μmol m⁻² and 6.4 μmol m⁻² s⁻¹) with lowering leaf position. The Cᵣ, Cᵣ(i) varied in a wide range of 630.0–988.6 μmol m⁻², 884.6–1291.4 μmol m⁻², 203.3–367.3 μmol m⁻² s⁻¹ for the leaves from the Top-1st to the Top-6th, and the TPU limitation did not occur for the Top-7th leaf. The Cᵣ(i) and Cᵣ increased with lowering leaf position, while the Pᵣ(i) and Pᵣ decreased with lowering leaf position.

Photosynthetic parameters in the FvCB model: The FvCB model performed well in modeling all individual P/Vc curves, and the parameters of Fᵥ, Vᵥ, Vᵥ, and gₑ were considerably different between leaves at various positions (Fig. 3). The Fᵥ, Vᵥ, Vᵥ, and gₑ reached the maximum (204.8, 244.3, 14.0, and 5.5 μmol m⁻² s⁻¹, respectively) for the Top-2nd to Top-3rd leaf, which were significantly higher than that for the Top-1st leaf, and then considerably decreased to the minimum (67.1, 70.1, 7.4, and 1.6 μmol m⁻² s⁻¹, respectively) for the Top-7th leaf with lowering leaf position. The g₀ of 0.3231 μmol m⁻² s⁻¹ for the Top-1st leaf was the highest, and the gₑ for the Top-2nd to Top-4th leaf changed insignificantly with the average of 0.2186 μmol m⁻² s⁻¹ was significantly higher than that for the Top-5th to Top-7th leaf (changed insignificantly with the average of 0.1297 μmol m⁻² s⁻¹) with rice canopy. Leaf-position-specific and canopy average FvCB models: The leaf-position-specific FvCB model fitted respectively for leaves at each specific position and canopy. The parameters of Fᵥ, Vᵥ, Vᵥ, and gₑ varied in a wide range of 57.1–218.6 μmol m⁻², 68.5–241.9 μmol m⁻² s⁻¹, 6.4–15.2 μmol m⁻² s⁻¹, 0.1344–0.3270 mol m⁻² s⁻¹ for the leaf-position-specific FvCB model, and were 157.7 μmol m⁻² s⁻¹, 167.3 μmol m⁻² s⁻¹, 9.7 μmol m⁻² s⁻¹, 0.1347 mmol m⁻² s⁻¹, and 3.4 μmol m⁻² s⁻¹ for the canopy-average FvCB model (Fig. 2). Generally, the parameters in the FvCB model of the Top-4th or Top-5th were near to these parameters in the canopy-average FvCB model, which indicated that the Top-4th or Top-5th leaf represented the photosynthetic parameters of rice canopy. The leaf-position-specific FvCB model performed much better than the canopy-average FvCB model in estimating leaf Pᵣ (Fig. 4). For leaves at different positions, the estimated Pᵣ based on leaf-position-specific FvCB model accounted for 97.8–99.9% of measured Pᵣ at the Top-1st leaf, and then decreased with lowering leaf position.

Table 1. The linear relationship of intercellular CO₂ concentration Cᵣ with ambient CO₂ concentration Cᵣ and the critical Cᵣ and net photosynthetic rate Pᵣ at which the transition from Rubisco- to RuBP-limited (Cᵣ, Cᵣ(i), Pᵣ, respectively) photosynthesis occurred for leaves at different positions. Top-1st, Top-2nd, Top-3rd, Top-4th, Top-5th, Top-6th, and Top-7th represent the top first to the top seventh leaf, respectively. Different letters represent significant difference in Cᵣ, Cᵣ(i), Pᵣ, and AE of the leaf-position-specific FvCB model between leaves at different positions at P<0.05.

<table>
<thead>
<tr>
<th>Leaf position</th>
<th>Cᵣ (μmol m⁻²)</th>
<th>Cᵣ(i)</th>
<th>Pᵣ (μmol m⁻²)</th>
<th>Cᵣ(i)</th>
<th>Pᵣ (μmol m⁻²)</th>
<th>Pᵣ (μmol m⁻² s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top-1st</td>
<td>0.7103</td>
<td>0.991</td>
<td>270.8 ± 29.8</td>
<td>378.5 ± 41.6</td>
<td>17.8 ± 3.9</td>
<td>660.0 ± 137.4</td>
</tr>
<tr>
<td>Top-2nd</td>
<td>0.6356</td>
<td>0.991</td>
<td>379.5 ± 95.3</td>
<td>94.8 ± 29.5</td>
<td>25.9 ± 2.0</td>
<td>716.7 ± 71.5</td>
</tr>
<tr>
<td>Top-3rd</td>
<td>0.6244</td>
<td>0.993</td>
<td>382.3 ± 73.7</td>
<td>610.8 ± 117.8</td>
<td>23.9 ± 4.1</td>
<td>754.5 ± 76.5</td>
</tr>
<tr>
<td>Top-4th</td>
<td>0.6468</td>
<td>0.991</td>
<td>399.8 ± 40.9</td>
<td>596.8 ± 73.2</td>
<td>21.1 ± 3.1</td>
<td>655.2 ± 91.3</td>
</tr>
<tr>
<td>Top-5th</td>
<td>0.7145</td>
<td>0.991</td>
<td>463.7 ± 73.2</td>
<td>945.4 ± 92.5</td>
<td>13.8 ± 2.3</td>
<td>1291 ± 136.4</td>
</tr>
<tr>
<td>Top-6th</td>
<td>0.8093</td>
<td>0.996</td>
<td>557.3 ± 21.0</td>
<td>441.0 ± 25.9</td>
<td>12.2 ± 1.3</td>
<td>988.6 ± 9.1</td>
</tr>
<tr>
<td>Top-7th</td>
<td>0.8459</td>
<td>0.996</td>
<td>264.8 ± 63.3</td>
<td>311.3 ± 74.4</td>
<td>6.4 ± 2.6</td>
<td>.</td>
</tr>
</tbody>
</table>
The vertical ratios of $J_{\text{Top-1st}}$ to $V_{\text{an}}$ agreed with the increasing research, the relationship between $J_{\text{Top-1st}}$ and $V_{\text{an}}$ varied with changed leaf attributes (Song et al., 2021). Moreover, the variation in ratios of $J_{\text{Top-1st}}$ to $V_{\text{an}}$ was also consistent with the $C_i$ (Table 1), as the increase in the ratios increased as leaf nitrogen concentration at which the photosynthetic rate was co-dominated by carboxylation and regeneration of RuBP (Ondoa et al., 2005).

The decreased $g_{\text{iso}}$ with lowering leaf position was similar as well as decreased $g_{\text{iso}}$ with leaf age (Flexas et al., 2008), while it was slightly different from positively correlated $g_{\text{iso}}$ with leaf nitrogen content (Yamani et al., 2011). The vertical profiles of parameters in the FvCB model provided important evidence that foliage physiological characteristics varied greatly within crop canopy. Coupling this information with the vertical distribution of leaf supply attributes, microclimate, etc., within crop canopy will offer a theoretical method for upsizing leaf supply parameters to their parameters canopy scale.

References


Gong X.W., Li J., Ma H.C. et al.: Photosynthetic characteristics, microclimate, and canopy average FvCB model. Top-1st, Top-2nd, Top-3rd, Top-4th, Top-5th, Top-6th, and Top-7th represent the top first to the top seventh leaf, respectively, and is the total number of $N_{\text{Mea}}$ data.

Discussion

The $P_{\text{iso}}$ initially increased linearly with the increase in $C_{i}$, then slowly up to the maximum, and kept at a steady state (Fig. 2), while the consistency of $V_{\text{an}}$ (Fig. 3A) with $P_{\text{iso}}$ was unremarkable under low CO2 concentration during the Rubisco-limited stage (Fig. 2), as the $P_{\text{iso}}$ was mainly affected by mitochondrial respiration. For $V_{\text{an}}$, $J_{\text{iso}}$, and $F_{\text{i}}$, the variation in leaf nitrogen status might be an important trait in interpreting their profile within the rice canopy (Yamani et al., 2011). The potential photosynthetic capacity of rice leaf was highly related to leaf nitrogen content (Xu et al., 2014, Yang et al., 2016), and $F_{\text{iso}}$–$V_{\text{an}}$–$J_{\text{iso}}$ marked increased with an increasing leaf nitrogen content (Nakano et al., 1997, Yin et al., 2009, Gu et al. 2012). Moreover, the leaf nitrogen content was low for the upper new-emerged and unexpanded leaf and usually decreased from the top to the bottom of rice canopy for the fully expanded leaf (Yang et al., 2014, Okami et al., 2016), which indicated the patterns of $V_{\text{an}}$–$J_{\text{iso}}$ and $F_{\text{i}}$ in Fig. 3D–C. Furthermore, the $V_{\text{an}}$ was positively related to both the content and activity of RuBP (Galimbas et al., 2013) and the $J_{\text{iso}}$ (Chen et al., 1999), Rubisco content and activity in rice with leaf expanding and declined with leaf senescence (Suetsugu et al., 2008), Wang et al., 2008, which also indicated the patterns of $V_{\text{an}}$ and $J_{\text{iso}}$ in Fig. 3D, B as new rice leaves emerged at the upper canopy.

The ratios of $J_{\text{Top-1st}}$ to $V_{\text{Top-1st}}$ were 1.05, 1.19, 1.18, 1.22, 1.07, 1.10, and 1.04 for Top-1st, Top-2nd, Top-3rd, Top-4th, Top-5th, Top-6th, and Top-7th leaves, respectively, and $J_{\text{Top-1st}}$ was usually calculated from the model-specific $V_{\text{an}}$ input with a predetermined and constant ratio of $J_{\text{Top-1st}}$ to $V_{\text{Top-1st}}$ (Gutierrez et al., 2010, Rogers et al. 2017). While the varied ratios of $J_{\text{Top-1st}}$ to $V_{\text{Top-1st}}$ agreed with the increasing research, the relationship between $J_{\text{Top-1st}}$ and $V_{\text{Top-1st}}$ varied with changed leaf attributes (Song et al., 2021). Moreover, the variation in ratios of $J_{\text{Top-1st}}$ to $V_{\text{Top-1st}}$ was also consistent with the $C_{i}$ (Table 1), as the increase in the ratios increased as leaf nitrogen concentration at which the photosynthetic rate was co-dominated by carboxylation and regeneration of RuBP (Ondoa et al., 2005).

The decreased $g_{\text{iso}}$ with lowering leaf position was similar with decreased $g_{\text{iso}}$ with leaf age (Flexas et al., 2008), while it was slightly different from positively correlated $g_{\text{iso}}$ with leaf nitrogen content (Yamani et al., 2011). The vertical profiles of parameters in the FvCB model provided important evidence that foliage physiological characteristics varied greatly within crop canopy. Coupling this information with the vertical distribution of leaf supply attributes, microclimate, etc., within crop canopy will offer a theoretical method for upsizing leaf supply parameters to their parameters canopy scale.


