ABSTRACT

Measurement and Modeling of Radiation and Water Fluxes in Plantation Forests

by

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Abstract

Projecting the effects of climate change on the global water and carbon cycles requires a combination of experiments and modeling. The experiments can provide insights and parameters to improve models and data to tests model performance. Duke’s Free-Air CO2 Enrichment (FACE) experiment is the longest running experiment on the effect of increasing atmospheric CO2 concentration and N amendment (in lieu of atmospheric deposition). Previous studies in our lab developed a hybrid carbon balance model, the so called Canopy Conductance Constrained Carbon Assimilation (4C-A) model, a research tool composed of three major submodels: (1) a 1-D radiative transfer scheme to estimate the vertical distribution of light quantity and intensity on leaf surfaces throughout the canopy, (2) a stomatal conductance model that estimate the vertical distribution of stomatal conductance subject to a constraint of sap flux-scaled mean canopy stomatal conductance, and (3) an empirical model utilizing the outputs from the first two to estimate the biochemical components of photosynthesis. Combining all, allowed estimation of photosynthesis at a range of spatial and temporal scales (Schäfer et al. 2003). The mean conductance is a critical input, requiring independent verification through a closure of the forest hydrological budget. In my dissertation I evaluated the three parts of the model based on field measurement and sensitivity analysis. I found: (1) sap flux-scaled transpiration, from
which mean conductance is calculated, was accurately estimated as evidenced by a closure of the budget to within ±3.6% of precipitation on average. [Note: under elevated CO₂, more foliage is produced, increasing the thickness of the litter layer and reducing overland flow and increasing soil moisture. Higher leaf area and thicker litter layer result in a greater evapotranspiration, mostly due to increased canopy interception and litter evaporation, thus reducing water yield.] (2) The inputs for the light calculation should include both shoot and tree level clumping to generate correct total canopy light absorption and light distribution down the canopy. And (3) 4C-A estimates of carbon assimilation provided enough carbon to support net primary production and respiration, and correctly predicted the depth in the in which branches die due to a negative carbon balance (i.e. photosynthesis < respiration).

Based on these results, the input-intensive 4C-A model can be used to generate accurate estimates of photosynthesis to assess the capacity of simpler, more applied growth and carbon cycling models to accurately estimate gross primary production.
Dedication

This thesis is dedicated to my family, friends and collaborators who supported me physically and mentally.
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Chapter 1. Introduction

Quantifying the exchanges of carbon, water and energy between the biosphere and atmosphere is a necessary step in addressing many current questions and in predicting future processes ranging from dynamics of populations within forest stands, range changes of biomes, transfer and transformation of materials in ecosystem and larger scale biogeochemistry, and feedback effects in biosphere-atmosphere flux exchanges. These processes occur at a range of scales and ultimately reach sufficient scale to be of economic relevance that dictates setting national and international policies (Milly et al. 2005).

Modeling is the preferred approach to quantify biosphere-atmosphere mass and energy exchange (e.g., Waring and Running 1998, Williams et al. 1995, Rind et al. 1992, Bonan 2008). The wide range of available models presents opportunities for matching models complexity to specific needs (e.g., Duursma and Mäkelä 2007; Norman and Jarvis 1975; Oker-Blom and Kellomaki 1982; Song and Band 2004; Stenberg 1998; Wang and Baldocchi 1989). Global scale models use simplified calculations to cover large spatial and temporal scales (e.g, Rind et al. 1992, Thornton et al. 2002, Berner 2003, Bonan 2008). However, these simplified calculations must be verified, often against estimates based on finer scale models (e.g., stand scale) which themselves can be tested against field measurements. Obviously, the more realistic these models become, the
more they rely on detailed input of parameters and driving variables and the more computationally demanding they are. Therefore, knowing under which stand conditions further simplification carries little penalty in terms of degraded accuracy of estimates would substantially decrease computational needs and the need for information that is difficult to obtain.

Fine scales model, thus, can be viewed along a spectrum of complexity, from the very complex ones used to answer specific scientific questions (e.g., Sperry et al. 1998, Sinoquet 2001), to simpler ones more suitable for practical operations and for verifying coarser scale models (Running and Coughlan 1988, Landberg and Waring 1997, Thornton et al. 2002). The Canopy Conductance Constrained Carbon Assimilation (4C-A) model, is a 1-D carbon assimilation model that is among the most realistic and accurate models, relying on information at a high temporal and spatial resolution (Schäfer et al. 2003). The model’s name is descriptive of its most important input, sap flux-scaled canopy conductance. Relying on measured sap flux takes away much of the uncertainty in calculating photosynthesis. Consider Fick’s diffusion equation: \( A = g \cdot c_a \cdot (1 - c_i / c_a) \), where \( A \) is assimilation, \( g \) is conductance, \( c_a \) is atmospheric concentration of \( \text{CO}_2 \) and \( c_i / c_a \) is the ratio leaf-internal to atmospheric concentration of \( \text{CO}_2 \). Empirical evidence shows that by and large, the most variable quantity on the right hand side of
the equation is $g$, so using this quantity as an input highly constrain the uncertainty in estimates of $A$. However, it also means that $g$ has to be well quantified.

The 4C-A model is composed of three main parts: (1) calculations of light distribution on leaf surfaces through the canopy, (2) constraining the vertical distribution of stomatal conductance based on mean canopy stomatal conductance, and (3) estimating $c_i/c_a$ based on (1) and (2), and calculating photosynthesis (Figure 1.1). Only some components of the model were evaluated, and no sensitivity analysis had been performed prior to my dissertation work. Such analysis is needed to determine the needed level of specification of canopy architecture, which can be one of the most difficult tasks in canopy photosynthesis modeling, often reduced for simplicity to a single layer turbid medium.

In the first chapter of my dissertation, I assess the accuracy of a 1-D light model. Although the model reduces the requisite input tremendously compared to light models requiring detailed description of 3-D canopy architecture, to capture the vertical distribution of the amount and intensity of light it requires more input than simpler models. It thus incorporate an account of shoot clumping and leaf-angle distribution, both of which can vary vertically, as well as tree clumping (e.g., Nilson 1999, 2004, Makela 2007). The question I ask is: How much simpler can the model be and still achieve a reasonable representation of the vertical distribution of light? I first evaluated
the light model by comparing modeled output of canopy openness and
photosynthetically active radiation (PAR) with measurements taken in a Pinus taeda
(loblolly pine) dominated stand at Duke Forest. Although the interception or
distributions of PAR have been assessed in a number of studies (e.g., Beaudet et al. 2002;
Bernier et al. 2001; Song and Band 2004; Stadt and Lieffers 2000, Duursma and Mäkelä
2007, Roupsard et al. 2008), rarely the effect of simplifying each structural attribute is
investigated over the natural range of each of the other attributes. I proceeded with a
sensitivity analysis, quantifying the effect of simplifying each structural properties of the
canopy (leaf angle distribution, and clumping at the shoot and the tree level) on the both
total absorbed PAR (APAR) and its vertical distribution based on multi-layer (1-D)
framework.

As stated, accurate estimates of mean canopy stomatal conductance is essential
for properly distributing conductance down the canopy (Figure 1.1), and then
calculating \( c_i / c_a \) and photosynthesis. (Figure 1.1 & 1.2). The vertical distribution of
stomatal conductance is based on stomatal-light response curves for sun and shade
foliage coupled with the distribution of light intensity, and then adjusted such that its
leaf-area weighted mean equal to sap flux-scaled mean canopy stomatal conductance
(Schäfer et al. 2003). Errors in sap flux-scaled conductance would directly translate to
errors in photosynthesis (Figure 1.1). Because the potential for errors is not small given
that the Granier-type constant heat dissipation probe measures flux in a small patch of
xylem and must be scaled to the tree or stand, it is necessary to assess the accuracy of the
scaled estimate. This was done by scaling sap flux to transpiration at a range of
temporal and spatial scales and comparing to independent measures as well as assessing
the closure of the entire hydrological balance in the same pine forest used for assessing
the 1-D light model.

Specifically, I compared evapotranspiration ($E_T$) values, calculated as the sum of
transpiration from sap flux-scaled measurements and modeled soil and litter layer
evaporation, with eddy covariance measurements from an ambient plot at Duke Forest.
Furthermore, data collected for up to 15 years in four treatments (atmospheric [CO$_2$
] enrichment and N fertilization in a split-plot randomized block design, $n=4$), including
wide ranges in weather and canopy conditions were used to estimate each component of
the water balance (Fig. 1-2). I used measurements of precipitation and precipitation
through-fall, scaled sap flux to transpiration, and models of evaporation, overland flow
and drainage. Not only this approach was used to assess the accuracy of scaling sap flux
to canopy level stomatal conductance for constraining photosynthesis calculations in the
4C-A framework, but it also permitted me to evaluate the effect of elevated CO$_2$ and N
fertilization on water balance components of a pine stand at Duke Forest, the longest
running free-air CO$_2$ enrichment (FACE) sites.
Finally, as an evaluation of carbon assimilation (photosynthesis) calculation, I estimated the photosynthesis of fast growing poplar plantation with high leaf area index. Using common physiological ratios, such as that between net primary production (NPP) and gross primary production (GPP; ~ 0.47± 0.04, Waring et al. 1998), between GPP and APAR (light use efficiency, LUE) and GPP and transpiration (water use efficiency, WUE), I assessed the performance of the model. Ultimately, I challenge the model to pinpoint the layer in the canopy where net photosynthesis reaches zero, and where I expected branch mortality to occur.
Canopy Conductance Constrained Carbon Assimilation (4C-A)

Figure 1.1. Schematic diagram of Canopy Conductance Constrained Carbon Assimilation (4C-A) model. The definitions of symbols and abbreviations are in Table 1.1

\[ A_{\text{net}} = g_s \cdot C_a (1 - C_i / C_a) \]
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<th>Parameter</th>
<th>Definition</th>
<th>Unit</th>
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<tr>
<td>$A_{net}$</td>
<td>net carbon assimilation</td>
<td>µmol C m$^{-2}$ leaf s$^{-1}$</td>
</tr>
<tr>
<td>$C_a$</td>
<td>leaf surface CO$_2$ concentration</td>
<td>ppm</td>
</tr>
<tr>
<td>$C_i$</td>
<td>CO$_2$ concentration in the intercellular space</td>
<td>ppm</td>
</tr>
<tr>
<td>$C_o$</td>
<td>ambient oxygen concentration (210000 µmol mol$^{-1}$)</td>
<td>µmol mol$^{-1}$</td>
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<tr>
<td>$E_C$</td>
<td>transpiration</td>
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<td>$E_L$</td>
<td>litter layer evaporation</td>
<td>mm</td>
</tr>
<tr>
<td>$E_S$</td>
<td>soil evaporation</td>
<td>mm</td>
</tr>
<tr>
<td>$F_O$</td>
<td>over land flow</td>
<td>mm</td>
</tr>
<tr>
<td>$I_C$</td>
<td>canopy interception</td>
<td>mm</td>
</tr>
<tr>
<td>GPP</td>
<td>gross primary production</td>
<td>g C m$^{-2}$ ground</td>
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<tr>
<td>$G_c$</td>
<td>sap flux scaled canopy conductance</td>
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<td>$g_s$</td>
<td>leaf stomatal conductance</td>
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<td>$K_C$</td>
<td>Michaelis constant for CO$_2$ fixation</td>
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</tr>
<tr>
<td>$K_o$</td>
<td>Michaelis constant for oxygen inhibition</td>
<td>mmol mol$^{-1}$</td>
</tr>
<tr>
<td>LAI</td>
<td>leaf area index</td>
<td>m$^2$ m$^{-2}$</td>
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<tr>
<td>LAP</td>
<td>vertical leaf area index profile</td>
<td>m$^2$ m$^{-2}$</td>
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<tr>
<td>NEP</td>
<td>net ecosystem production</td>
<td>g C m$^{-2}$ ground</td>
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<td>NPP</td>
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<td>g C m$^{-2}$ ground</td>
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<tr>
<td>P</td>
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<td>$P_T$</td>
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<td>R</td>
<td>residual</td>
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<td>$R_a$</td>
<td>autotrophic respiration rate</td>
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<td>$R_c$</td>
<td>constructional respiration rate</td>
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<td>$R_m$</td>
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<td>g C m$^{-2}$ ground</td>
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<td>$V_m$</td>
<td>maximum Rubisco capacity per unit leaf area</td>
<td>µmol CO$_2$ m$^{-2}$ leaf s$^{-1}$</td>
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<td>leaf absorptivity (0.83)</td>
<td>dimensionless</td>
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<tr>
<td>$e_m$</td>
<td>maximum quantum efficiency (0.08)</td>
<td>mol mol$^{-1}$</td>
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<tr>
<td>$\Delta S$</td>
<td>change in water storage</td>
<td>mm</td>
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<tr>
<td>$\Gamma^*$</td>
<td>CO$_2$ compensation point</td>
<td>µmol mol$^{-1}$</td>
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Chapter 2. Assessing canopy and stand conditions in which specification of vertical canopy architecture is needed for estimating the amount of absorbed light and the vertical profile of light intensity

2.1. Abstract

We analyzed the effect of simplifying assumptions in canopy representation of radiation transfer models by first comparing estimated openness and photosynthetically active radiation (PAR) with measured values at different layers down the canopy of composed of pine and broadleaved species and at seasons with greatly differing leaf area index ($L$). Using the actual $L$ and its vertical profile, the most detailed model included tree density (TD) to represent clumping of foliage into individual trees at the canopy and sub-canopy layers, and a realistic vertical specification of leaf angle distribution (LAD) and shoot clumping ($\Pi$). A less detailed model replaced the vertically specified variables with their mean value. In the most parsimonious single-leaf model, neither $\Pi$ nor TD were accounted for. We show that in our stand the laborious vertical specification of $\Pi$ and LAD slightly improved openness and PAR estimates down the canopy and during a period representing large $L$ dynamics – using the mean values produced very similar results. Further simplification was more risky in terms of the estimates of vertical distributions of openness and PAR absorbed by the canopy (APAR), but had little effect on canopy total APAR. We performed a sensitivity analysis to assess
the ranges in TD, and mean Π and LAD affecting APAR and, potentially, photosynthesis; the analysis was performed along a range of $L$, keeping the vertical distribution of $L$ as in the real stand. The sensitivity analysis showed that not accounting for shoot clumping would result in an overestimation of total APAR, potentially by substantial amounts, with errors increasing with decreasing $L$. Not accounting for tree density would also lead to substantial overestimation of APAR, but only in low density stands, and the effect is largely independent of $L$. Like the effect of changing shoot clumping, that of changing LAD from spherical increased with decreasing $L$, and was larger and more persistent along the $L$ range where shoots are more clumped. Overall, accounting for the effect of tree level clumping on APAR and its vertical distribution is most important in stands of broadleaved species where leaves are not very clumped on shoots. However, even in coniferous forests with highly clumped shoots, accurate estimation of APAR distribution in stands of high $L$ requires that tree density is also incorporated in the model.

2.2. Introduction

Photosynthesis is the process supplying the basic material for plant growth and ecosystem carbon cycling, and its spatial and temporal variation is determined primarily by the rate and total amount of absorbed photosynthetically active radiation (PAR). The
interception of PAR is determined by canopy and crown architecture, including the spatial distribution of crowns in stands, the clumping of leaves in shoots, the dimensions of leaves and shoots, and the angle distribution of leaves (Ross 1981). In turn, the prevailing PAR at each location in the canopy affects leaf clumping and angles (Stenberg 1998) as well as leaf photosynthetic characteristics, including mesophyll properties and leaf biochemistry (Niinemets 1997; Niinemets and Kull 1995; Sprugel 1989; Stenberg et al. 2001; Terashima and Hikosaka 1995). Through the effect on photosynthesis, the distribution of PAR influences stand dynamics vis-à-vis regeneration, growth and mortality.

High spatiotemporal variation of PAR in the canopy renders direct measurement impractical (Palmroth et al. 1999), particularly when stand-level information is needed over the many years of stand development. This led to a proliferation of models that were developed from simple one-layer turbid-medium models designed to estimate the total amount of absorbed PAR (APAR; e.g., Landsberg and Waring 1997) to highly detailed, three-dimensional (3D) models that account for horizontal heterogeneities in canopies and are often designed to estimate PAR distribution on leaf surfaces down the canopy (e.g., Canham et al. 1994; Chen and Reynolds 1997; Norman and Wells 1983; Wang and Jarvis 1990; Brunner 1998; Cescatti 1997; Stadt and Lieffers 2000; Mariscal et al. 2000; Martens et al. 2000; Sinoquet et al. 2001).
Simpler models are commonly employed as a component of more comprehensive models of stand growth or ecosystem (or larger scale) carbon dynamics (e.g., Mäkelä 1997; Running and Coughlan 1988). Because they require much more detailed information to represent the canopy (Kubo et al. 2008), 3D models are more commonly used to address specific scientific questions, e.g., for testing specific hypotheses or for validation of simpler models (Drouet 2003; Mariscal et al. 2004; Roupsard et al. 2008; Sinoquet and Rivet 1997). Between the simple and complex extremes, a wide range of models simplify the non-random foliage area distribution and non-homogenous stand structure of real forest stands, translating spatially explicit description of the canopy to more generic statistical distributions of properties of canopy layers or individual trees (e.g., Duursma and Mäkelä 2007; Norman and Jarvis 1975; Oker-Blom and Kellomäki 1982; Song and Band 2004; Stenberg 1998; Wang and Baldocchi 1989). Thus, in case of a layered-model (instead of a single tree) the canopy can be described using idealized leaf angle distribution, typically spherical (Campbell 1986), average shoot clumping, typically used in conifers (Thérézien et al. 2007), and tree clumping (Nilson 1999). These simplifications, of canopy representation make estimates of APAR or PAR distribution computationally less intensive.

The wide range of model complexity presents opportunities for matching models complexity to specific needs. Indeed, even some models of intermediate complexity
often require site-, species-, and canopy-depth-specific parameterizations. Knowing under which stand conditions further simplification carries little penalty in terms of degraded accuracy of PAR estimates would substantially decrease the need for information that is difficult to obtain. Although the interception or distributions have been assessed in a number of studies (e.g., Beaudet et al. 2002; Bernier et al. 2001; Song and Band 2004; Stadt and Lieffers 2000; Duursma and Mäkelä 2007; Roupsard et al. 2008), rarely the effect of simplifying each structural attribute is investigated over the natural range of each of the other attributes. The purpose of this study is to quantify the effect of simplifying important structural properties of canopy elements (leaf angle distribution, and clumping at the shoot and the tree level) on the both total APAR and its vertical distribution based on multi-layer (1D) framework, the most commonly used approach in models of canopy photosynthesis.

The canopy PAR interception and attenuation with depth in a horizontally homogenous canopy is commonly modeled based on the Beer-Lambert law (BL). A simple representation of BL for estimating mean PAR interception by the canopy \( Q \) is

\[
Q = Q_0 (1 - e^{(-K_{be}(θ)L)})
\]

(1)

where \( Q_0 \) is the incident PAR above the canopy, \( K_{be}(θ) \) is mean leaf horizontal projection per unit leaf area, i.e. the canopy extinction coefficient for direct beam PAR, and \( L \) is the leaf area index. \( K_{be}(θ) \) which depends on the solar zenith angle \( (θ) \) and the distribution of
leaf inclination angles (Campbell 1986). This BL formulation assumes a random
distribution of leaves in the canopy space, thus intercepting PAR more efficiently than
real canopies, where leaves are clumped at the shoot and tree scale. Often, however, the
formulation is simplified by assuming a constant “effective” extinction coefficient that
allows using daily or longer term average $Q_0$ instead of values at diurnal resolution
(Duursma and Mäkelä 2007; Landsberg and Waring 1997).

Another widely used simplification in models that operate at time scales <1 day
is based on the assumption that leaf angle is spherically distributed in the canopy space
(Campbell and Norman 1998). Perhaps an unintended joint outcome of these
simplifications (random distribution and spherical orientation of leaf elements) is that in
some situations it compensates for neglecting leaf clumping, allowing light penetration
deeper into the canopy (Kim et al. 2008). However, in other cases, when compared to
vertically measured PAR distribution, the assumption of spherical leaf angle distribution
caused an underestimation of light transmission (Stadt and Lieffers, 2000), or had little
influence on APAR and net photosynthesis (Goudriaan 1988; Oker-Blom and Kellomaki
1982; Chen et al. 1998). Leaf angle distribution (LAD) was found not spherical for many
tree species, with some oriented more vertically and others more horizontally (Thomas
and Winner 2000; Wirth et al. 2001). It is possible that assuming spherical LAD caused
variable impact among studies on total APAR and vertical PAR distribution is the
degree and direction of the difference with the actual LAD in the canopy. In this study we aim to delimit the canopy conditions under which each architectural variable affects APAR, thereby informing on situations in which simple BL representation would suffice versus other situations requiring more complex canopy structure and optical representation.

Although some canopy PAR absorption models account for the effects of shoot- or stand-level clumping, most tend to ignore the vertical variation in shoot characteristics, i.e. the changes in the interception efficiency of shoots along the PAR gradient (Palmroth et al. 2002; Sprugel et al. 1996; Stenberg et al. 1999). By assuming a constant value for each characteristic these models avoid the added complexity and data required for vertically specified architectural properties (e.g., Alton and North 2007; Bernier et al. 2001). While this simplification may have relatively small effect on total APAR over longer integration periods, it can affect the distribution of PAR among canopy layers. Thus, we also investigated the effect on APAR of representing the canopy with variable versus constant leaf angle distribution and shoot clumping, accounting for tree level clumping by incorporating tree density and crown shape into the 1D framework (Nilson and Kuusk 2004; Song 2007).
2.3. *Materials and methods*

2.3.1. Model description

To calculate PAR absorption by different layers in the canopy, above canopy incident PAR ($Q_o$) was partitioned into direct ($Q_{ob}$) and diffuse ($Q_{od}$) components (Spitters et al. 1986) using measured and expected clear day radiation (Campbell and Norman 1998). Scattered light ($Q_s$) was assumed zero above the canopy. The interception of direct beam ($Q_b$) diffuse ($Q_d$) and $Q_s$ was estimated separately in each 1 m deep layer downward through the canopy. Computationally, it is more efficient to calculate PAR at each level based on the value at the top of the layer and layer-specific properties than based on the value at the top of the canopy and average properties from the top of the canopy to that layer. However, certain parameters for calculating $Q_d$ are available only for the second approach (Campbell and Norman 1998), and only $Q_b$ and $Q_s$ at the bottom of each layer were calculated based on the first approach.

In every layer, $Q_b$ on *sunlit* horizontal surface is the same as the top of the canopy and is calculated as

$$Q_b(z) = Q_{ob}$$

Clumping of canopy elements can be incorporated into radiation transfer models using an average quantity that integrates shoot and tree level clumping (Niinemets et al. 2004). However, as tree density increases it is likely that shoot clumping decreases faster
with depth in the canopy, and this approach does not permit evaluating the effect of each change independently, nor does it allow delineating the tree density at which accounting for shoot level density is required. Thus, we calculated the proportion of sunlit area on horizontal surface at each sun angle, i.e. the transmission of direct beam PAR (τₜ,θ), based on the tree-level clumping calculation accounting for crown shape and tree density (TD; Nilson 1999) as

$$\tauₜ(z,θ) = e^{\sum_{j=1}^{n} -N_j \sum_{k=1}^{N_j} S_j(z,θ)(1-a_j(z,θ))}$$

(3)

where

$$a_j(z,θ) = e^{\sum_{k=1}^{N_j} \left( \frac{-K_{be,stem,branch,leaf}(z)BA_j(z)K_{be,non,leaf}(z)SA_j(z)}{S_j(z,θ)} \right)}$$

(4)

and Nᵢ is the stand density of the jth species, S(z,θ) is the projected area of crown for the jth species, aᵢ(z,θ) is the mean gap fraction in a single tree crown at the zenith angle θ (Nilson 1999). The extinction coefficients (Kₑₑ) of stem and branch area of all species and leaf area of broadleaved species is calculated according to Campbell and Normal (1998) as

$$Kₑₑ(z,θ) = \frac{\sqrt{x(z) + \tan^2 θ}}{x(z) + 1.774(x(z) + 1.182)^{-0.733}}$$

(5a)

The extinction coefficient of a conifer leaf (needle) is calculated as

$$Kₑₑ,leaf(z,θ) = G(z,x(z),θ)/\cos θ .$$

(5b)
The G-function, or the projection of unit foliage hemi-surface (or half total surface) area on the plane perpendicular to the view direction $\theta$, is calculated according to Stenberg (2006). $x(z)$ is the average ratio of canopy elements on horizontal and vertical surfaces (Campbell 1986). $x(z)$ for branches was assumed equal to that of leaf, essentially reflecting the observation that branches tend to orient more vertically at the top of the canopy and more horizontally at the bottom, just as leaves do. Because stems are nearly vertical in orientation, $x(z)$ was set to 0.01 for $K_{\text{be,stem}}$.

$L_j(z), BA_j(z)$ and $SA_j(z)$ are defined as leaf, branch and stem hemisurface area of $z^{th}$ layer for $j^{th}$ species, respectively. Shoot clumping ($\Pi(z)$) is defined as the average ratio of shoot silhouette area to the projection area of all leaves with their natural orientation, but spread out so they do not shade each other (Stenberg 1998).

Scattered radiation ($Q_s$) was also calculated based on layer specific information as

$$Q_s(z) = (\tau_d(z, \theta) - \tau_b(z, \theta))Q_b(z)$$  \hspace{1cm} (7)

The attenuation of diffuse radiation ($Q_d$) was calculated as

$$Q_d(z) = \tau_d(z)Q_{od}$$  \hspace{1cm} (6)

The transmission of diffuse PAR ($\tau_d(z)$) and the sum of PAR (direct, diffuse and down scattered radiation; $\tau_{bt}(z, \theta)$) were calculated according to Campbell and Norman (1998) as
\[
\tau_d(z) = 2 \int_0^{\pi/2} \tau_{b,\text{total}}(z, \theta) \sin \theta \cos \theta \, d\theta
\]

and

\[
\tau_{\text{tot}}(z, \theta) = e^{\tau_d(z)}
\]

where \( \alpha \) is canopy absorptivity, set to 0.83 (Lai et al. 2000) after finding that using different values for leaves (0.80; Long et al., 1992) and bark (0.9; Henrion and Tributsch 2009) did not have a detectible effect, \( \tau_{b,\text{total}}(z, \theta) \), the average direct radiation transmission coefficient from the top to the \( z \)th layer, is calculated based on \( L_{C,\text{total},j}(z) \), \( K_{b,\text{total},j}(z, \theta) \) and \( \Pi_{\text{canopy},j}(z) \):

\[
\tau_{b,\text{total}}(z, \theta) = e^{\tau_d(z)}
\]

\[
a_{\text{total},j}(z, \theta) = e^{\frac{K_{b,\text{total},j}(z)L_{C,\text{total},j}(z)\Pi_{\text{canopy},j}(z)}{N_j S_j(z, \theta)}}
\]

\( L_{C,\text{total},j}(z) \), \( K_{b,\text{total},j}(z) \) and \( \Pi_{\text{canopy},j}(z) \) were cumulative average values weighted with leaf, branch and stem area for \( j \)th species from the canopy top to each layer.

The average of total PAR on a horizontal surface was calculated by summing direct, diffuse and scattered radiation. \( Q_{\text{avg}}(z) \) was calculated as:

\[
Q_{\text{avg}}(z) = \tau_b(z)(Q_b(z) + Q_d(z) + Q_s(z)) + (1 - \tau_b(z))(Q_d(z) + Q_s(z))
\]
APAR of the layer was calculated by subtracting the $Q_{avg}(z)$ from $Q(z-1)$ and canopy total APAR was calculated by subtracting the $Q_{avg}(z)$ at the bottom of canopy from $Q_0$.

PAR both down the canopy and below the canopy is highly variable and contain errors associated with difficulties of holding the sensors perfectly horizontal. Thus, PAR measurements may not provide for a very good benchmark for model testing. Measurements of canopy openness, the fraction of open sky above the layer, integrate over a large portion of the canopy and are thus less variable and less sensitive to imperfect orientation of the sensor. As canopy openness, here defined as $\tau_d$, is estimated in the model we used these estimates as a more robust test of the model.

### 2.3.2 Model Evaluation

Model-based estimates of canopy openness and PAR on horizontal surface were compared to measurements obtained at a loblolly pine (*Pinus taeda* L.) plantation (Duke Forest; 35° 58' N, 79° 05' W, NC, USA), which included spatially and temporally varying components of broadleaved deciduous foliage (Figure 1. A-C). Canopy openness was measured with LAI-2000 canopy analyzer (Li-Cor, Lincoln, NE, USA) from six free-air CO$_2$ enrichment (FACE) plots six times throughout 2002-2003 representing a wide range of $L$ among plots and seasons. Measurements from the central tower were made from
the top of the canopy down at two-meter intervals. Four measurements were made from each side of the tower while blocking three quarter of the sensor lens on the tower side, and averaged. The diffuse non-interceptance (DIFN, LAI-2000 User Manual) is calculated by multiplying the five concentric gap values from LAI-2000 with the corresponding area proportions. DIFN was used as a measure of canopy openness as it corresponds to \( \tau_d \) estimated in the model.

\( Q_0 \) on horizontal surface above the canopy was measured with a quantum sensor (Q190, Li-Cor, Lincoln, NE, USA), and PAR inside and below the canopy was measured with a ceptometer (AccuPAR LP-80, ICT international, Armidale, Australia). The quantum sensor provided one spot measurement, while the ceptometer measurements provided the average of 80 quantum sensors located on 80 cm bar. Three different types of measurements were done in March 2004 and October 2005 representing \( L \) (here expressed as projected leaf area) range from 1.5 to 6 m\(^2\) m\(^{-2}\). In March 2004, 40 or more PAR measurements were taken below the canopy at six FACE plots (plot 1 was measured twice) and averaged for each plot. In October 2005, below canopy measurements were taken for two days at plot 4, a plot with average leaf area index at the site. Measurements were taken at 5-minute interval and averaged every 30 minutes to synchronize with the measurements of \( Q_0 \), providing 41 daytime measurements. In addition, measurement profiles from the central tower of plots 1 and 2 having the lowest
and highest proportion of broadleaved species leaf area index were taken in October.
The eight profiles were spaced from mid-morning to late afternoon, and were composed of four measurements taken at two-meter intervals from the top of the canopy to the ground level in the direction of each tower side, and averaged by layer.

For model validation, we evaluated seven models with different complexities (v1-7, Table 2). Model v1 used the simple Beer-Lambert model obtaining $L$ estimates for hardwood and conifers on each measurement date from McCarthy et al. (2007) and unpublished data (e.g. Figure 1.A). No shoot clumping ($\Pi=1$) and spherical leaf angle distribution (LAD) were assumed for both conifer and hardwood species. Vertical leaf area distribution of the stand was calculated by summing the vertical leaf area for individual tree assuming normal distribution of leaf within the live crown (Vose et al. 1994), and corresponded to the shape observed over time based on the LAI-2000 measurements (McCarthy et al. 2007).

We added shoot clumping as a constant in model v2, with $\Pi=0.6$ representing the average of the pine (Thérézien et al. 2007) and 0.95 for broadleaved species according to Kim et al. (2008) (Figure 1.D).

In model v3 we replaced shoot clumping with tree-level clumping. To calculate tree-level clumping, stem density, height, diameter at breast height (DBH), crown length and branch biomass of individual trees in six FACE plots were obtained from McCarthy
et al. (2007) and unpublished data. Stem surface area, $SA(z)$ was calculated from the height of individual trees and using segmented polynomial taper equation (Sharma and Burkhart 2003). Branch surface area, $BA(z)$ was calculated from a combination of observation, measurements and assumptions regarding branch number and dimensions (dimensional approach; see below). This was converted to total branch volume and finally to biomass and checked against a more direct and accurate estimate of total branch biomass for individual trees (McCarthy 2007). The dimensional approach, needed for estimating $BA(z)$, produced estimates of biomass larger than the direct approach, mostly due to branch loss at the bottom of the canopy. Therefore, $BA(z)$ was adjusted downward as described later.

For the dimensional approach, first the number of whorls in the live crown was estimated from crown length; the live crown length was estimated from diameter and height of individual trees using a regression model developed from measurements at the end of 2005 and 2006 growing seasons (McCarthy, 2007). The number of whorls within the live crown was estimated from crown length and tree average height growth which vary by dominance class. The average annual height growth for pine tree was ~1 m over three-year periodic measurements; height growth of sub-canopy species was calculated from annual diameter increment and the relationship between height and diameter. From measurements we learned that intra-whorl branches were few, small and short
lived, and ignored their contribution to $BA(z)$. We also found that on average, branches bifurcated trice, with a fifth year length increment rarely exceeding 1% of the total branch length, and occurring on only few shoots. A branch of any order was considered dead and gone once its youngest bifurcation was older than four years. The first-year length increment of branch originating at the main stem was set to ~90% of the height increment of that year. A second year length increment along the branch axis was 90% of the previous year’s length, and that of the two laterals was 90% of this year’s axial increment. This was replicated in the second bifurcation (third year growth) and third bifurcation for three axial and six lateral branches, at which point no further branch length increment was recorded for that whorl. Using this design, the total length of the main branches originating from the stem was calculated based on their age.

The diameter of each branch was calculated by assuming that, due to lower hydraulic conductivity at the branch base, the sum of branch sapwood area at the base of branches exceeds the sapwood area of the stem supporting these branches (Oren et al. 1986). Knowing the taper of the stem allows calculating the sapwood area below and above a whorl, with the reduction in sapwood area assumed to be divided among the four branches and then increased to account for the effect of reduced hydraulic conductivity at the junction. Thus, excluding bark thickness, the sapwood area of
current year stem and branches was ~14% larger than the previous year’s stem sapwood. The same design was used to calculate the diameter of higher order branches.

Based on the basal diameter and length of each branch order, the both branch surface area and volume of an idealized branch was estimated in each whorl, and multiplied by four representing the average number of branches per whorl. For the correction described above, branch volume was converted to biomass using wood density interpolated between 0.37 g cm$^{-3}$ at the top whorl to 0.52 g cm$^{-3}$ at the bottom most whorl (McCarthy et al. 2007). Summing provided the total branch mass which was then compared with the estimate from the direct method. The dimensional estimate was reduced by removing the biggest branches, representing bottom branches with a high likelihood of self pruning, until it matched the direct estimate, and $BA(z)$ was recalculated from the remaining branches. When $L$ was at maximum, $SA$ and $BA$ summed to ~30% of $L$; the contribution of these components to the surface area of the canopy increased as leaves are shed during the winter and early spring, becoming nearly equal to $L$ when it reaches its minimum (Figure 1.A-C).

In model v4, shoot clumping was added back as a constant as in v2. In model v5, we used vertically variable pine $Π(z)$ with spherical LAD. The vertically variable shoot clumping ($Π(z)$) values were calculated based on four shoots harvested at the top of the canopy and four at the bottom as described in Thérézien et al. (2007). In model v6,
vertically variable LAD was added. In calculating LAD of the pine, \( x(z) \) was estimated based on pictures taken perpendicular to the shoot axis. Five pictures were taken at each of the top, middle and bottom layers of the canopy. LAD was obtained by measuring the angle from horizontal surface of at least 40 needles oriented along the shoot axis in each picture. For the hardwood species, values of \( x(z) \) were assumed similar to an oak canopy from Kull et al. (1999) and Wirth et al. (2001), changing from 1 (i.e. spherical) at the top of the canopy to 2.5 at the bottom (Figure 1.E). And lastly, in model \( v7 \), the most complete model, we vertically varied \( \Pi(z) \) and LAD.

### 2.3.3. Sensitivity Analysis

For the sensitivity analysis, we calculated total APAR and PAR in each canopy layer (1 m depth) on the summer solstice. Based on the seasonal dynamics of diameter increment, the growing season in the study area lasts from the beginning of April to the end of September. During the growing season, the maximum sun angle ranged from a high of 77.5 to a low of 51.6, with angles > 70 degrees in 52% of growing season days, making the summer solstice a fairly typical growing season day. We calculated the diurnal light intensities during a clear and a cloudy day using the same sun angle, according to Campbell and Norman (1998; see Figure 2). For clear day, atmospheric transmittance was assumed to be 0.75 (Campbell and Norman 1998) and for cloudy day
it was set at 0. The maximum light densities on the clear day reached \( \sim 2100 \, \mu \text{mol m}^{-2} \text{s}^{-1} \) versus \( \sim 790 \, \mu \text{mol m}^{-2} \text{s}^{-1} \) on the cloudy day. On a clear day, direct light composed the majority of total PAR; on cloudy day, there was no direct light (Figure 2).

To increase the generality of our findings, we used wide range of values for shoot clumping, LAD, \( L \) and stand density. Shoot level clumping ranges from 0.2 at the canopy top to 0.9 at the bottom of species with short needles versus 0.4 to 0.9 in long needed species (Palmroth et al. 2002; Thérézien et al. 2007). \( BA(z) \) and \( SA(z) \) used in model validation were assumed zero in the sensitivity analysis, meaning that the effects of simplification represent a likely maximum.

The effect of variations in LAD, tree density (\( N \)) and \( L \) were also investigated. The effect of constant LAD evaluated based on the assumption that it is spherical (e.g., \( x = 1 \), in Equation 5), closer to vertical (0.5), or closer to horizontal (3). We used constant \( \Pi(z) \) and \( x(z) \) throughout the canopy depth for sensitivity analyses because the additional accuracy from vertically variable \( \Pi(z) \) and \( x(z) \) was relatively small (Figure 1. D&E). However, the effects of vertically varying \( \Pi(z) \) and \( x(z) \) are demonstrated at the end of the discussion.

Given the size of the trees, set to a height of 21 m in all simulations, the effect of tree density was evaluated from a low of 100 trees ha\(^{-1} \) to a high of 3000 trees ha\(^{-1} \). Crown length and width were modified to reflect tree density based on Schultz (1997; see Table
4). For each tree density level, the effect of $L$ on APAR was evaluated from a low of 2 (projected leaf area) to a high of 10, commonly found in stands of shade tolerant species (Oren et al. 1988). The vertical distribution of leaf area was assumed to follow Weibull distribution (e.g., Mori and Hagihara 1991; Utsugi et al. 2006) with 1.5 and 3 as scale and shape parameter, respectively, generating nearly normal distribution.

2.4. Results and Discussion

We begin by describing how well the different versions of the model quantified canopy openness and PAR on horizontal surface in one stand where spatial and seasonal variation of $L$ are large (McCarthy et al. 2007). Comparisons are based on below-canopy measurements taken at various times over the year, and measurements made from towers, representing vertical transects through the canopy. Following, we concentrate on APAR, which it is calculated from mean PAR on horizontal surfaces through the canopy because it is the variable often used in modeling canopy photosynthesis. We analyze the effects of incorporating constant shoot and stand clumping ($\Pi$ and TD, respectively), and leaf angle distribution (LAD) on absorbed PAR (APAR) during one “typical” growing season clear day and one cloudy day. We conclude by analyzing the effect of vertically variable canopy properties on estimated PAR distribution in one stand.
2.4.1. Model validation

The most complete model (v7) estimates of canopy openness and PAR on horizontal surface well agree with measurements (Figure 3A&B). The slope of modeled versus measured openness (1.02) and PAR (0.97) were not different from unity (P = 0.13, and 0.34 respectively), and the intercepts (-0.02, and -7.62 μmol m\(^{-2}\) s\(^{-1}\), respectively) not different from zero (P=0.15, and 0.50). Considering that the model was specified with a broadleaf and needle-leaf foliage in the canopy and broadleaf subcanopy, all collapsed into 1-D configuration (Fig. 1.A & C), demonstrate that it can combine the effect of individual components in complex canopy on mean PAR on horizontal surface just as well as most of other models including 3-D models (Mariscal et al. 2004, Mottus 2004, Stadt and Lieffers 2000).

Although all model versions that accounted for shoot and tree clumping (v4-v7) reproduced a reasonable estimate of vertical PAR distribution, the most complex version (v7, see Table 3) showed the best agreement with the data. Nevertheless, all model configurations accounting for both attributes straddled the zero error line, meaning that overestimation at one canopy level was compensated by an underestimation lower down (Figure 3.E & F). Not accounting for either shoot and/or stand clumping resulted in a large overestimation of light absorption high in the canopy and underestimation of light levels in all lower canopy layers. A number of 3D radiation transfer models can
predict well the vertical distribution of mean PAR in the canopy (Wang and Baldocchi 1989, Brunner 1998, Canham et al. 1999, Gersonde et al. 2004, Mariscal et al. 2004), including mixed-species canopies (Stadt and Lieffers 2000). Our novel 1D model performs just as well in mixed-species stands (Fig. 3A & B) as in uni-specific stands (see openness in the non-growing season when broadleaved species are leafless; Figure 3.A). However, unlike 3D models requiring spatially explicit information on tree crowns, our model operates based on statistical representation of the canopy (Figure 1). It is noteworthy that even in 3D models the point-by-point comparisons between modeled and measured show little agreement because small errors in canopy element positions can translate into large errors in estimated PAR (e.g. Mariscal et al. 2004).

Because the greatest effect on the vertical distribution of PAR is realized once shoot and stand clumping are incorporated, either as constant or vertically varying quantity, we concentrate our sensitivity analysis on the effects of including these factors in the simplest, constant form. This analysis is restricted to a coniferous (needle-leaf) canopy because of its added complexity of shoot level clumping. Because additional improvements in predictions of the vertical distribution of PAR are realized when all the investigated canopy properties are set to vary vertically (Table 3), we conclude with an analysis of the relative deterioration in accuracy caused by holding each constant in the test stand.
2.4.2. Sensitivity analysis

The absolute negative intercept observed between the modeled values of modeled openness and PAR and their measured values (Figure 3A & B) cautions of large uncertainties relative to the signal at very small values of these variables. This suggests that expressing estimates obtained from various configurations of the model relative to a base configuration would produce volatile ratios at low light regimes, making it difficult to compare the effects of different simplifications on APAR. Thus we limited our sensitivity analyses to conditions in which PAR on horizontal surface is estimated to exceed 40 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). While making comparisons clearer, eliminating these ratios did not allow comparisons of the effect of all simplifications at each canopy level. We also note that we show all interaction effects on APAR among all factors studies only if the effects were more than 1% of APAR, and that the effect we show represent a maximum because we do not account for the surface area of branches and stems.

2.4.2.1. Total Absorbed PAR

2.4.2.1.1. The effect of shoot clumping

Estimating photosynthesis in canopies of stands and forests based on semi-empirical models is commonly done by estimating total APAR and multiplying by potential light use efficiency reduced via stress-related modifiers (Duursma and Mäkelä
2007; Hilker et al. 2008; Landsberg and Waring 1997; Makela et al. 2008). If the potential light use efficiency is relatively invariant and the modifiers well defined (e.g., Landsberg and Waring 1997), improving estimates of APAR is the only way users of these models can improve estimates of canopy photosynthesis.

Shoot clumping affected total APAR slightly less on cloudy than clear days, and while the effect of tree clumping was slightly larger on cloudy days, but for both canopy attributes the differences between days were very small. Accounting for shoot clumping affected APAR more than accounting for any of the other investigated canopy properties. As expected, APAR decreased with increasing clumping especially at low $L$ (compared to having non-clumped shoots, i.e. $\Pi = 1$, Figure 4.A). Thus, while estimated total APAR of a canopy with $\Pi = 0.9$ and $L = 2$ was only 3.5% lower than would be estimated for a similar canopy with unclumped shoots, APAR was estimated ~40% lower with highly clumped shoots ($\Pi = 0.2$), such as those found at the canopy top of coniferous stands (Thérézien et al. 2007 and references therein). This means that not accounting for shoot clumping in such stands could cause APAR to be overestimated by two thirds. In dense canopies ($L = 10$), the effect of these clumped shoots on APAR was smaller, allowing only 20% of PAR to go unabsorbed, yet still overestimating APAR by 25%. Even in more typical, less dense canopies (e.g., $L = 6$), and with typical value of $\Pi =$
0.6 (Thérézien et al. 2007), APAR in models with non-clumped shoots would be overestimated by >15%.

Thus, not accounting for the shoot clumping would result in an overestimation of total APAR and canopy photosynthesis, potentially by substantial amounts, with errors increasing with decreasing canopy density.

2.4.2.1.2. The effect of tree clumping (tree density and projection area of a tree)

Estimates of total APAR were affected by tree density (i.e. tree clumping) only at low densities (Figure 4.C & D). Relative to scenarios without tree clumping, APAR was 16 -18% lower at the lowest density (100 tree ha\(^{-1}\)). Thus, not accounting for tree clumping in very open stands would result in ~20% overestimate of APAR. With increasing stand density, the effect on estimated APAR quickly diminished such that at 500 trees ha\(^{-1}\) total APAR was estimated only 5% or less lower than APAR without accounting for stand clumping (5% overestimation of APAR).

The pattern of APAR with \(L\) observed at stands with low tree densities relative to modeling the stand as randomly distributed shoots in the canopy (i.e., no tree clumping) reflects the combined effect of a number of processes. Starting at low \(L\), increasing canopy density (i.e. canopy leaf area) increases the density of shoots in the crowns of few trees, which is not as effective for intercepting PAR as the same increase of \(L\) randomly distributed in the canopy. At high \(L\), distributed canopies reach a point in
which most PAR is already absorbed, and further increase generates very little gain in APAR. Thus, even the small increases in APAR with the additional $L$ crammed in crowns of few trees helps close the APAR gap with distributed canopies, resulting in the upturn of the ratios observed in Figures 4.C & D. As demonstrated by this and earlier studies (Brunner 1997, Oker-Blom et al. 1989, Duursma and Mäkelä 2007) tree clumping affects APAR by controlling the spatial distribution of canopy elements, specified through crown dimensions and tree density that are highly variable among species and affected by stand conditions.

More generally, the control of tree clumping on APAR can be viewed via the area shaded by the trees, which reflect stand and crown characteristics and the sun angle. When and where the shade area equal the ground area ($NS = 1.0$ in Eqn. 3), canopy elements are presumably positioned in the way of incoming light anywhere in the stand. However, the random distribution of crowns means that there is some overlap and estimated APAR increases less with $L$ when tree clumping is imposed (Figure 5). The pattern is similar but the stable minimum decreases with $NS$ below 1.0. As $NS$ increases above 1.0, even randomly positioned crown will approach complete cover, especially early and late in the day when the sun elevation angle is low. In open stands, as the sun elevation angle steepens, the solitary crowns will fail to intercept much of the light, but as stand density increases (especially for species that can maintain large crowns in dense
stands), NS will be much greater than 1.0 all day, and interception will approach that estimated without accounting for tree clumping (Figure 5). The ratios presented in Fig. 4.C & D, produced from daily integrated sums, smoothen the different patterns representing the changing NS with diurnal changes in sun angles.

Accounting for tree density had a substantial effect on APAR. In contrast, the interaction effect between tree density and $L$ reflect <3% difference between maximum and minimum APAR estimated at each density. Nevertheless, we feel that, given the model complexity, it is important to provide a physical explanation for each observed phenomenon.

2.4.2.1.3. The effect of leaf angle distribution

Unlike shoot and stand clumping, LAD affected the estimates of total APAR differently on clear and cloudy days, but the effect on diffuse radiation was so small it merits no further discussion (Figure 4.E-H). At low $L$ canopies, more vertically oriented leaves (LAD0.5) decreased estimates of APAR up to 7% ($\Pi = 0.6$) compared to spherical distribution (LAD1.0) (Figure 3.C&D) and more horizontally oriented leaves (LAD3.0) increased APAR by up to 13% (Figure 3.E&F). Generally, the effect of LAD was larger and more persistent along the $L$ range where shoots are more clumped.

In summary, our analysis show that total APAR was most affected by shoot clumping (Figure 4.A &B). Because leaves are less clumped on shoots of broadleaved
species than on shoots of conifers (Niinemets et al. 2004, Théré et al. 2007), it was found to affect APAR in a dense, high L poplar plantation much less than tree clumping (TD, e.g., Kim et al. 2008). However, most widely-used growth and ecosystem carbon dynamics models do not account for either variable (e.g., Landsberg and Waring 1997, Running and Coughlan 1988). Incorporating shoot and stand clumping into model for improved estimates of total APAR and canopy photosynthesis should not be particularly difficult. Tree density, useful for estimating APAR in both types of forests is commonly available from stand inventories and can be obtained for larger scale applications from certain remotely sensed products (Lefsky et al. 2002). Shoot clumping, on the other hand, has been quantified for many conifer species (see Thérezien et al. 2007).

Recently, Duursma and Mäkelä (2007) proposed recently a new structural parameter, tree leaf area per crown surface area ($L_A/S_A$), that can be used to estimate the effective extinction coefficient ($K_{eff}$) of the canopy (see their eqn. 9b). Our sensitivity analysis covers the range of values in their analysis and extends it to a much higher value. The relationship between $K_{eff}$ and $L_A/S_A$ changes with a lumped parameter $K_H$ (the extinction coefficient of homogeneous canopies, Duursma and Mäkelä (2007)) that was derived in their study from simulations done with a detailed 3D model and depends on the zenith angle ($\theta$) and shoot characteristics. Simulating PAR attenuation with our
model and extracting $K_{\text{eff}}$ based on either the average $L_A/S_A$ over the year or a dynamic $L_A/S_A$ reflecting the dynamics of leaf area and crown dimensions in the stand, produced a higher $K_{\text{eff}}$ than the one predicted from Duursma and Mäkelä (2007) parameterized with our average $L_A/S_A$ of 1.55 and $K_H$ which reflects our latitude but their shoot clumping ($K_H = -0.29$; Fig. 9A). Simulating our stand with all inputs the same except for varying crown width to generate a range of $L_A/S_A$, recovered the same shape of the relationship between $K_{\text{eff}}$ and $L_A/S_A$. Our line is shifted upward due in part to a differential account for shoot clumping (fixed $k$ in their paper and $\Pi^*G$ as a function of $\theta$ in our model). Running our model without tree clumping allowed us to extract $K_H$ for our stand (~0.34).

Although changing $K_H$ shifts the relationship between $K_{\text{eff}}$ and $L_A/S_A$ based on our model relative to Duursma and Mäkelä (2007), it does not change its curvature. In other words, there is little effect of shoot clumping and zenith angle on the relationship and the ratio of $K_{\text{eff}}$ between our and expected was $1.199 \pm 0.004$ (s.d). There is, however, an interaction effect of $\Pi$ and $\theta$ on $K_H$ (Fig. 9B) because in our model $G$ depends on $\theta$ (Eqn. 5b). We ran the model for a range of shoot clumping representing a large number of species (Thérézien et al. 2007) over a latitudinal range from 10° to 65° (and thus the mean $\theta$ in Fig 9) , and found that the latitudinal influence on $K_H$ increases with decreasing shoot clumping (i.e. increasing $\Pi$; Fig. 9C). Because the relationship for each
Π can be approximated as linear considering the range in values (Fig. 9B), we described the model results as linear (Fig. 9C), extracted the intercept and slope of the relationship between K_H and zenith angle at Π ranging by 0.1 from 0.2 to 0.9, and produced a relationship between the two parameters and Π (Fig. 9D; Note the two parameters are linearly related as Slope = -4.463*Intercept + 0.020). In this way, K_H can be estimated for any shoot clumping and zenith angle, thus allowing generalizing Duursma and Mäkelä (2007) approach globally and across forest types.

2.4.2.2. Effects on the vertical distribution of APAR

The model validation (Fig. 2) showed that in coniferous forests similar to the one at Duke Forest, not accounting for either shoot or stand clumping has a large impact on estimations of the vertical distribution of canopy openness and APAR. The sensitivity analysis of total APAR demonstrated that the impact of certain canopy specification may increase or decrease with increasing L. We therefore proceeded with the assessment of the effect of varying each component on the vertical distribution of APAR. To keep the comparisons manageable, we limited the stand/canopy conditions to four extreme cases, the combinations of the highest and lowest L and stand density, and we use vertically constant parameters.
Shoot clumping increases APAR in deeper canopy layers by decreasing absorption in the upper layers (Figure 6.A-D), and the effect increases with clumping as has been demonstrated in earlier modeling studies (e.g., Stenberg 1998, Niinemet et al. 2004). At low $L$, the redistribution of light benefits lower canopy strata but only where tree densities are high. At high $L$, moderate to high shoot clumping increases light penetration and APAR in mid-canopy, but does not enhance absorption of APAR at the bottom of the canopy. At high $L$ and tree density, absorption of PAR in canopies without shoot clumping is so high at the top that estimates of APAR lower in the canopy were very low. Although we did not represent the relative effect of clumping in these situation because the ratios are quite high and uncertain, these are the conditions in which shoot clumping would generate a substantial relative increase in lower canopy PAR conditions. Accounting for shoot clumping under such conditions would be essential for correctly estimating the carbon balance that permit trees to hang onto lower branches and for the success of recruitment and sub-canopy species (Brunner 1997, Kull and Kruijt 1998).

The effect of shoot clumping on the vertical distribution of APAR was different in cloudy and clear days. During cloudy days shoot clumping decreased APAR less in the upper canopy (relative to a canopy with no shoot clumping) than in clear days, and increased it more in mid-canopy in stands of low tree density, shifting to an increase in
lower canopy in stands of high density. Overall, in stands of low tree and canopy
density (both low TD and L), shoot clumping did not increase APAR at any layer in the
canopy. An increase in either density affected the distribution of APAR such that lower
absorption high in the canopy was compensated by higher absorption in mid-to-low
canopy.

Similar to shoot clumping, tree-level clumping decreased APAR in the upper
canopy and increased it in lower canopy layers (Figure 6.E-H). The effect was
particularly high at stands of low tree density, especially when L was high. At stands
with high tree density, the distribution of crowns approximates the continuous surface
of the canopy without specification of tree clumping. The interaction effect on the
distribution of APAR of stand clumping and shoot clumping is apparent by comparing
model estimates for the same L. (Note the difference in scales.) In all situations, the
effect of tree clumping increased with decreasing shoot clumping (i.e. as Π increased).
This means that accounting for the clumping of foliage in crowns has an increasing
effect on APAR distribution with decreasing shoot clumping, and the effect is larger in
cloudy than clear days. Indeed, accounting for tree level clumping on APAR and its
vertical distribution is most important in stands of broadleaved species where leaves are
not very clumped on shoots (Kim et al. 2008; Chen et al. 1996, Niinemets et al. 2004), and
optical estimates of total clumping reflect clumping at levels larger than a shoot (Chen et
al 1996, Nilson et al. 1999, Mottus et al. 2004, Niinemets et al. 2004). However, in stands of high $L$, accurate estimation of APAR distribution requires that tree density is explicitly incorporated in the model, even in coniferous forests with highly clumped shoots.

Leaf angle distribution can have large effect on the penetration of light through the canopy (Figure 7). Foliage oriented more vertically (LAD0.5) than a spherical distribution (LAD1.0) decreases the absorption of PAR in the upper canopy, making more light available for absorption in lower canopy layers. Conversely, more horizontally oriented foliage absorbs much of the PAR high in the canopy, allowing less to penetrate into the lower canopy. Under cloudy conditions, the LAD-imposed redistribution of APAR relative to that with a spherical distribution was not very large in any combination of tree densities and $L$. However, in clear days, very large effects were observed in dense stands with dense canopies (Fig. 7 D & H), especially when foliage was not very clumped in shoots. Even in stands and canopies of lower densities, APAR redistribution generated an increase or decrease of the estimate of APAR of $>10\%$ in some layers. In such stands the changes were particularly large when foliage was clumped. The vertical pattern observed in APAR with changing LAD relative to APAR with spherical distribution is caused by similar reasons generating the pattern with introducing shoot clumping (Figure 6.A-D).
Orienting foliage vertically in open stands resulted in a reduced APAR at all canopy layers, much like having highly clumped foliage on shoots. On the other hand, horizontal orientation in such stands increased absorption of PAR at all layers, regardless of the shoot clumping, but the effect was largest in canopies with highly clumped shoots. Among the published results on the effects of leaf angle distribution on APAR and vertical PAR, some show a small effect (Gourdiaan 1996, Oker-Blom and Kellomäki 1982) and others a relatively large effect (Stadt and Leffers 2000, this study). This disagreement likely reflects the degree and direction of the difference between the modeled and actual LAD in the canopy (Thomas and Winner 2000, Wirth et al. 2001), and the mean sun angle (Oker-Blom and Kellomäki 1982). Moreover, as is shown here it is also controlled by the interaction between LAD and clumping into shoots.

Overall, our sensitivity analysis shows similar priority as other studies. Stadt and Lieffers (2000) claimed that the highest influence of the parameters in the model on stand level light transmission predictions was $L$ followed by the crown radius, crown length and foliage inclination.

2.4.2.3. Effects of varying shoot and stand clumping and leaf angle distribution on the vertical distribution of APAR

In forest canopies, decreasing shoot clumping with depth in the canopy and changing leaf angle distribution should distribute light more evenly relative to the
constant specification we used in the sensitivity analysis (Stenberg 1998). For most applications, the information needed for such detailed specification of canopy attributes may be impractical.

We tested the effects of using constant versus vertically variable shoot clumping and leaf angle distributions (see Figure 1 for the parameterization), changing tree clumping from the canopy to the sub-canopy layer. The results show that, depending on the simplification and the canopy layer, estimated openness ranged from -5% to +8% relative to the most realistic model (v7), while APAR ranged from -8% to +15%. Using constant values for both shoot clumping and leaf angle distribution (v4) underestimated both quantities at the top of the canopy and overestimated them at the bottom, representing the worst overall agreement. Allowing LAD to vary vertically but keeping $\Pi$ constant (v6) resulted in overestimation at the top similar to that of v4, but a very good agreement at the bottom, and the best overall agreement with the most realistic model. Finally, allowing $\Pi$ to vary vertically but keeping LAD constant (v5) produced a very close agreement with v7 at the top of the canopy, but the agreement deteriorated with depth in the canopy.
2.5. Conclusions

Our validation exercise showed that in a stand with a canopy dominated by pine with a substantial component of broadleaved species, and a sub-canopy composed entirely of broadleaves species, accounting for mean shoot and tree clumping was needed to reproduce measured openness and PAR gradient with depth the canopy, but had little effect on total APAR. Further improvements incorporating variable leaf angle distribution and shoot clumping made only small additional changes in the vertical distribution of APAR.

The sensitivity analysis showed, however, that not accounting for shoot clumping would result in an overestimation of total APAR, potentially by substantial amounts, with errors increasing with decreasing canopy leaf area. Not accounting for tree density would also lead to substantial overestimation of APAR, but only in low density stands. The effect of tree clumping on APAR is largely independent of canopy leaf area index.

Altogether, accounting for tree clumping is most important in stands of broadleaved species where leaves are not very clumped on shoots, while, even in coniferous forests with highly clumped shoots, accurate estimation of APAR distribution in stands of high $L$ requires that tree density is explicitly incorporated in the model. At present, information on both variables, tree density and shoot characteristics, are
commonly available and their incorporation into canopy photosynthesis models relatively simple.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Unit</th>
</tr>
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<tbody>
<tr>
<td>BA</td>
<td>branch surface area</td>
<td>m&lt;sup&gt;2&lt;/sup&gt; m&lt;sup&gt;-2&lt;/sup&gt;</td>
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<tr>
<td>G(z,x(z),θ)</td>
<td>G-function</td>
<td>dimensionless</td>
</tr>
<tr>
<td>K&lt;sub&gt;be&lt;/sub&gt;(θ)</td>
<td>extinction coefficient in the zth layer</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>K&lt;sub&gt;be&lt;/sub&gt;&lt;sub&gt;-&lt;/sub&gt;branch(z)</td>
<td>branch extinction coefficient in the zth layer</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>K&lt;sub&gt;be&lt;/sub&gt;&lt;sub&gt;-&lt;/sub&gt;leaf(z)</td>
<td>leaf extinction coefficient in the zth layer</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>K&lt;sub&gt;be&lt;/sub&gt;&lt;sub&gt;-&lt;/sub&gt;stem(z)</td>
<td>stem extinction coefficient in the zth layer</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>K&lt;sub&gt;be&lt;/sub&gt;&lt;sub&gt;-&lt;/sub&gt;total(z)</td>
<td>average extinction coefficient to the zth layer weighted with leaf area in each layer</td>
<td>dimensionless</td>
</tr>
<tr>
<td>L</td>
<td>leaf area index</td>
<td>m&lt;sup&gt;2&lt;/sup&gt; m&lt;sup&gt;-2&lt;/sup&gt;</td>
</tr>
<tr>
<td>L(z)</td>
<td>leaf area density in the zth layer</td>
<td>m&lt;sup&gt;2&lt;/sup&gt; m&lt;sup&gt;-2&lt;/sup&gt;</td>
</tr>
<tr>
<td>L&lt;sub&gt;c&lt;/sub&gt;(z)</td>
<td>cumulative leaf area index to the zth layer</td>
<td>m&lt;sup&gt;2&lt;/sup&gt; m&lt;sup&gt;-2&lt;/sup&gt;</td>
</tr>
<tr>
<td>N</td>
<td>stand density</td>
<td>trees m&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td>Q</td>
<td>photosynthetic photon flux density</td>
<td>µmol m&lt;sup&gt;2&lt;/sup&gt; ground s&lt;sup&gt;-1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Q&lt;sub&gt;o&lt;/sub&gt;</td>
<td>photosynthetic photon flux density above the canopy</td>
<td>µmol m&lt;sup&gt;2&lt;/sup&gt; ground s&lt;sup&gt;-1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Q&lt;sub&gt;avg&lt;/sub&gt;</td>
<td>canopy average photosynthetic photon flux density</td>
<td>µmol m&lt;sup&gt;2&lt;/sup&gt; leaf s&lt;sup&gt;-1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Q&lt;sub&gt;b&lt;/sub&gt;</td>
<td>direct radiation</td>
<td>µmol m&lt;sup&gt;2&lt;/sup&gt; ground s&lt;sup&gt;-1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Q&lt;sub&gt;b&lt;/sub&gt;(z)</td>
<td>direct radiation at the bottom of the zth layer</td>
<td>µmol m&lt;sup&gt;2&lt;/sup&gt; ground s&lt;sup&gt;-1&lt;/sup&gt;</td>
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<tr>
<td>Q&lt;sub&gt;d&lt;/sub&gt;</td>
<td>diffuse radiation</td>
<td>µmol m&lt;sup&gt;2&lt;/sup&gt; ground s&lt;sup&gt;-1&lt;/sup&gt;</td>
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<tr>
<td>Q&lt;sub&gt;d&lt;/sub&gt;(z)</td>
<td>diffuse radiation at the bottom of the zth layer</td>
<td>µmol m&lt;sup&gt;2&lt;/sup&gt; ground s&lt;sup&gt;-1&lt;/sup&gt;</td>
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<td>Q&lt;sub&gt;ob&lt;/sub&gt;</td>
<td>direct radiation at the top of the canopy</td>
<td>µmol m&lt;sup&gt;2&lt;/sup&gt; ground s&lt;sup&gt;-1&lt;/sup&gt;</td>
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<tr>
<td>Q&lt;sub&gt;od&lt;/sub&gt;</td>
<td>diffuse radiation at the top of the canopy</td>
<td>µmol m&lt;sup&gt;2&lt;/sup&gt; ground s&lt;sup&gt;-1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Q&lt;sub&gt;s&lt;/sub&gt;</td>
<td>scattered radiation</td>
<td>µmol m&lt;sup&gt;2&lt;/sup&gt; ground s&lt;sup&gt;-1&lt;/sup&gt;</td>
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<tr>
<td>Q&lt;sub&gt;s&lt;/sub&gt;(z)</td>
<td>scattered radiation at the bottom of the zth layer</td>
<td>µmol m&lt;sup&gt;2&lt;/sup&gt; ground s&lt;sup&gt;-1&lt;/sup&gt;</td>
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<tr>
<td>S(z,θ)</td>
<td>projected area of tree crown in zth layer at the zenith angle θ</td>
<td>m&lt;sup&gt;2&lt;/sup&gt;</td>
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<td>SA</td>
<td>stem surface area</td>
<td>m&lt;sup&gt;2&lt;/sup&gt; m&lt;sup&gt;-2&lt;/sup&gt;</td>
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<tr>
<td>a(θ, z)</td>
<td>the mean gap fraction of the zth layer in a single tree crown at the view angle θ</td>
<td>dimensionless</td>
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<tr>
<td>x(z)</td>
<td>ratio of average projected areas of canopy leaves on horizontal and vertical surfaces in the zth layer</td>
<td>dimensionless</td>
</tr>
<tr>
<td>Z</td>
<td>height from the ground</td>
<td>m</td>
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Table 2.1. Continued

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<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Unit</th>
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<tr>
<td>$\tau_b$</td>
<td>sunlit proportion</td>
<td>dimensionless</td>
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<tr>
<td>$\tau_b(z, \theta)$</td>
<td>sunlit proportion in the $z$th layer at the zenith angle $\theta$</td>
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<td>$\tau_{b,\text{total}}(z, \theta)$</td>
<td>average direct radiation transmission coefficient to the $z$th layer weighted with leaf area in each layer at the zenith angle $\theta$</td>
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<td>$\tau_{b}(z, \theta)$</td>
<td>total radiation transmission coefficient in the $z$th layer at the zenith angle $\theta$</td>
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<td>$\tau_d(z)$</td>
<td>diffuse radiation transmission coefficient in the $z$th layer</td>
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<tr>
<td>$\Pi$</td>
<td>shoot clumping</td>
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<tr>
<td>$\Theta$</td>
<td>zenith angle of the sun</td>
<td>radian</td>
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Table 2.2 Model descriptions for various versions

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<tr>
<th>Ver</th>
<th>Description</th>
<th>Shoot clumping</th>
<th>Tree clumping</th>
<th>Leaf angle distribution</th>
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<tr>
<td></td>
<td></td>
<td>Constant</td>
<td></td>
<td>Spherical</td>
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<tr>
<td>1</td>
<td>Simple Beer-Lambert</td>
<td>x</td>
<td></td>
<td>x</td>
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<tr>
<td>2</td>
<td>Shoot clumping ($I_f$)</td>
<td>x</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>3</td>
<td>Tree clumping</td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>4</td>
<td>Constant $I_f$ and LAD</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>5</td>
<td>Vertically variable $I_f$</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>6</td>
<td>Vertically variable LAD</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>7</td>
<td>Complete model</td>
<td>x</td>
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Table 2.3. Regression outputs from different model versions

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<th>Openness</th>
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<th></th>
<th>PAR</th>
<th></th>
<th></th>
<th></th>
<th>difference in total APAR(%)</th>
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<tbody>
<tr>
<td></td>
<td>slope</td>
<td>intercept</td>
<td>r^2</td>
<td>MSE</td>
<td>slope</td>
<td>intercept</td>
<td>r^2</td>
<td>MSE</td>
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Table 2.4. Stand density and crown characteristics

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<th>Tree density (trees ha(^{-1}))</th>
<th>100</th>
<th>500</th>
<th>1000</th>
<th>1500</th>
<th>2000</th>
<th>3000</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree height (m)</td>
<td></td>
<td></td>
<td></td>
<td>21</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crown length (m)</td>
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<td>12</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>Crown width (m)</td>
<td>5</td>
<td>4</td>
<td>3.6</td>
<td>3.35</td>
<td>3.1</td>
<td>2.8</td>
</tr>
</tbody>
</table>
Figure 2.1. A sample of the vertical distribution of the surface areas of (A) leaves, (B) branches and (C) stems as was used in all models, with broadleaved species represented by dashed lines. In (A) a continuous thin line represent the foliage profile in the non-growing season. Vertical distributions of (D) shoot clumping (Π) and (E) the parameter describing leaf angle distribution (x) used in the most detailed model (v7, see text), and the extremes of crown dimensions and shape used in all models except v1 and v2, which did not include tree clumping.
Figure 2.2. Diurnal pattern of incoming photosynthetically active radiation during the summer solstice assuming either a cloudy day with only diffuse component or a clear day with both diffuse and direct components (thick lines). These patterns were used as input to all model versions.
Figure 2.3. Comparison of (A) canopy openness and (B) photosynthetically active radiation (PAR) estimated based on the most complete model (v7) with measured values taken vertically in the canopy and on the ground. The measurements taken vertically are presented against relative canopy height (C & D) along with the estimates from v7 and the simplest model (v1). The relative difference between measured (E) openness and (F) PAR and estimates from each model version at each canopy layer are shown along with the standard error. See Table 2 for a brief description of each model version. A comparison between (G) openness and (H) PAR estimated with each model version and normalized by the measured values along a range of leaf area index. The data was selected for heights in the canopy and seasons in which broadleaved species do not affect light attenuation so the effect of accounting for pine shoot clumping is amplified.
Figure 2.4. The effect on absorbed photosynthetically active radiation (APAR) by the entire canopy of accounting for (A & B) shoot clumping of different degree (most clumped \( \Pi = 0.2 \)), (C & D) tree clumping representing three densities (and crown properties, see Figure 1) and (E – H) leaf angle distribution that is more vertically orientated than spherical (LAD0.5/LAD1.0) and more horizontally oriented (LAD3.0/LAD1.0) over a range of leaf area index. Results are shown for a clear day (left panels) and a cloudy day (see Figure 2).
Figure 2.5. The effect on absorbed photosynthetically active radiation (APAR) of tree clumping, which is calculated based on crown shape and size and tree density and changes with the sun angle, can be effectively represented based on the ratio of the crown shadow area relative to the ground area (NS, see Equation 3). At low values of NS, the effect of tree clumping is to reduce APAR with increasing leaf area index relative to randomly distributed canopy, reaching a stable minimum. As NS increases above 1.0, the pattern changes and the effect of tree clumping decreases (see text for explanation).
Figure 2.6. The effect on absorbed photosynthetically active radiation (APAR) at each layer in the canopy of accounting for (A - D) shoot clumping of different degree (most clumped Π = 0.2) at four combinations of low and high tree densities and low and high leaf area index, and (E - H) tree clumping at the same combinations. Thin lines represent effects during a cloudy day of a subset of shoots. Note the differences in scales among the four panels representing the effects of tree-clumping on APAR.
Figure 2.7. The effect on absorbed photosynthetically active radiation (APAR) at each layer in the canopy of accounting for (A - D) leaf angle distribution that is more vertically orientated than spherical (LAD0.5/LAD1.0) and (E – H) more horizontally oriented (LAD3.0/LAD1.0) with shoot clumping of different degree (most clumped $\Pi = 0.2$) at four combinations of low and high tree densities and low and high leaf area index. Thin lines represent effects during a cloudy day of a subset of shoots. Note the differences in scales among the panels.
Figure 2.8. The relative difference in (A) openness and (B) absorbed photosynthetically active radiation between the most complete, vertically specified model (v7) and models that allow either shoot clumping (v5) or leaf angle distribution (v6) or neither (v4) to vary down the canopy.
Figure 2.9. (A) The effect of leaf-to-crown surface area ($L_A/S_A$) on the effective light extinction coefficient ($K_{eff}$) based on Duursma and Mäkelä (2007; the extinction coefficient of homogeneous canopies, $K_H = \sim 0.29$) in comparison to results produced based on our model (see text for details). (B) The effect of zenith angle on $K_H$ based on Duursma and Mäkelä (2007) versus results from our model, with differences reflecting the influence of different shoot clumping and the G function in our model. (C) Relationships as shown in (B) but linearized for stands with a range of shoot clumping ($\Pi$). (D) The effects of $\Pi$ on the intercept (Intercept = $-0.405*\Pi + 0.022$) and slope (slope = $1.808*\Pi + 0.081$) extracted from the linear relationships shown in (C).
Chapter 3. Fifteen-year response of the water budget and its components to elevated atmospheric CO$_2$ and nitrogen fertilization in a loblolly pine forest

3.1. Abstract

The terrestrial balance between precipitation and evaporation determines drainage and surface runoff, recharging the water table and reservoirs. Forests play an important role in this balance by mediating the transfer of water from the land to the atmosphere. Thus, evaporative responses of forests to increasing atmospheric CO$_2$ concentration and nitrogen (N) deposition may have appreciable implications to the hydrological cycle and water availability, with considerable ecological and economical consequences. Here we perform in a Pinus taeda (loblolly pine) forest the most comprehensive assessment of the hydrological budget and all its components over 15 years (1993-2007), including 14 years of CO$_2$ enrichment (whole plot, $n=4$) and nine years of N fertilization (split plot), on the background of naturally varying climatic conditions. The budget was based on up to 240 sap flux (constant heat dissipation) sensors measuring up to four species and scaled to canopy transpiration ($E_c$), environmental sensors, and modeling. Using the budget components we evaluated whether treatment-induced increase in leaf area index ($L$) led to (1) higher evaporation from canopy rainfall interception ($I_c$), and (2) higher $E_c$. We also evaluated whether higher thickness of the
litter layer led to (3) higher evaporation from rain water stored in the litter \((E_L)\), compensated for by (4) lower evaporation from the soil surface \((E_S)\) due to decreased amount of soil moisture and increased resistance to vapor exchange with the atmosphere. Ultimately, we wished to assess how the combined evapotranspiration (i.e., the sum of the four components) responded to the treatments and assess the effect on water yield (i.e. the sum of overland runoff and drainage below the rooting zone). We found that none of the components responded to the N amendment. On the other hand an average of 14% increase in \(L\) under elevated CO\(_2\) was accompanied by a (not significantly) higher \(I_c\) (~15%), reducing throughfall precipitation \((P_T)\) by up to 6% during the last few years of the study. In contrast, the increase in \(L\) had little to no effect on \(E_c\). \(E_l\) indeed increased slightly (but not significantly) under elevated CO2 while \(E_s\) decreased such that their sum was largely unaffected. The CO\(_2\)-induced (and perhaps N-induced) routing of water from overland flow \((F_o)\) to infiltration, via the increased amount of litter on the forest floor, results in higher average soil moisture despite the lower \(P_T\). The increase was small and coupled with a layer of very low hydraulic conductivity below the rooting zone resulted in no increase in drainage. Thus, the increased evaporation due to higher \(L\) and thus rainfall interception resulted in a lower water yield, and might ultimately be the main effect of elevated CO\(_2\), especially if N is not limiting (McCarthy et al. 2007), in similar forests.
3.2. Introduction

The balance between precipitation and evaporation over land determines surface runoff, returning water from continents to oceans (Gedney et al, 2006) and, on the way, recharging the water table and reservoirs. Forests play an important role in the global hydrological cycle by mediating the transfer of water from the land surface to the atmosphere (i.e. evapotranspiration; Drake et al. 1997, Sarmiento and Wofsy, 1999). Thus, evaporative responses of forest ecosystems to increasing atmospheric CO$_2$ concentration and nitrogen (N) deposition may have appreciable implications to the hydrological cycle and water availability (Rind et al. 1992, Reay et al. 2008), with considerable effects on ecosystem function and composition and on economics at regional and larger scales (Milly et al. 2005).

Elevated CO$_2$ reduces stomatal conductance of many species (e.g. Bazzaz 1990, Drake et al. 1997, Bunce 1998, Lockwood 1999, Medlyn et al. 2001, Herrick et al. 2004) and, provided that drivers of transpiration do not change much, reduce transpirational water loss at the leaf scale. Thus, increases of surface runoff observed over the past century were attributed to increasing atmospheric CO$_2$ concentrations (Matthews 2006), and further substantial increases are projected in many regions based on results from general circulation models (Milly et al. 2005), despite the accompanying potential warming-induced increases in the saturation vapor pressure of air (Allen and Ingram...
2002). Indeed, although a reduction in forest evapotranspiration would increase runoff and provide for downstream users of all sorts, it may also lead to warmer surface and further climate consequences.

However, elevated CO$_2$ may also lead to a higher canopy leaf area index ($L$). Where water availability limits $L$, water savings accrued via CO$_2$-induced reductions in transpiration rates at the leaf scale may allow an increase of $L$ (Woodward 1990). Where water is less or not limiting, higher atmospheric CO$_2$, commonly stimulating photosynthesis regardless of stomatal response (e.g., Wong et al. 1978, Sage 1994; Drake et al. 1997; Saxe et al. 2001, Schäfer et al. 2003, Crous and Ellsworth 2004, McCarthy 2007), would increase the availability of carbohydrates for production of all plant parts, again leading to stands carrying higher $L$ (Pataki et al., 2005, McCarthy et al. 2007). Increased $L$ where it is limited by water availability would result in the ecosystem recovering a similar amount of water used in evapotranspiration; although total evapotranspiration would recover, the partitioning to transpiration may be lower and compensated for by increased evaporation of intercepted water (Woodward 1990, Sage 1994; Drake et al. 1997; Saxe et al. 2001; Schäfer et al. 2002, Urban 2003). Increased $L$ where it is not limited by water availability would result in increasing evapotranspiration and decreased runoff, unless stomatal conductance decreases in response to higher [CO$_2$] or greater mutual shading within the denser canopy.
Increased N supply might lead to higher stand scale transpiration rate ($E_c$) by increasing both the physiological activity of foliage and the stand $L$ (Ewers et al. 2000, 2001, Samuelson et al. 2008). Although foliage richer in N invested in photosynthetic enzymes photosynthesizes at higher rates (McGuire et al. 1995; Sand 1995; Crous et al. 2008, Luis et al. 2009), and thus likely has higher conductance (Samuelson et al. 2008), photosynthetic enhancements in response to fertilizer applications are typically transient (Maier et al., 2008). Furthermore, where N limitation is alleviated, more of the extra carbohydrates produced under elevated CO$_2$ are allocated to the production of aboveground components (Palmroth et al., 2006), leading to further increases in $L$ (McCarthy et al., 2007). Higher $L$ increases the rate at which water is used, forcing more extended periods of water stress even in wet climates and causing plants to produce tissues of lower vulnerability to cavitation, accompanied by lower hydraulic conductivity and lower maximum stomatal conductance (Ewers et al. 2000, Domec et al. 2009). Taken together, the effect of increased N availability would likely lead to increased $E_c$ only if concomitant reductions in stomatal conductance do not fully compensate.

The combined effects of high [CO$_2$] and N deposition on the hydrological cycle will likely reflect the relative changes in physiology (stomatal conductance) and canopy structure ($L$), and their integrated effect on transpiration and evaporation (Woodward
Furthermore, treatment-induced changes in litter and soil organic matter may affect evaporation, runoff, infiltration and drainage, the overall effect of which would be reflected in soil moisture, forming a feedback to transpiration. Thus, only a comprehensive assessment of all components of the hydrologic budget would allow identifying which has changed under treatment and which compensated for that change.

*Pinus taeda* L. (loblolly pine) is the most planted species worldwide, covering in the United States alone an area of 130,000 square kilometers, in both managed and unmanaged forests (Schultz 1997, Martin and Jokela 2004). This makes the response of loblolly pine to changing atmospheric conditions important regionally to the southeastern super region of the U.S., and increasingly in other continents as well. Moreover, a managed forest of this species has been subjected to elevated CO$_2$ in otherwise unaltered state since 1994 (+200 ppmv), transitioning from an open to closed canopy conditions (McCarthy et al., 2007), doubling in height (McCarthy et al., in press), and experiencing droughts, storms and an additional sub-plot N addition implemented partway into the study. This longest running free-air CO$_2$ enrichment (FACE) experiment comes closest than any to informing us of the future hydrologic behavior of forests composed of similar species, because all components of the hydrological cycle were measured or, if this was not possible, parameters and variables necessary for
modeling were obtained continuously for 15 years. In this study we concentrate on annual values of the hydrological budget components to determine whether elevated atmospheric [CO$_2$], without or with N amendment, altered the balance in favor of runoff at the expense of evapotranspiration.

*P. taeda* is a shade intolerant species and has been shown highly sensitive to soil drought (Oren et al., 1998, Ellsworth 1995, Ewers et al. 2000, Ellsworth and Roger 2004, Stoy et al. 2006), leading to the observation that evapotranspiration ($E_T$) of *P. taeda* stands is more sensitive to precipitation ($P$) than that of nearby Oak-Hickory type forests (Pataki and Oren 2003, Stoy et al. 2006). The hydrological budget of the pine forest subjected to the Duke FACE experiment for the period 1998-2000 showed no effect of elevated CO$_2$ on evapotranspiration, although the average soil moisture was higher in plots enriched with CO$_2$ (Schäfer et al. 2002). The higher moisture was attributed to topographically driven routing of water out of two of the current CO$_2$ plots and into two of the elevated CO$_2$ plots, a reduction in forest floor evaporation due to increased thickness of the litter layer in elevated CO$_2$ plots, and perhaps increase in water holding capacity of the soil due to increased soil organic matter content (Schlesinger and Lichter 2001). During that period of the study, investigations showed that *P. taeda*, the dominant species in the forest, has foliage with stomata that is insensitive to increasing CO$_2$ (Ellsworth 1995, 1999, Pataki et al. 1998, Schäfer et al. 2002), and that $L$ did not seem
to increase under elevated CO$_2$ (Schäfer et al. 2002). It was therefore not particularly surprising that $E_T$ was unaffected as well.

However, since then, investigations revealed a number of hydraulic and hydrological changes under elevated CO$_2$ that could influence $E_T$ and the hydrological budget. First, stomatal conductance of $P.\text{taeda}$ foliage seems to be lower under elevated than current CO$_2$ when the soil is moist due to hydraulic adjustments (Domec et al., 2009). Second, new calculations showed that $L$ has indeed increased by elevated CO$_2$ an average of $\sim$14% (beginning already in 1998), reaching $\sim$40% enhancement when combined with N fertilization (McCarthy et al. 2007). Third, standing biomass of fine roots also increased (e.g., Matamala and Schlesinger 2001, Pritachard et al. 2008, Jackson et al. in press), allowing better access to soil moisture (Sperry et al. 1998, Hacke et al. 2000, Ewers et al 2001). However, addition of N reduced the amount of fine roots under both [CO$_2$] conditions (Butnor et al. 2003, Palmroth et al. 2006, Drake et al. 2008). And forth, the increase of $L$ under elevated CO$_2$ produced a thicker litter layer (Schlesinger and Lichter 2001 Finzi et al. 2007, McCarthy et al. 2007 Lichter et al. 2008), which might be further thicken by N fertilization, with potential implication to surface evaporation and runoff (Schäfer et al. 2002). Furthermore, CO$_2$-induced lower canopy vulnerability to ice storm (McCarthy et al., 2006) infused potential inter-annual dynamic to the effect of CO$_2$ on the hydrologic budget of the forest.
The hydrologic budget at the site has been established a few times at the site, often concentrating on only a few components or a short time (Oren et al. 1998, Phillips and Oren 2001) or on many components during few years (Schäfer et al. 2002). Here we perform the most comprehensive assessment of the budget and all of its components over 15 years (1993-2007), including 14 years of CO\(_2\) enrichment and nine years of N fertilization, on the background of naturally varying climatic conditions. Using the budget components we evaluated whether treatment-induced increase in \( L \) led to (1) higher evaporation from canopy rainfall interception (\( I_C \)), and (2) higher \( E_C \). We also evaluated whether higher thickness of the litter layer led to (3) higher evaporation from rain water stored in the litter (\( E_L \)), compensated for by (4) lower evaporation from the soil surface (\( E_S \)) due to decreased amount of soil moisture and increased resistance to vapor exchange with the atmosphere. Ultimately, we wished to assess how the combined evapotranspiration (i.e., the sum of the four components) responded to the treatments and assess the effect on water yield, the sum of overland runoff and drainage below the rooting zone.

**3.3. Material and Methods**

**3.3.1. Setting**

The experiment is located in a plantation established in 1983 on a site of fairly even terrain in the Blackwood division of Duke Forest, North Carolina (35°58′ N, 79°08′
W, elevation 163m). The moderate fertility site contains acidic clay-loam soil (Enon series), increasing in depth and fertility with slight changes of elevation (McCarthy et al. 2007). The climate is characterized by warm and humid summers and moderate winters with a mean annual temperature of 15.8 °C. Precipitation is distributed approximately evenly throughout the year, with a 111-year average of 1145 mm. In early 2007 pines reached 24 m in height and comprised over 80 % of the sapwood area at breast height (Table 1). Common broadleaf species include sweetgum (*Liquidambar styraciflua*) and tulip (yellow) poplar (*Liriodendron tulipifera*) in the mid to upper canopy, and red maple (*Acer rubrum* L.), winged elm (*Ulmus alata* Michx.) and flowering dogwood (*Cornus florida* L.) in the mid to lower canopy.

In 1993 an untreated 15 m radius plot (plot 8) was established as a part of another study, followed in 1994 by the nearby FACE prototype plot of similar dimensions (FACEp; plot 7). CO₂ enrichment (550 ppmv during daylight hours of the growing season) delivered by 32 vertical pipes surrounding plot commenced in 1994 according to the FACE protocol (Hendrey et al. 1999). The infrastructure for the replicated FACE experiment (plot 1-6) was completed in 1996 and CO₂ enrichment (+200 ppmv) commenced in three of the plots in August of that year. The enrichment with CO₂ continues the entire year at times in which the ambient temperature was higher than 5 °C and wind speed was less than 5.0 m s⁻¹. Beginning 2006, CO₂ enrichment was
performed during the daylight only in all plots. Each plot has radial boardwalks
oriented north-south and east-west, and a central tower.

In the fall 1998, plots 7 and 8 were split in half, using impermeable barrier to a
depth of 0.7 m – well below the rooting zone, and one half of each plot as well as 7.5 m
buffer arching outside the plot received annual nitrogen addition (11.2 g N m\(^{-2}\) yr\(^{-1}\)).
Since 2005, plots 1-6 began to receive a similar treatment.

Each tree of diameter ≥ 20 mm at 1.35 m aboveground was equipped with a steel
dendrometer band from which diameter has been calculated weekly (McCarthy et al., in
press). Before the installation of dendrometer band, diameter of all trees had been
measured during the non-growing season of each year (Phillips and Oren 2001, Schäfer
et al. 2002), as has been diameter of trees <20 mm in diameter during the period in which
dendroband data was available (See McCarthy et al. 2007 for detailed description).
Diameter measurements were corrected for bark thickness (McCarthy et al., in press)
and used to estimate sapwood area per unit ground area (\(AS:AG\)) for each species. \(L\) was
obtained from McCarthy et al. (2007) and leaf litter mass (\(LM\)) from Lichter et al. (2008),
interpolating between the measurement years using a relationship between \(LM\) and
yearly maximum \(L\) and the continuous record of maximum \(L\) from McCarthy et al.
(2007).
3.3.2. Environmental measurements

Air temperature (T\text{air}) and relative humidity, used for calculating vapor pressure deficit (VPD), was measured in the upper third of the canopy in each plot (Vaisala HMP35C and HMP45C; Helsinki, Finland). Beginning in 1997, volumetric soil water concentration of the upper 30 cm soil layer was measured continuously at four locations in each of plots 1-6 (CS615 or CS616; Campbell Scientific, Logan, Utah, USA); since 2001, volumetric soil water content was measured continuously at eight locations, with four probes measuring at 5-10 cm depth and four probes at 25-30 cm depth in each of plots 7 and 8 (ThetaProbe ML1x or ML2x; Delta-T Devices, Cambridge, UK). On the central tower above the canopy of plot 4, sensors for measurements of photosynthetic photon flux density PPFD (Q190; LiCor, Lincoln, Nebraska, USA), net radiation R\text{n} (REBS Q*7; Radiation and Energy Balance System Inc., Seattle, Washington, USA), and precipitation P (tipping bucket TI; Texas Instruments, Austin, Texas, USA) were mounted. All sensors were sampled every 30 s, and 30 minute averages were logged (CR21X or CR23X; Campbell Scientific, Logan, Utah, USA). In addition, in each measurement plot precipitation throughfall (P_{t}) was measured with four to eight 10 cm diameter rain gauges (Productive Alternatives Inc., Fergus Falls, Minnesota, USA) randomly distributed in each plot in 1998 and manually recorded (at 0.2 mm accuracy) at approximately weekly intervals.
3.3.3. Sap flux measurements

In each plot, *P. taeda* and *L. styraciflua*, and for a period of time *C. florida* and *U. alata* were selected for sap flux measurements based on the Granier-type constant heat dissipation sensor (Granier et al. 1987). The sensor consists of a heated (200 mW) and a reference probe, 20 mm long and 2 mm in diameter. The heated probe was placed 12-15 cm above the reference probe to prevent thermal interference; the distance is sufficiently small to avoid large thermal gradients in the tree trunk (Goulden and Field, 1994). Sensors were installed in the outer 20 mm of the xylem towards north and covered with a radiation shield to protect from direct radiation. Heat flux density was monitored every 30 s, and 30 min averages were stored on the logger used for storage of environmental data. The signal was converted to sap flux density (J$s$ in g H$_2$O m$^{-2}$ sapwood s$^{-1}$).

The number of sensors increased as the experimental setup changed and as tree sapwood depth increased (Table 2). The deeper sensors were positioned only in trees with wide hydroactive xylem and did not protrude into the heartwood, so corrections were not needed (Clearwater et al., 1999). In plot 8, sap flux was monitored in 10 *P. taeda* and two *L. styraciflua* trees beginning in April, 1993. In April, 1997, three *L. styraciflua* trees were added and in April, 1999, following fertilization, sensors where assigned such
that five *P. taeda* and one of five *L. styraciflua* trees were in the fertilized half and five and four trees of these species, respectively, in the unfertilized half. In plot 7, sap flux was monitored in 10 *P. taeda* and three *L. styraciflua* trees beginning in April, 1994. In April, 1997, nine *P. taeda* and two *L. styraciflua* trees were added and in April, 1999, after fertilization, 11 of 19 *P. taeda* and two of five *L. styraciflua* monitored trees were in the fertilized half, with the remaining in the unfertilized half. In early 2001, both plot 7 and 8 had 15 outer sensors (0 – 20 mm from the cambium), 5 mid-depth sensors (20 – 40 mm) and 5 inner sensors (40 – 60 mm) in *P. taeda* trees and 5 outer sensors in *L. styraciflua* in each fertilized and unfertilized halves (Phillips and Oren 2001, Schäfer et al. 2002). In plots 1-6, flux in eight *P. taeda* and four *L. styraciflua* trees was monitored since May, 1997. In October, 1998, two mid sensors were added to two of the *P. taeda* trees, and in February, 2002, additional two mid-depth and two inner sensors were installed. Also, two mid-depth sensors were added to two of the *L. styraciflua* trees. At the end of the study, a total of 240 sensors were continuously monitored.

For approximately three years, beginning in April, 1998, flux in five *C. florida* and *U. alata* in each CO₂ treatment was monitored (Schäfer et al., 2002). Sample *C. florida* were one per plot while sample *U. alata* trees were distributed regardless of plot due to uneven distribution of individuals of these species, and were followed only as long as
necessary to ascertain that their contribution to stand-level transpiration was very small, due to low values of both flux and sapwood area per unit of ground area.

3.3.4. Scaling flux to transpiration

Transpiration of trees in each size class (see Results for class definition) was calculated by multiplying treatment average $J_S$ with the corresponding sapwood area, assuming that the average flux of the innermost sensors apply across the deeper hydroactive xylem (mm).

$$E_{\text{class}} = \frac{J_{S_{0-20}} AS_{0-20} + J_{S_{20-40}} AS_{20-40} + J_{S_{40-60}} AS_{40-\text{MAX}}}{AG}$$

Canopy transpiration ($E_C$, mm m$^{-2}$ ground area s$^{-1}$) was calculated by summing the transpiration of the classes (Oren et al. 1998).

3.3.5. Hydrological balance

In closed systems, water input, output and storage in the system should balance out, with the combined errors reflected in the residual component ($R$). Thus,

$$P = I_C + E_C + E_L + E_S + F_o + Q + \Delta S + R$$

where $P$ is precipitation, $I_C$ is precipitation interception in the canopy, $E_C$ is stand level transpiration, $E_L$ and $E_S$ are evaporation from litter and soil layer, respectively, $F_o$ is
overland flow, $Q$ is drainage below the rooting zone – here set at 30 cm, $\Delta S$ is the change in soil moisture content (i.e., change in water storage) measured within the soil column between 0-30 cm, and $R$, the residual component, including the sum of lateral flow within the soil. In our study of the annual hydrologic budget, all variables are expressed in mm yr$^{-1}$.

Canopy interception (approximately equal to evaporation from wet canopies) was calculated as the difference between $P$ and throughfall precipitation ($P_T$) beginning in 1998, and was estimated during earlier years based on the strong relationship between $P$ and $P_T$ generated from the data collected at the site (Uebelherr 2008).

Evaporation from the litter and soil ($E_l$ and $E_s$) was calculated according to Park et al. (1998) by solving in the litter layer a vapor transfer equation given by Bussière and Cellier (1994)

$$\frac{C_{lw}}{\rho_{lw}} \frac{\partial \rho_{lw}}{\partial t} = -D_{lw} \frac{\partial \rho_{lw}}{\partial z},$$

where $\rho_w$ and $\rho_{lw}$ are the density of water vapor (kg m$^{-3}$) and water (kg m$^{-3}$), respectively. $D_{lw}$ is the litter layer vapor diffusivity (m$^2$ s$^{-1}$) from Fosberg (1975), $C_{lw}$ is the litter layer water capacity (kg m$^{-2}$) from Bristow et al. (1986), $t$ is time (s), $z$ is the vertical coordinate (m). The equations was solved to estimate $\rho_{lw}$ in each layer. This was used to estimate $E_l$ and $E_s$ in each layer according to
\[ E_L = \frac{\rho_{v,n-1} - \rho_{v,0}}{r_l} \]
\[ E_S = \frac{\rho_{sv} - \rho_{v,n-1}}{r_l + r_s}, \]

where \( \rho_{sv} \) is vapor density at the soil surface (kg m\(^{-3}\)), set as the bottom boundary layer condition, \( n \) is the resistance of the litter layer (s m\(^{-1}\)) calculated according to Kondo et al (1993), and \( r_s \) the resistance of the soil surface(s m\(^{-1}\)) calculated according to Camillo and Robert (1986).

Overland flow (\( F_O \)) was calculated according to Paul et al. (2003) using leaf litter mass (\( LM \)) and the average slope angle at each plot (Table 3). Drainage (\( Q \)) from a plane positioned at the bottom of the 30 cm root zone was modeled based on numerically solving the Richard’s equation:

\[ \frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z} \left[ K(\theta) \left( \frac{\partial \psi}{\partial z} + 1 \right) \right] \]

based on the soil moisture at the bottom of the layer and the physical properties of the soil. A two-layer model was constructed to account for differences in soil properties between the upper 35 cm layer and the layer below (Table 3). The model was parameterized from a relationship between \( \psi \) and \( \theta \) after Clapp & Hornberger (1978). Because \( \theta \) was measured only as an average for the upper layer, \( \theta \) at the bottom of the layer was based on estimating a vertical profile of \( \theta \) to 70 cm at discrete 1.5 cm intervals.
The $\Theta$ profile was generated by setting the initial conditions of mean $\Theta$ through the profile on January 1, 1993 equal to the average soil moisture (~30%) on that day during 1998-2007, allowing $E_c$ to remove water from the soil in proportion to the root distribution (Matamala & Schlesinger 2000) and $E_s$ (the first layer only) to remove water based on soil water potential ($\Psi$) according to Katul et al. (1997). This creates a $\Psi$ gradient that causes redistribution of moisture within the soil, and may result in water flow into the rooting zone from below.

The accuracy of the estimated evapotranspiration ($=I_C+E_C+E_L+E_S$), representing a large portion of the hydrologic budget, was evaluated against latent heat flux ($LE$) measured with eddy-covariance system (Stoy et al. 2006, Novick et al. 2009 and unpublished data). Conventional eddy covariance measurements were made at the central tower of plot 1, an ambient CO$_2$ plot, 1 m above the canopy with a 3-D sonic anemometer (CSAT3; Campbell Scientific, Logan, Utah, USA) and an infrared gas analyser (LiCor 6262; Li-Cor, Lincoln, Nebraska, USA). For details on measurement frequency, gap-filling methodology, and data analysis see Lai et al.(2000) and Novick et al. (2009). Latent heat flux was compared to estimates of transpiration and stand water use averaged for the ambient plots only because $LE$ represents the entire stand and is largely uninfluenced by the elevated CO$_2$ plots.
### 3.3.6. Statistical analysis

Statistical analyses of $J_s$ responses to CO$_2$ enrichment and N fertilization were made on the original data sets. However, in calculating the hydrological budget components, missing data were gap-filled via regression of a given variable among plots, e.g. $T_{air}$ from plot 1 to plot 2, etc, generating a continuous data set from June 1993 (plots 7 and 8) or May, year (plots 1-6) to the end of 2007. After finding no trend over time, a repeated measure (years as repetition) ANOVA with a block design for the CO$_2$ treatment, and a split-plot for the fertilization treatment were employed to assess treatment effects on the yearly sum of the hydrological budget components ($P$, $I_c$, $E_c$, $E_t$, $E_s$, $F_o$, $Q$, $\Delta S$) and on the means of air temperature ($T_{air}$) vapor pressure deficit (VPD), soil moisture ($\Theta$), and $J_s$ using SAS 9.1.0.

### 3.4. Results

Analysis of variance of environmental effects and water flux components was performed on subset of years representing similar experimental settings, revealing very few CO$_2$ effects and no fertilization effect (Table 4).

#### 3.4.1. Environmental variables

The yearly averages of environmental variables between 1993 and 2007 are presented in Figure 1 (A-G), showing high inter-annual variability in precipitation ($P$, $T_{air}$, $\Theta$, $E_c$, $E_t$, $E_s$, $F_o$, $Q$, $\Delta S$).
~80% differences between 1996 and 2007), and inter and intra-annual variation in photosynthetically active radiation (PAR). Air temperature ($T_{air}$) and vapor pressure deficit (VPD) were similar in all treatment at any year (Figure 1.C&D, Table 4), showing inter-annual variation reflecting differences between wet (e.g., 1995 and 1996) and dry (2002 and 2007) years. However, as has been found in an earlier study (spanning 1998 – 2000; Schäfer et al. 2002), soil moisture ($\Theta$) was higher under elevated CO$_2$, particularly at the end of the study (Figure 1.E, Table 4; $P<0.01$). On average, the difference in soil moisture increased over the study period at an average rate of 0.1% per year ($P<0.01$), beginning at 1.7% in 1997 when soil moisture measurements began and reaching at 2.6% in 2007. Similar to $\Theta$, leaf area index ($L$; from McCarthy et al. 2007) and leaf litter mass ($LM$; from Lichter et al. 2008) were significantly greater under elevated CO$_2$ (Figure 1.F&G, Table 4). However, unlike $\Theta$, the differences of $L$ reached a plateau in 1998 as canopy closed, followed as expected by $LM$ in 2002. Both variables show fluctuations reflecting inter-annual variation in weather.

### 3.4.2. Sap flux density and scaling up to stand transpiration

Changes of the sap flux measurement scheme to accommodate changes in the focus of the study (Table 2) meant that in the past different scaling schemes were used in different periods (e.g., Phillips and Oren 2001 *versus* Schäfer et al. 2002). It is well know
that both systematic and random variation of $J_s$ in the sapwood can be very large (Phillips et al., 1996; Oren et al. 1998; Infante et al. 2001). Having a 15-year long record based on many sap flux sensors allowed us to test whether patterns that appeared significant and were used in scaling at certain stages of the study were truly important and persistent when considered in the context of the entire time series.

Following a detailed analysis showing that the scaling rules used earlier did not work well for the entire time-series, we proceeded with a series of tests to identify the sources of variation in sap flux density ($J_s$), both spatially and temporally. We found that sap flux density in the outer 20 mm of xylem was unaffected by either CO$_2$ or fertilization in both $P.\ taeda$ and $L.\ styraciflua$ trees ($P>0.26$ at minimum).

Some studies showed no relationship between sap flux density and tree size (e.g. Jiménez et al. 2000, Kumagai et al. 2005, Fiora and Cescatti 2006). However, other studies found that trees protruding into the upper canopy have higher $J_s$ (e.g., Granier et al. 1996, 2000, Oren et al. 1999, Jimenez et al. 2000), perhaps reflecting greater amount of absorbed radiation. We divided the trees equipped with sap flux sensors into three canopy position categories according to diameter (lower, mid, and upper thirds of the diameter distribution), and found that $J_s$ of the outer xylem in large $P.\ taeda$ and $L.\ styraciflua$ trees was mostly higher than that of the smaller two categories, both showing similar $J_s$ (Figure 2). The ratio increased over the years (Figure 2 A&B) with trees
growing under elevated CO$_2$ having higher ratios (P<0.001 for $P$.taeda), although there was convergence of the ratio between treatments with time, especially in $L$. styraciflua (making the lines for this species statistically indistinguishable (P>0.20).

The ratio of $J_S$ of mid-depth and inner xylem to that of the outer xylem decreased with trees size, with the pattern of small trees steeper than that of medium and large trees, and the decrease was generally steeper under ambient CO$_2$ conditions (Figure. 2.C-F). This is similar to the finding at the site of Schäfer et al. (2002). Having measured in only two depths and fewer sample trees in $L$. styraciflua prevented a clear pattern from emerging among tree size classes and treatments. In most cases, there was no temporal component to the $J_S$ ratio, except that the ratio of flux in the inner sensors to that in the outer sensors decreased with time in large trees under elevated CO$_2$ (P < 0.001) and showed tendency to decrease in medium size trees under ambient CO$_2$ (P = 0.0571). Nevertheless, these temporal changes were small relative to those in the outer sensors among tree size classes (Fig. 2.A&B), and relative to the variation with depth (Fig. 2. C-F).

Phillips et al. (1996) and Schäfer et al. (2002) have shown that the flux deeper in the xylem decreased relative to that in the outer xylem as the soil dries, an opposite trend to that reported by Ford et al. (2004). Thus, we assessed whether the ratio of the mid-depth or inner flux to the outer flux changed consistently with environmental
conditions. Our longer and better replicated measurement scheme produced data showing no relationship of the rations with any environmental variable (minimum P = 0.15).

Using these findings as scaling rules, Js of outer sensor were scaled to canopy transpiration of individual trees based on sapwood area within each depth category per unit of ground area. Sapwood area of individual trees was estimated based on relationship between diameter and sapwood depth (McCarthy 2007), and is shown at the treatment scale in Table 1.

The estimated annual values of the hydrological budget components are shown in Figure 3 A-G and in Table 5. The analyses did not reveal significant N fertilizer effect on any component (P > 0.41). Elevated atmospheric CO₂ decreased Pr (and thus its corollary Ic) but not significantly, and did not affect Ec, Q, storage in the rooting zone, or the modeled evaporation from the litter (Eₜ; Table 4). Evaporation from the surface, Eₛ, was modeled to be significantly lower under elevated CO₂ plots during the last two periods of the study because of a higher insulation and resistance to water vapor transfer through the thicker litter layer, but the absolute difference is very small relative to other components of the budget (Figure 3.D & Table 5). More litter on the soil surface in elevated CO₂ plots decreased the modeled Fₒ, but this effect did not increase the amount of water infiltrating the soil due to the lower Pr (Figure 3.E).
Summing the components of the budget comprising evapotranspiration during periods in which the canopy is not wet (i.e. $I_C = 0$, and $E^* = E_C + E_L + E_S$), we evaluated these most uncertain estimates by comparing the mean $E^*$ with $LE$, an independent estimate of evapotranspiration (Figure 4). Similar to Schäfer et al. (2002), our estimate of $E_T$ was larger than $LE$ in wetter months with low radiation and slightly lower in high radiation months, during which understory contribution to total evapotranspiration is larger but was not measured in our study.

3.5.Discussion

Neither soil moisture nor any of the hydrological budget components responded significantly to N addition despite the observed responses of L. This is probably a reflection of the low replication of fertilization in the middle part of the experiment (n=1 from 1999 through 2004), and the short period (n=4 from 2005 – 2007) during which the rest of the plots had time to respond to the treatment in terms of increasing canopy leaf area and, after a few years’ lag, increasing forest floor litter mass. These changes do not follow monotonically the commencement of a treatment because inter-annual variation in weather conditions, especially precipitation and evapotranspiration, can greatly reverse the response (McCarthy et al. 2006 a&b, 2007; Palmroth et al., 2006). Without such changes, there is no reason for the hydrology of the forest to change. As a result, we
did not detect any significant main or interaction effect of N fertilization, and can focus on the effects of elevated CO$_2$.

Elevated CO$_2$ increased $L$ an average of 14% (McCarthy et al. 2007), leading us to hypothesize (1) that canopy rainfall interception loss, $I_c$, would increase resulting in lower amount of water reaching the forest floor as throughfall precipitation, $P_t$. In contrast to Schäfer et al. (2002) and Uebelherr (2008), but consistent with Lichter et al. (2000) who reported 7% decrease in $P_t$ during years in which $L$ increased by 3%, we found about 6% CO$_2$-induced reduction of $P_t$ (insignificant). Indeed, detecting small differences in $P_t$ is difficult due to high spatial variations of canopy structure (Van Dijk et al. 2001, Stogsdill et al. 1989; Uebelherr 2008).

We also hypothesized (2) that CO$_2$-induced increase in $L$ would lead to higher canopy transpiration ($E_c$). The expectation that $E_c$ would decrease under elevated CO$_2$ is pegged to the often observed reductions in stomatal conductance (Medlyn 1996), predicted to result in a greater savings of water in ecosystems with well coupled canopies (Woodward 1990). However, although some studies show CO$_2$-induced decrease of stomatal conductance (Dixon et al. 1995; Tissue et al. 1997), including of the $L. styraciflua$ at the Duke FACE experiment, many forest tree species show little or no effect under long-term exposure to elevated CO$_2$ (Eamus & Jarvis 1989; Bunce 1992;

Canopy transpiration, $E_c$, increased in all treatments as the study progressed in part reflecting the increase of $L$. The absence of CO2-induced increase in $E_c$ despite 14% increase in $L$ may reflect the observed decrease of maximum stomatal conductance under well-watered conditions due to hydraulic constraints (Domec et al., 2009). Is it possible that the approach is not sensitive enough to detect treatment-induced changes? Perhaps so, but the inter-annual variation in $E_c$ did actually mapped well to changes in other environmental conditions (soil moisture and VPD), as have been shown previously in this and nearby forests of the same or different species (Stoy et al. 2006). Indeed, relative to 2001, the 2002 drought caused ~22% decrease of $E_c$ in elevated CO2 and fertilized plots, significantly more ($P=0.04$) than the ~14% decrease in ambient and unfertilized plots. An overall significant decrease in 2007 drought year of ~11% relative to 2006 ($P<0.001$) show that the method is sensitive enough to pick up differences of this amount.

Our results, of unchanging $E_c$ with $L$ fall between the increased in $E_c$ reported from two other FACE experiments on regenerating forest stands in which $L$ developed faster under elevated CO2 (Uddling et al. 2008, Tricker et al. 2009) and decreasing $E_c$ observed in another FACE study on L. styraciflua, in which a large CO2-induced
reduction of stomatal conductance translated to a reduction in Ec on the background of unchanging L (Wullschleger and Norby 2001, Norby et al. 2003). In that study, the reduction in Ec was proportionally lower (13%) than that of stomatal conductance (18–29%), presumably because the canopy was not coupled very well to the atmosphere.

We also expected thicker litter layer under elevated CO2 to lead to (3) higher evaporation from rain water stored in the litter (E_l), and (4) lower evaporation from the soil surface (E_s) due to decreased amount of soil moisture and increased resistance to vapor exchange with the atmosphere. Increased thickness of the litter layer under elevated CO2 has been found both in our experiment (see Figure 1.G, after Schlesinger and Lichter (2001) and Lichter et al. 2008-) and other FACE sites (Liu et al. 2005; Hoosbeek and Scarascia-Mugnozza 2008). Although these predictions were supported by the data, the analysis confirmed only the latter predictions. Nevertheless, the sum of these two components (total forest floor evaporation, E_{LS}) comprised a small fraction of the budget and, as predicted, was unaffected by elevated CO2, a finding in contrast to those from a shorter study in the site showing lower evaporation under elevated CO2 (Schäfer et al., 2002).

The increase of LM in elevated CO2 plots decreased Fo (Table5). However, due to a reduced amount of throughfall precipitation, the effect on the amount of water entering the soil was only sufficient to increase soil moisture (Figure. 1.G & 3.E), but had
no effect on water loss from the soil through evaporation, transpiration or drainage (Figure 3, Tables 4 and 5). Groundwater flow and storage are continually changing in response to human activities and climatic variation (Alley et al. 2005).

Our ultimate objective was to assess how the combined evapotranspiration (i.e., the sum of the four components) responded to the treatments and assess the effect on water yield, the sum of overland runoff and drainage below the rooting zone. Prior to performing such an assessment, it is necessary to ascertain that the sum of the measured and modeled components of the hydrological budget match, on the long term, the input in precipitation. Figure 5 shows that the budget of all treatments was balanced with incoming precipitation, with significant bias at low precipitation years, the slope was 0.86 and the intercept was 159.75 ($r^2=0.95$), or 1.01 ($r^2 = 0.93$) if forced through the intercept. Similarly, the sum of modeled output was within 95% confidence interval of $P$ over most of the range (Figure 5). Based on this closure, we proceeded with a simple evaluation of treatment effects on water yield, defined as the sum of drainage and overland flow.

We compared precipitation with additive components of hydrologic budget of each treatment (Figure 6). Note that, because the fertilization treatment began later than the elevated CO$_2$ treatment, the range of precipitation is somewhat narrower. We focused primarily on three components, one representing the sum of all the evaporation
components, one representing yield, and one representing transpiration. Two points quickly become apparent: (1) among the three components, annual transpiration is least sensitive to precipitation within the wide natural range covered in the 15-year record. And (2), because of the insensitivity of $E_c$ to $P$, the variation in precipitation is absorbed by evaporation, and to even a greater extent by water yield. These observations are similar to results from a four-year study in a nearby Oak-Hickory forest (Oishi et al., in review).

Although overland flow was reduced under elevated CO$_2$, leading to a higher soil moisture, the increase of $I_c$ with $L$ over time during the experiment lead to higher total evaporation progressively reducing water yield (Tables 4 and 5). In the nearby study of the Oak-Hickory forest, water yield calculated as in this study was the most influential determinant of inflow to local reservoirs (Oishi et al., in review). The CO$_2$-induced (and perhaps N-induced) routing of water from overland flow to infiltration, via the increased amount of litter on the forest floor, resulted in higher average soil moisture. This could have support increased drainage, thus compensating water yield for lower $F_0$. However, a lower throughfall precipitation under elevated CO$_2$, coupled with the low hydraulic conductivity of the soil below the rooting zone, a legacy of historical cultivation practices, resulted in no observable increase in drainage. This
prevented such compensation of water yield, indicating that the water yield from similar forests are likely to decrease as elevated CO$_2$ increases canopy leaf area.
Table 3.1. Yearly maximum sapwood area at breast height for pine and broadleaf species in each treatment. Values in parenthesis are the standard error with \( n = 4 \).

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<th>Elevated CO(_2)</th>
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a: In addition to 17 sweetgum trees, five *Cornus florida* L. and seven *Ulmus alata* Michx. trees had sensors in ambient sites.

b: Five *C. florida* and seven *U. alata* trees had sensors in elevated sites.
Table 3.3. Site and soil characteristics of each plot. Shaded plots are under elevated CO$_2$. When there were no differences between plots, one value was used for all plots. Slope is the average value of East-West and North-South slope. Rock is the average volumetric rock content from four pits with standard errors in parenthesis. Ks represent the saturated hydraulic conductivities in each soil depth. Subscript 0-20, 20-40 and 40- represents the values of each soil characteristic variables at the soil depth of 0-20 cm, 20-40 cm and 40 cm and below, respectively. b represents the b value from soil water characteristic curve ($\Psi = -\Psi_s(\Theta/\Theta_s)^b$) and hydraulic conductivity function ($K=K_s((\Theta/\Theta_s)^{-2b+3}$) according to Clapp and Hornberger (1978). $\Psi_s$ and $\Theta_s$ represent the saturated soil water potential and volumetric soil water content, respectively. $\Psi$, K and $\Theta$ represent the soil water potential, hydraulic conductivity and volumetric soil water content at the time of calculation, respectively.

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<th>Plot 4</th>
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Table 3.4. Statistical p-values of environmental variables and water balance components were tested with repeated measure anova using complete block design for CO$_2$ and split plots for fertilization. The numbers in parenthesis represent the average ratio between ambient and elevated plots. $T_{\text{air}}$ is air temperature, VPD is vapor pressure deficit, $\Theta$ is volumetric soil water content to 30 cm depth, $L$ is yearly maximum leaf area index, $LM$ is litter mass, $P_T$ is precipitation throughfall, $E_C$ is canopy transpiration, $E_L$ is litter layer evaporation, $E_S$ is soil layer evaporation, $F_O$ is the overland flow, $Q$ is drainage, $\Delta S$ is the change of water storage in soil to 30 cm depth, water yield is the sum of $Q$ and $F_O$, evaporation is the sum of canopy interception, $E_L$ and $E_S$, evapotranspiration is the sum of $E_C$ and evaporation. The statistical test was performed at four different periods depending on the number of replications (1993-1996: $n=1$ for CO$_2$, 1997-1998: $n=4$ for CO$_2$, 1999-2004: $n=4$ for CO$_2$, $n=1$ for N fertilization and 2005-2007: $n=4$ for CO$_2$ and N). The statistical test was only available from 1997, since there was one replication before. However, p-value for CO$_2$ effect is shown here, since there was no effect of fertilization in any years.\footnote{*: $P_T$ began to measure 1998. Therefore, output was modeled from 1993 to 1997 and they are not used for this analysis}

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Table 3.5. Individual water balance components for each treatment from 1993 to 2007 in mm yr⁻¹. Values in the middle of rows are an average for the corresponding treatments. Values in parenthesis represent one standard error (n=4). N is nitrogen fertilization, P is precipitation, Ic is precipitation interception, Pt is precipitation through fall, LE is latent heat flux, Ec is canopy transpiration, El is litter layer evaporation, Es is soil layer evaporation, Fo is overland flow, Q is drainage to below 30cm in depth, ∆S is change of soil water storage to a 30 cm depth in the soil and R is the residual.

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Fertilized

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Figure 3.1. A) The yearly sum of precipitation, \( P \), B) monthly sum of photosynthetically active radiation, PAR, C) yearly average of air temperature, \( T_{\text{air}} \), D) yearly average of vapor pressure deficit, VPD, E) yearly average of volumetric soil water content, \( \Theta \), F) yearly maximum leaf area index, \( L \) and G) yearly maximum litter mass, \( LM \). AU (○) and EU (●) represent the average of ambient and elevated CO₂ unfertilized plots, respectively. AF (Δ) and EF (▲) represent the average of ambient and elevated CO₂ fertilized plots, respectively. Bar represent standard errors with \( n=4 \).
Figure 3.2. Outer sap flux density and its relationship with mid and inner sap flux density in *Pinus taeda* (A,C and E) and *Liquidambar styraciflua* (B, D and F). In each panel open symbols represent ambient CO₂ plots and closed symbols represent elevated CO₂ plots. A) Outer *J*ₜ ratios between large size trees (upper one third in diameter) and small and medium trees for *Pinus taeda*. The slope and intercept for ambient plots (○) are 0.035 and -68.63, respectively (r²=0.48, P<0.001). The slope and intercept for elevated plots (●) are 0.028 and -55.69, respectively (r²=0.51, P<0.001). B) Outer *J*ₜ ratios between large size trees and small and medium trees in *L. styraciflua*. The slope and intercept for ambient CO₂ plots (○) are 0.144 and -287.40, respectively (r²=0.48, P<0.001). The slope and intercept for elevated CO₂ plots (●) are 0.092 and -183.26, respectively (r²=0.15, P<0.044). C) The average ratios of mid-depth (20-40mm in sapwood) and inner (40-60mm) *J*ₜ to outer *J*ₜ of *P. taeda* for large (circle), medium(inverted triangle) and small (square) trees in ambient CO₂ plots. D) The average ratios of inner (20-40mm) *J*ₜ to outer *J*ₜ(0-20mm) of *L. styraciflua* for large (circle), and medium and small (inverted triangle) trees in ambient CO₂ plots. E) The average ratios of mid-depth and inner *J*ₜ to outer *J*ₜ of *P. taeda* for large (circle), medium (inverted triangle) and small (square) trees in elevated CO₂ plots. F) The average ratios of inner *J*ₜ to outer *J*ₜ of *L. styraciflua* for large (circle), and medium and small (inverted triangle) trees in elevated CO₂ plots.
Figure 3.3. Yearly water balance model outputs: A) precipitation through fall, $P_T$, B) canopy transpiration, $E_C$, C) litter layer evaporation, $E_L$, D) soil layer evaporation, $E_S$, E) over land flow, $F_o$, F) drainage, $Q$ and G) the change of soil water storage to 30 cm depth, $\Delta S$. AU (○) and AF (●) represent the average of ambient and elevated CO$_2$ unfertilized plots, respectively. EU (△) and EF (▲) represent the average of ambient and elevated CO$_2$ fertilized plots, respectively. Bar represent standard errors.
Figure 3.4. Comparison of canopy evapotranspiration ($E_T^* = E_C + E_S + E_L$) excluding canopy interception under ambient CO$_2$ with latent heat flux ($LE$) above the canopy. $E_C$, $E_S$ and $E_L$ represent canopy transpiration, soil and litter layer evaporation, respectively. Vertical bars represent one standard error ($n = 4$). Inset figure shows the yearly comparison between the two.
Figure 3.5. Comparison between precipitation and sum of water balance components from four different treatments from 1993 to 2007. AU(○) and EU(●) represent ambient and elevated CO\textsubscript{2} unfertilized plots with standard errors (n=4, since 1996), respectively. AF (△) and EF (▲) represent ambient and elevated CO\textsubscript{2} fertilized plots, respectively. Symbols with error bars represent the average of 4 plots with standard errors. AU and EU have error bars since 1996 and AF and EF have error bars since 2005. Green line represents the regression line and black solid line represents 1:1 line and dashed lines represent 95% confidence interval.
Figure 3.6. Comparisons of precipitation with additive components of hydrologic balance from four treatments. AU, AF, EU and EF represent ambient CO\textsubscript{2} unfertilized, ambient CO\textsubscript{2} fertilized, elevated CO\textsubscript{2} unfertilized and elevated CO\textsubscript{2} fertilized plots, respectively. I\textsubscript{c} is precipitation interception, E\textsubscript{ls} is the sum of litter and soil evaporation, E\textsubscript{c} is canopy transpiration, F\textsubscript{o} is overland flow and Q is drainage. All are in mm yr\textsuperscript{-1}. Closed symbols represent components of evapotranspiration and open symbols represent components of water yield. The vertical lines represent the minimum (800 mm) and maximum (1449 mm for unfertilized and 1363 mm for fertilized plots) precipitation during the study period for each treatment. Solid diagonal lines represent linear regressions for each component of the hydrologic balance to precipitation except 1:1 line at the top.
Chapter 4. Actual and Potential Transpiration and Carbon Assimilation in an Irrigated Poplar Plantation

4.1. Abstract

An increasing number of experimental studies attempt to maximize biomass production of trees in plantations by removing nutrient and water limitations. The results from these studies begin to inform operational managers. We investigated a *Populus trichocarpa* Torr. × *P. deltoides* Bartr. & Marsh plantation with a combined irrigation and nutrient supply system designed to optimize biomass production. Sap flux density was measured continuously over four of the six growing season months, supplemented with periodic measurements of leaf gas exchange and water potential. Measurements of tree diameter and height were used to estimate leaf area and biomass production using allometric relations. Sap flux was converted to canopy conductance, and analyzed based on an empirical model to isolate the effects of water limitation. Actual and soil water-unlimited potential CO$_2$ uptakes were estimated using a Canopy Conductance Constrained Carbon Assimilation (4C-A) scheme, which couples actual or potential canopy conductance with vertical gradients of light distribution, leaf-level conductance, maximum Rubisco capacity ($V_{\text{max}}$) and maximum electron transport ($J_{\text{max}}$). Net primary production (NPP) was ~0.43 of gross primary production (GPP); when estimated for individual trees, this ratio was independent of tree size. Based on the same ratio, we found that current irrigation reduced growth by ~18 % compare to growth with no water limitation. To achieve this maximum growth, however, would require 70%
more water for transpiration, and would reduce water use efficiency by 27%, from 1.57 to 1.15 g stem wood C kg\(^{-1}\) water. Given the economic and social values of water, plantation managers appear to have optimized water use.

**Key words**: gas-exchange, gross primary production, leaf area index, leaf water potential, light-use efficiency, net primary production, soil moisture, water-use efficiency

### 4.2. Introduction

Managers of plantations traditionally increase yield by controlling genotype, tree density and nutrient availability. A few intensively managed plantations also irrigate to increase production further (Romero et al. 2004, Coyle and Coleman 2005). Although irrigation can be tailored to completely alleviate soil water limitation, it would be inefficient as yields do not increase proportionally to water use (Harvey and van den Driessche 1999, Romero et al. 2004, Choi et al. 2005). Given the increased scarcity of water resources (Vörösmarty et al. 2000), an approach to assess the tradeoffs between stand-level water use and carbon uptake (Jackson et al. 2005) that can be employed accurately and broadly is highly desirable. Here we develop a data-intensive approach to assess the carbon-water tradeoff, and compare the outcome to simpler approaches that can be more broadly applied. In addition to using our estimates to evaluate carbon-
water tradeoffs estimated with less realistic yet simpler approaches, ours is designed to accurately distribute assimilation down the canopy, thus facilitating spatially explicit physiological studies.

Although CO$_2$ uptake and transpiration ($E$) by forests are not easily measured, models are available to estimate these variables (Collatz et al. 1991, Leuning 1995, Williams et al. 1996, Landsberg and Waring 1997, Thornton et al. 2002). Canopy-level gas exchange models rely on estimates of stomatal conductance ($g_s$). Jarvis (1976) empirically described stomatal response to the external environment as:

$$g_s = g_{sm} f_1(D)f_2(Q)f_3(\Psi).$$

(1)

where, $g_{sm}$ is maximum stomatal conductance, which is largely determined by hydraulic characteristic of a plant under optimal conditions, $D$ is vapor pressure deficit, $Q$ is photosynthetic photon flux density, and $\Psi$ is soil or leaf water potential. Carbon assimilation is related to stomatal conductance through Fick's law:

$$A_{net} = g_c (C_a - C_i)$$

(2)

where, $A_{net}$ is net carbon assimilation, $g_c$ is canopy conductance for CO$_2$, which includes the boundary layer conductance ($g_{bl}$) in addition to $g_s$, $C_a$ is atmospheric CO$_2$ concentration and $C_i$ is the CO$_2$ concentration in the intercellular space of the leaf. The component ($C_a - C_i$) in Equation 2 can be re-written as $C_a (1-C_i/C_a)$. Measures of $C_a$ are readily available. The ratio $C_i/C_a$ is often assumed constant (Norman 1982) or can be estimated from knowledge of $Q$, $D$ (or relative humidity), water use efficiency (WUE)
and $g_c$ (Cowan and Farquhar 1977, Collatz et al. 1991, Katul et al. 2000). To scale leaf-
level $C_i/C_a$ to the canopy, the vertical distribution of leaf area is needed for estimating $Q$
on leaf surfaces, which in turn is used to estimate $g_c$ and the biochemical properties
controlling photosynthesis. Such a scheme is incorporated in the canopy conductance
constrained carbon- assimilation (4C-A) model (Schäfer et al. 2003) where the leaf-level
estimates of $g_c$ are matched with averaged canopy stomatal conductance ($G_s$) obtained
from measurements of sap flux, leaf area, and evaporative demand. Hereafter, ‘$G$’ is
used to represent conductance based on sap flux scaled measurements and ‘$g$’ is used for
conductance from gas-exchange measurements.

In this paper, we investigated the regulation of stomatal conductance and carbon
assimilation of 3-year-old *Populus trichocarpa* Torr. × *P. deltoides* Bartr. & Marsh trees in
an intensively managed hybrid poplar plantation situated on the east side of the
Washington Cascades. Poplars are known to transpire up to 8 mm day$^{-1}$ when growing
in non-arid environments (Allen et al. 1999), and even higher rates have been recorded
in trees along streams in arid areas (9.3 mm day$^{-1}$; Pataki et al. 2005). Thus, hybrid poplar
plantations in arid environments require large quantities of irrigation water. The
objectives of this study are to: 1) analyze the effect of various environmental factors on
actual conductance and model ‘potential conductance’ under non-limiting soil water,
thus allowing estimates of transpiration in absence of water stress, and 2) calculate
carbon assimilation with both actual and potential conductance, and assess the effect of soil water limitation on both the reduction in biomass production and stand-level WUE.

4.3. Materials and methods

4.3.1. Setting

Most poplar plantations in the Pacific Northwest are either on flood plain sites (west side of the Cascade Mountains) or on irrigated land (east side). This study was conducted at the Boise Cascade Corporation’s Wallula Cottonwood Fiber Farm (46° 10’ N 118° 28’ W) located on a sandy soil near Wallula, in eastern WA, during four growing season months (mid-June to mid-October). Mean annual temperature is 12.3 °C and mean annual precipitation is 160 mm. This plantation was established in the late 1980’s on formerly irrigated agricultural land. The study block was harvested in 1996 and replanted in July, 1997 with *P. trichocarpa* x *P. deltoides* hybrid cuttings at 0.9 x 3.5 m spacing. Drip irrigation was initiated at leaf expansion and terminated in mid- to late-October of each year. Frequent additions of dissolved nutrients were supplied in the irrigation stream and herbicides were applied during the first two growing seasons to control weed. Trees were in their third growing season when this study began, with mean height >8 m. During the study, average maximum temperature was 28.3 °C and average minimum temperature was 14.7 °C. Total precipitation over this period was 19.3 mm.
### 4.3.2. Measurements

Diameter at breast height \((d_{1.4})\) of 50 to 51 trees (4 rows \(\times\) 12–13 trees per row), at least 15 m from the block’s edge, was measured with a diameter tape three times: at the start and end of the study, and approximately in the middle of the period when the heat dissipation probes (see below) were moved from the first to the second set of five trees. This re-location of the probes defines the two study periods (before and after re-location) for which some of the analyses were performed separately. Leaf area of individual trees was estimated five times during the study period, spaced four to six weeks apart. At each time, a relationship between branch diameter and its projected leaf area was developed from a sub-sample of branches from the crowns of four to five trees covering a wide range of canopy positions and diameter classes. A total of forty-five sample branches representing nine to ten, \(\sim\)1-m deep canopy layers were harvested, keeping track of the branch diameter and its insertion height. Samples were taken from trees on which sap flux was not monitored, except at the end of the study after the sensors were removed. The area of each leaf was measured with a Li-Cor 3200 leaf area meter (Li-Cor, Inc., Lincoln, NE), summed for each branch, and related to branch diameter.

Concurrently with branch sampling, diameter and branch height of all branches were measured on four of the trees monitored for sap flux and accessible from two towers. The study trees represented the 22nd to 94th, and 24th to 84th percentile of the \(d_{1.4}\) range in the two periods. Using the relationships derived for branches, the leaf area of
each branch was estimated, and summed to tree level leaf area ($A_t$). $A_t$ was then related to the percentile of $d_{1.4}$ represented by the four sample trees in each of the five times.

Leaf area index ($L$) was estimated from the leaf area of the 50th percentile tree multiplied by tree density (3175 trees ha$^{-1}$). $A_t$ and $L$ were converted to biomass based on leaf mass per area (LMA; 65 g m$^{-2}$ on average, ranging from 81 g m$^{-2}$ at the top to 48 g m$^{-2}$ at the bottom of the canopy) obtained from 32 oven dried (78 °C for 48 hours) circular disks (2 cm in diameter) collected from leaves in the outer envelope of crowns and in the inner core from top and bottom branches about halfway through the study. Leaf nitrogen concentration (g g$^{-1}$) was determined six times over the growing season, corresponding to most of the eight gas exchange measurement campaigns. At each time 16 leaves, four collected in each of the outer envelope and inner core of crowns from canopy top and bottom branches, were dried for 48 hours, ground to a fine powder, and 0.05 g sample was sent to the Phytotron at Duke University for a mass spectrum analysis.

The bottom of the canopy extended to the ground throughout the study, and top height increased from ~8 to ~11 m. The profiles of leaf characteristic dimension ($d$) and leaf area density ($L(z)$) were estimated in each 1-m canopy layer. $d$ was estimated assuming circular leaf shape, calculating diameter from the average area of a leaf in the layer and multiplying by 0.81 (Campbell and Norman 1998). $L(z)$ and its seasonal variation were obtained from the four sample trees for which branch diameter and insertion height were measured. Based on observations, the leaf area of branches with
basal diameter < 25 mm was assigned to the layer in which the branch was attached, while the leaf area of those ≥ 25 mm was split between the layer of insertion and that above. \( L(z) \) was unrelated to tree size. Therefore, \( L(z) \) was expressed relative to total tree leaf area, normalized with respect to height, and the product averaged for the four sample trees and employed with all the trees in the plot. The sum of \( L(z) \) of individual trees produced the canopy level \( L(z) \).

Sap flux density \( (J_{sf}) \) was measured using Granier-type sensors. Due to the fast growth of the trees, the sensors had to be re-positioned after six weeks, and were moved to a different set of trees to increase the sample size. The trees sampled during the first period ranged from the 10\(^{th} \) to 94\(^{th} \) percentile, and during the second period from 24\(^{th} \) to 84\(^{th} \) percentile of \( d_{1.4} \). Four sensors were installed in each tree, except for the smallest tree, in which two sensors were installed. Sensors were installed in the outer 20 mm on the north and south sides, and towards east and west in the next 20 mm of the hydro-active xylem (Granier 1987, Phillips et al. 1996, Oren et al. 1998, Oliveras and Llorens 2001).

Meteorological variables were obtained using a weather station positioned at the top of a 12 m tower, the approximate crown-top-height of the dominant trees. Incoming solar radiation was measured with a pyranometer (Li200S, Li-Cor, Lincoln, Nebraska). Air temperature and humidity were obtained from a shielded combination of a capacitance relative humidity sensor and a thermistor probe (HMP35C, Campbell Scientific, Inc., Logan, UT). Wind speed was measured with a cup anemometer (Model
03001-5, R.M. Young, Traverse City, Michigan). Meteorological variables and sap flux were measured every 10 s and 30-min averages were recorded (CR10 datalogger, Campbell Scientific). Repositioning of sensors and power outages resulted in a loss of data for 11 days during the 126 day study.

Leaf-level stomatal conductance ($g_s$) was measured with a steady state porometer (Li 1600, Li-Cor, Lincoln, NE) and leaf water potential ($\Psi_L$) with a Scholander-Hammel pressure chamber (PMS Instruments, Corvallis, OR) on the four trees accessible from the towers. Eight two-to-three day measurement campaigns, beginning at 0800 h, later on two windy days, and lasting till darkness, allowed diurnal $g_s$ representation based on five to eight sets of measurements per day. Each set of measurements was represented by the total of 24 leaves, four leaves each taken from a sunny and a shady microenvironment of each of three crown thirds (i.e. top, middle and bottom). To eliminate variation from leaf development, we measured only mature leaves (Leaf Plastochron Index>3). On seven of these campaigns leaf water potential was measured on eight leaves per tree, four from the top and four from the bottom of the crown, split between crown envelope and core foliage. The measurements were taken at predawn and solar noon.

4.3.3. Data processing

Biomass production of stems and branches was estimated from species-specific allometric equations based on diameter and height at the beginning and the end of each
period (Scarascia-Mugnozza et al. 1997, Zabek and Prescott 2006), and then calculating weighted average based on the density of trees in this study relative to the densities in the published studies. Foliage biomass production, occurring only in the first period, was calculated by multiplying the increase in leaf area with the average LMA. Root biomass production was assumed to be 14% of total above biomass production, as estimated for another, similar age hybrid poplar stand supplied with drip-irrigation (Gielen et al. 2005).

**Modeling of actual net carbon uptake** ($A_{\text{net}}$) by the canopy ($A_{\text{netC}}$) and gross primary productivity (GPP) was based on the 4C-A scheme (Schäfer et al. 2003). 4C-A is a multi-layer canopy photosynthesis model where sap-flux-scaled total conductance constrains estimates of stomatal and aerodynamic of boundary layer conductance, and the constrained conductance is coupled to a Farquhar-type photosynthesis model (Farquhar et al. 1980, Farquhar and von Caemmerer 1982). For details, refer to Appendix B.

To calculate the solar energy available for photosynthesis, incoming solar radiation ($R_t$) was partitioned into incoming photon flux density ($Q$) according to Alados et al. (1996). The interception and transmission of $Q$ were calculated based on Beer and Lambert’s law with two levels of clumping: (1) tree and shoot, and (2) tree only (Nilson 1999, Niinemets et al. 2004). For details, refer to Appendix C.
Total canopy conductance ($G_c$) was calculated from the sum of the boundary layer and stomata conductance to water vapor. The boundary layer conductance to water vapor ($G_{bl}(z)$) was calculated as in (Campbell and Norman 1998) based on the wind speed at each layer $U(z)$ – modeled based on measured $U$ above the canopy and the $L(z)$ (see Appendix D for $U(z)$ calculations) – and the $d$ profiles in the canopy. Boundary conductance for the entire canopy was scaled from $G_{bl}(z)$ based on $L(z)$:

$$G_{bl} = \frac{\sum_{z=1}^{12} G_{bl}(z) L(z)}{L}.$$

Canopy stomatal conductance $G_s$ was estimated from sap flux-scaled $G_c$ after adjusting for $G_{bl}$

$$G_s = \frac{G_c G_{bl}}{G_{bl} - G_c}.$$  \hspace{1cm} (3)

$G_c$ was calculated based on a simplified equation (Köstner et al. 1992):

$$G_c = \frac{G_v (T_a + 273) \rho E_L}{D}$$  \hspace{1cm} (4)


where $G_v$ is the universal gas constant adjusted for water vapor, $T_a$ is the air temperature, and $\rho$ is the density of water. Only conditions of $D \geq 0.6$ kPa (~70% of the time) were used to ensure that errors in estimates of $G_c$ remained below 10% (Ewers and Oren 2000).

The stomata conductance to water vapor ($g_s$) was estimated based on distribution of $Q$ within the canopy, response functions of $g_s$ to $Q$, and constrained by sap flux scaled
$G_s$ (Equation 3). At each layer, $g_s$ of sunlit ($g_{s,sun}(z)$) and shaded ($g_{s,shade}(z)$) leaves is estimated from the response functions of $g_s$ to $Q$, obtained from porometric measurements. These rates are converted to a mean canopy stomatal conductance by scaling based on the sunlit fraction of leaf area ($\tau_b$) and $L(z)$ (Appendix C), summing up for the entire canopy, and dividing by $L$. This value was then constrained with sap flux-scaled $G_s$ by linearly adjusting $g_s(z)$, such that

$$G_s = rf \sum_{z=1}^{12} L(z) \left[ g_{s,sun}(z) \tau_b(z) + g_{s,shade}(z)(1 - \tau_b(z)) \right] L$$  \hspace{1cm} (5)

where $rf$ is the linear reduction factor, which makes the leaf-area weighted $g_s$ equal to $G_s$. This operation is used to account for conditions not captured by the curves describing the light response stomatal conductance. In optimal conditions, $rf$ was ~1.

The above calculations produced two profiles, one of $G_{bl}$ and one of $g_s$, the sum of which for the entire canopy was forced to match the sap flux scaled $G_s$ by adjusting the total $g_s$. $G_{bl}$ to water vapor was converted to its equivalent for CO$_2$ by dividing by 1.42, and $g_s$ by dividing by 1.6 (Jones 1992) before employing in the calculations of photosynthesis (Appendix B).

*Canopy stomatal conductance*, $G_s$, was modeled for gap-filling during hours in which $D$ was low (<0.6kPa) or days of missing data due to power outage and switching of sample trees. We used a modified Jarvis-type model (Equation 1) to simulate values for these missing data.
In Equation 1, \( f(Q) \) was best described as a piece-wise linear function with a saturated region, effectively similar to a saturation function (Jarvis 1976). For \( f(D) \), the stomatal sensitivity to \( D \) (i.e. the relative change in both \( G_s \) and \( g_s \) with a change in \( D \)), is proportional to the conductance at low \( D \) (Sandford and Jarvis 1986, Oren et al. 1999). Thus, the response of \( G_s \) to \( D \) can be predicted by:

\[
G_s = b - m \ln(D)
\]  

(6)

where \( b \) is a reference \( G_s \) at \( D = 1 \) kPa (hereafter, \( G_{sref} \)) and \(-m\) is the sensitivity of \( G_s \) to \( D \) (\(-dG_s/d \ln D\)). For various species under moderate environmental conditions, \( m \) averages \(-0.6b\) (e.g., Oren et al. 1999, Ewers et al. 2000, Ewers et al. 2001). However, the ratio of \( m \) to \( G_{sref} \) (denoted as \( \gamma \)) is higher in regions in which the average \( D \) is lower and the range of \( D \) is narrower; it also increases with decreasing ratio of \( G_{bl} \) to \( G_{sref} \) (Oren et al. 1999). The expected value of \( \gamma \) can be calculated by (1) assuming a constant leaf-specific hydraulic conductivity and water potential gradient driving flow, (2) solving for \( G_c = c (1/D) \), where \( c \) is a constant (mmol m\(^{-2}\) s\(^{-1}\)) for a wide range of \( D \), (3) based on assumed values of \( G_{bl} / G_{sref} \), extracting the corresponding values of \( G_s \) from \( G_c \), and (4) regressing \( G_s \) over different ranges of natural log transformed \( D \).

The functions described thus far do not account for soil water limitation on \( G_s \), and therefore can be used to estimate \( G_s \) and \( G_{sref} \) only when the soil is very moist, or when predicting potential \( G_s \) and \( G_{sref} \). Ideally for our approach, the model would estimates \( G_{sref} \) based on \( Q \) and some measure of moisture availability, such as reflected
in predawn leaf water potential ($\Psi_{pd}$), and adjust it to $G_s$ based on $D$ and stomatal conductance sensitivity to $D$. Thus, the following equation would emerge:

$$G_s = G_{sref} \left( \frac{G_{avg}, \Psi_{pd}}{m(D_{range}, G_{hi}, G_{sref}, G_{sref})} \right) \ln(D)$$

where $D_{range}$ is the daily range of $D$ to which the stand had been exposed.

However, we do not have continuous measurements of any variable reflective of soil moisture availability, and thus $f(\psi)$-type function. We solved this problem by assessing whether $G_{sref}$ estimated using a model that did not account for water limitation (i.e., the above model but without $f(\psi)$) over-estimated sap flux-based $G_{sref}$, and whether the overestimation could be explained by $\Psi_{pd}$ over the subset of days with this measure. If so, we rescaled $G_{sref}$ estimated by the model for a specific data gap by its average ratio to $G_{sref}$ calculated from sap flux in the period immediately before and after the gap.

The transpiration per unit leaf area ($E_L$) used in calculating $G_c$ was estimated based on leaf area ($A_L$), sapwood area ($A_S$, assumed all cross-section area inside bark) and average $J_{SF}$. To account for potential nighttime conductance (Oren et al. 2001, Daley and Phillips 2006), the baseline for each sap flux sensor output was set between nights in which $D$ was $\sim0$ kPa, rather than between consecutive nights. Because $J_{SF}$ changed radially but not azimuthally, average $J_{SF}$ was calculated by weighting the outer $J_{SF}$ by the sapwood area represented in that xylem band and the inner $J_{SF}$ by the remaining sapwood area (Ewers et al. 2001, Oren and Pataki 2001). The transpiration per unit leaf area ($E_L$) was estimated from the average $J_{SF}$ using:
\[ E_L = J_{SF} \frac{A_S}{A_L} \]  \hspace{1cm} (8).

*Actual photosynthetic rates* were calculated as explained in Appendix B based on \( Q \) and \( g_c \) estimated for each layer. Net photosynthesis \((A_{\text{net}})\) integrated for an individual tree and for the entire canopy \((A_{\text{netC}})\) was calculated as

\[ A_{\text{netC}} = \sum_{z=1}^{12} L(z) \left[ A_{\text{net,sun}}(z) \tau_b(z) + A_{\text{net,shade}}(z)(1 - \tau_b(z)) \right] \]  \hspace{1cm} (9)

where \( \tau_b(z) \) is the proportion of sunlit area, \( A_{\text{net,sun}}(z) \) and \( A_{\text{net,shade}}(z) \) are the net assimilation of sunlit and shaded leaves in the \( z \)th layer, respectively. Using a similar approach, but accounting for day respiration (Appendix B), GPP was similarly calculated and integrated to the canopy.

To estimate potential \( A_{\text{netC}} \) and GPP in the absence of soil water limitation to \( g_s \), we modeled \( G_s \) based on Equation 7 without \( \Psi_{pd} \), by performing a boundary-line analysis on the sap flux scaled \( G_s \) (Schäfer et al. 2000; see Data Analysis below) fitting only \( G_{sref} \), \( f_1(D) \) and \( f_2(Q) \). Doing so ignores limitation imposed by \( \Psi \), thus generating potential \( G_s \).

Whole plant liquid phase hydraulic conductance \((K_L)\) was calculated after Granier and Loustau (1994) to check the equality of gas and liquid phase:

\[ K_L = \frac{E_L}{\psi_s - \psi_L} \]  \hspace{1cm} (10)
where $\Psi_s$, the soil water potential, is substituted by $\Psi_{pd}$ of the lower canopy, and $\Psi_l$, the leaf water potential is taken as the leaf area weighted average $\Psi_{md}$. Daily $g_{sref}$ and $K_l$ of each individual tree were calculated for days in which both $\Psi_l$ and $g_s$ were measured. $K_l$ was calculated by dividing the morning maximum $E_l$ with the differences between predawn and noon water potential. Daily $g_{sref}$ was calculated by selecting $g_s$ values, the $g_s(z)$ scaled by leaf area, beginning at the time of daily maximum $g_s$ to the time of daily maximum $D$, then by fitting through Equation 6.

### 4.3.4. Data Analysis

Parameters for the functions describing stomatal response to variations in $Q$ and $D$ were generated with boundary line analyses of $g_s$ and $G_s$ versus $D$ using a method described in (Schäfer et al. 2000). Briefly, conductance was partitioned into six $D$ intervals, the mean and standard deviation (s.d.) of $g_s$ were calculated, and outliers were removed using Dixon’s test (Sokal and Rohlf 1995). The data, represented by $\geq 5$ observations, were selected for the subset falling at least 1 s.d. above the mean, which were averaged and used to generate the response to $D$. Leaf-level data from the same canopy position were treated as a single dataset because of the small number of measurements from individual trees. At the tree level, two sets of data were generated for boundary line analysis: (1) data were partitioned to five canopy average $Q$ ($Q_{avg}$, estimated from $Q$ in the light model; Appendix C) classes, four classes were 65 $\mu$mol $m^{-2}$
s^{-1} wide from 0 to 260 μmol m^{-2} s^{-1}, and one for \( Q_{\text{avg}} > 260 \mu \text{mol m}^{-2} \text{s}^{-1} \), and (2) data were partitioned into two sets, one above and one below \( G_{\text{is}}=700 \mu \text{mol m}^{-2} \text{s}^{-1} \).

\( G_{\text{s}} \) estimates were gap-filled based on the above functions and meteorological data (air temperature, relative humidity and wind speed available from a weather station located within 0.6 km). This gap-filled dataset was used to estimate transpiration and carbon assimilation over the entire study period.

All statistical analyses were made with SAS procedures GLM and Repeated Measures of ANOVA (version 8.02, SAS Institute Inc., Cary, N.C.). Non-linear curve fits were performed in SIGMAPLOT (version 8.0, SPSS, Inc., San Rafael, CA).

### 4.4. Results

Daily values of meteorological conditions, diameter increment and water potential measurements are presented in Figure 1. Except for an occasional cloudy day, the pattern in incoming total radiation followed the maximum sun angle, with daytime mean \( T_a \) and \( D \) lagging the maximum radiation by about six weeks. Maximum mean daytime daily \( T_a \) and \( D \) were 31.3°C and 3.26 kPa, averaging 21.7°C and 1.5 kPa over the 126-day study during which 19.3 mm of rainfall were delivered in 10 events. Maximum half-hourly \( D \) was 5.5 kPa. The quadratic mean diameter increased more during the first phase of the study (1.11 cm, from 7.66 to 8.77 cm) than in the second period (1.0 cm, from 8.77 to 9.77 cm); however, the change in basal area increment was not as
pronounced (14.3 vs 14.5 cm² for the average tree during the first and second period, respectively). Leaf water potential varied slightly over the study period, was always greater at the lower canopy during midday, but mostly similar to the upper canopy at predawn.

Sap flux density was unrelated to tree size (P = 0.85) and was not affected by azimuth (P = 0.71), but decreased appreciably moving from the outer 20 mm of the xylem to the next 20 mm layer (P = 0.006; Figure 2). Scaling $J_{sf}$ to $E$ resulted in a similar seasonal pattern to that observed in $D$ (Figure 1D), with $E$ reaching maximum of ~6.2 mm day⁻¹ in mid July, averaging 3.4 mm day⁻¹ for the study period.

Leaf area of branches was linearly correlated with branch diameter at each sampling time with $r^2 > 0.72$ (maximum $P < 0.001$), and the relationship did not vary by height (minimum $P = 0.18$). Whole tree $A_L$ was linearly correlated with the percentile of $d_{L4}$ at each sampling time with $r^2 > 0.88$ (maximum $P = 0.04$). $A_L$ was distributed vertically based on the vertical distribution of branch diameter (Figure 3A); normalizing the distribution by each tree height and maximum $A_L(z)$ revealed no height-related pattern. Based on the time-specific equations and stand level diameter measurements, $L$ was 5.9 at the beginning of the study in May, rapidly rising to a maximum of 9.5 in July, followed with a slow decline to 6.0 by the end of the study in September (Figure 1E).
4.4.1. Conductance

The 4C-A scheme for estimating $A_{net}$ and GPP relies on leaf-level gas exchange measurements to generate $g_s(z)$ versus $Q$ response at several layers in the canopy, scale $g_s(z)$ to $g_s$, and constrain it with sap flux-scaled $G_s$ to account for the effects of other factors such as $D$ and soil moisture. We constructed $Q$ response curves using data from campaigns in which large number (~1650) of $g_s(z)$ measurements were made and assessed how well $g_s(z)$ scaled to $g_s$ agreed with $G_s$.

Leaf-level $g_s$ measurements for sun and shaded leaves from different canopy positions showed a commonly observed pattern of increasing conductance with increasing light, and decreasing conductance with increasing $D$ (Figure 4A). Using a boundary line analysis, the result of which for one category (canopy-top envelope or sun leaves) is shown as an example (the line through large symbols in Figure 4A), $g_{sref}$ and the sensitivity to $D$ (i.e. $m$) was estimated using Equation 6 for each of the six categories of crown positions (Figure 4B). The average leaf-level $\gamma$ (the slope of the relationship between $-dg_s/d\ln D$ and $g_{sref}$) for the six categories was $-0.45\pm0.06$ (P = 0.003). The expected $\gamma$ was estimated from the ratio $g_{bl}/g_{sm}$ (Oren et al. 1999), calculated from the porometry-generated constant wind speed (generating a steady high boundary layer conductance of ~2800 mmol m$^{-2}$ s$^{-1}$), and the maximum $g_s(z)$ measured (~500 mmol m$^{-2}$ s$^{-1}$). Based on the resulting $g_{bl}/g_{sm}$ of ~5.6 and the range in $D$ used in the measurements, the expected $\gamma$ was estimated at 0.53, similar to the observed sensitivity (P=0.58).
A diurnal pattern of photosynthetic photon flux density at the top of the canopy, \( Q \), on the same cloudy day depicted in Figure 2, is shown in Figure 3B. In Figure 3C, we show the corresponding estimate of average \( Q \) modeled based on the light model with tree clumping (LM2; see Appendix C for details on different light models) on the horizontal surface in each layer. These estimates were done with four light models differing in their specification of canopy structure, and converted to light at the leaf surface in order to estimate \( g_s(z) \). The porometry data for each leaf category were related to \( Q \) in order to generate the \( g_s-Q \) responses. After testing whether the lines are different or not, the crown envelope and core foliage in each canopy layer were combined into three relationships (Figure 4C); this was supported by the observation that LMA differed between canopy layers but not within a layer (\( P=0.60 \) and 0.11 for top and bottom, respectively).

Tree level \( G_s \) also decreased with \( D \) once \( D > 0.6 \) kPa. The boundary analysis was performed for each tree after partitioning the data to five consecutive ranges of \( Q_{avg} \), two of which are shown for one tree in Figure 5A. From this analysis, \( G_{sref} \) and \( m \) were obtained for each period. For both periods, \( m \) was similarly related to \( G_{sref} \) with a slope \( (\gamma, \text{i.e. the sensitivity of } G_s \text{ to } D \text{ at a given } G_{sref}) \) of 0.64 (Figure 5B), not different (\( P=0.75 \)) from the general slope obtained from a large number of studies (\( \sim 0.6 \), Oren et al. 1999). This analysis does not account for the effects on \( \gamma \) of (1) the range in \( D \) values occurring during the time in which \( G_s \) was analyzed, and (2) \( G_{bol}/G_{sref} \) (see surface in Figure 6). We
evaluated more precisely the change in the sensitivity of \( G_s \) to \( D \) with changes in \( G_{sref} \) by accounting for the effects of both factors. To do this we first partitioned data for individual trees into two categories, above and below \( G_{bl} = 700 \text{ mmol m}^{-2}\text{ s}^{-1} \). \( G_{sref} \) and \( m \) were estimated from boundary line analysis by \( G_{bl} \) and plotted these values against the observed range in \( D \) and the average ratio \( G_{bl}/G_{sref} \) (Figure 6). The inset in Figure 6 shows that the actual \( \gamma \) was similar to that predicted (Oren et al. 1999).

As final diagnostics of the consistency between \( g_s \) and both sap flux-scaled \( G_s \) and \( K_L \), daily values were calculated for the measurement campaign days. For each measurement, \( g_s(z) \) was scaled to the canopy by estimating the sunlit and shaded leaf area in each of the three canopy layers based on the light model (Appendix C; see example for average light in Figure 2), summing and dividing by \( A_L \). This generated a diurnal pattern of \( g_s \) for each tree. Selecting the portion of the diurnal patterns between the time of maximum conductance and the time of maximum \( D \), the relationships of \( g_s \) and \( G_s \) with \( D \) were analyzed (Equation 6) to obtain \( g_{sref} \) and \( G_{sref} \) for the same day for each tree. Excluding a cold morning, a windy day (not permitting measurements at the top of the canopy) and a pesticide application, allowed 15 comparisons showing a close agreement between the two estimates (Figure 7A; \( P=0.87 \) based on a paired t-test).

Similarly, \( g_{sref} \) was closely correlated to \( K_L \) (\( P = 0.003 \); Figure 7B). Thus, both in terms of expected \( G_s-D \) behavior and in relations to \( g_s \) and \( K_L \), \( G_s \) provides a good representation of the canopy, and can therefore be scaled based on light and \( A_L \) or \( L \) profile to \( G_s(z) \).
Next we established the relationship between $G_{sref}$ and $Q_{avg}$ for each tree (Figure 5C). The mean of the two parameters in the fit $G_{sref} = bQ_{avg} + a$ (a = 34.5, s.e. = 4.79; b = 0.40, s.e., = 0.03) described the average response ($r^2$=0.81, p<0.001). In general, $G_{sref}$ increased with $Q_{avg}$ similarly in both periods (P=0.18), saturating when $Q_{avg} > 195 \mu mol m^{-2} s^{-1}$.

To fill gaps in the data during the study period, and to estimate $G_s$ when $D < 0.6$ kPa, we predicted $G_s$ of *P. trichocarpa* x *P. deltoides* from $Q_{avg}$, $D$ and its daily range, $G_{bl}/G_{sref}$, and the functional relationships established above, such that:

$$G_s = G_{sref}(Q_{avg}) - \gamma(D_{range}, G_{bl}/G_{sref}) * G_{sref}(Q_{avg}) * \ln (D) \quad (10)$$

thus ignoring the effect of soil moisture limitations, which were indicated in low predawn leaf water potential days (Figure 1F). Clearly, this model overestimated $G_s$ over much of the range (Figure 8A), and we considered these values as the potential canopy conductance used in calculating the potential $A_{netC}$ and GPP. Daily $G_{sref}$ values from the modeled $G_s$ were expressed as a ratio of the observed $G_{sref}$ for individual trees. The ratio was linearly correlated with predawn water potential during days in which it was measured, showing overestimation under low soil moisture and underestimation under high soil moisture. We therefore calculated a soil water dependent correction factor (actual $G_{sref}$ / modeled $G_{sref}$ for $D>0.6$ kPa) for each day, and employed it to adjust the modeled $G_{sref}$ used in estimating $G_s$ during hours of $D<0.6$ kPa. The same ratio was used
to gap-fill 11 days of missing data, by averaging the correction factor before and after each gap.

**4.4.2. Actual and Potential Carbon Assimilation and Biomass Production**

Most of the biomass produced during the whole study period was in the stem (Table 2). We missed the early part of the growing season in which, based on the foliage produced before and during the study period, about 90 g C m\(^{-2}\) were invested in foliage production. We have no estimates of production in other components during the growing season before and after the study period.

The estimates of photosynthesis are sensitive to the specification of canopy properties in models employed to calculate light at the leaf surface at different layers in the canopy. The most realistic canopy specification employed (LM1) included both tree level and shoot level clumping, the latter varying vertically. A less detailed model employed only tree level clumping (LM2), and the least detailed was a simple Beer-Lambert without clumping (LM3). A comparison based on the output from the models with data collected on a light sensor of porometry demonstrated that light attenuation in LM3 was excessive, but that LM1 and the LM2 attenuated light similarly and without bias (Figure 9 and Figure A.3). Below we present the results of photosynthesis estimated based on 4C-A with LM2, the simplest of the unbiased models. In the discussion we provide some contrast with the estimates based on more complex and simpler models.
Individual tree $A_{\text{netC}}$ per unit of time was related to $A_L$, and the relationship did not change between the early and late part of the growing season ($r^2=0.90; P=0.07$ for differences between periods). Net primary productivity (NPP) during the study period increased with $A_{\text{netC}}$ at a rate of 0.41 (s.e. 0.08; $r^2=0.67; P<0.01$), similar to the average NPP/$A_{\text{netC}}$ of the 10 trees (0.50, s.e. 0.03), with the difference attributable to a significant intercept of the relationship ($P<0.001$). At the stand level, NPP/GPP was 0.43, and just as NPP/$A_{\text{netC}}$, increased from the first to the second period (Table 2). To assimilate 2371 g C m$^{-2}$ ground (LM2 in Table 2) over the study period, the stand used 438 mm of water. After removing soil water limitations to stomatal conductance and associated effects on photosynthesis, potential GPP was estimated to increase to 2900 g C m$^{-2}$ ground for the study period, associated with an increase in water use to 742 mm water.

4.5. Discussion

Poplar trees are typical of other fast growing species. Expected annual biomass production from a short-rotation poplar plantation is 12-15 Mg ha$^{-1}$ yr$^{-1}$ (Ben Brahim et al. 2000), but can reach ~45 Mg ha$^{-1}$ yr$^{-1}$ (Dawson 1976). Heights during the study period increased about 4.5 m, similar to other studies (e.g., Dawson 1976, Ben Brahim et al. 2000). The high rate of biomass production is attributed to high photosynthetic capacity and carboxylation efficiency (Nelson 1984) and high leaf area. Both $A_L$ and $L$ in the study stand were high, with $L$ reaching a maximum of 9.5, similar to published values for
hybrid poplar trees (Hinckley et al. 1994, Ceulemans et al. 1997). As expected based on the coupling between photosynthesis and transpiration, stands of these trees use large quantities of water (Allen et al. 1999, Zhang et al. 1999), especially in an arid environment. Thus, even with irrigation, soil moisture limitation may develop that impose constraints on water use and photosynthesis.

4.5.1. Stomatal conductance

Because the mechanism of stomatal function remains unclear (Buckley and Mott 2002, Comstock 2002), empirical models are more commonly used to describe stomatal behavior (e.g., Jarvis 1976, Ball 1987, Tardieu and Davies 1993, Leuning 1995, Gao et al. 2002). Empirical models are usually parameterized by varying individual environmental variables and describing their effects on stomatal conductance (Rayment et al. 2000). Our model is a modified version of the Jarvis (1976) type model with six variables (Equation 7).

Not including soil water limitation, the model overestimated $G_s$ because the other variables – $G_{sref}$, $f(Q_{avg})$, $f(D)$ and $f(G_{bol}/G_{sref})$ – were generated with boundary line analyses thus representing the highest values (except outliers) within specified ranges of environmental conditions (e.g., Figure 4A and 5A). Stomatal conductance has often been shown to increases linearly with light up to a maximum, as we show at both the leaf and canopy levels (Figure 4C and 5C). At the canopy level, $G_{sref}$ reached maximum at
$Q_{\text{avg}} = 290 \, \mu\text{mol m}^{-2} \text{s}^{-1}$, about 75% of the maximum value of canopy average light ($\sim 380 \, \mu\text{mol m}^{-2} \text{s}^{-1}$), corresponding to incoming $Q = 1320 \sim 1440 \, \mu\text{mol m}^{-2} \text{s}^{-1}$. Again, at both the leaf and canopy levels, the response of stomatal conductance to $D$ was similar to that expected based on theory for isohydric plants (Oren et al. 1999, Sperry et al. 2002), such as *Populus*, attempting to maintain leaf water potential above a minimum below which excessive cavitation occurs in the xylem (Figure 4 & 5AB, 6). We also show that stomatal responses to $D$ at different light levels can be described as a general increase in both $g_{\text{sref}}$ and $m$ with light, consistent with previous studies (Tinoco-Ojanguren and Pearcy 1993, Meinzer et al. 1997, Yong et al. 1997, Allen and Pearcy 2000). However, the absolute increase of the sensitivity of stomatal conductance to $D$ did not lead to a change in the relationship between these parameters (Figures 4B and 5B), a behavior observed in many species (Oren et al. 2001, Addington et al. 2004, Ewers et al. 2005).

In this study, $\Psi_{\text{md}}$ ($\sim -2.0 \text{ MPa}$) was lower than some published data for *P. trichocarpa*, its hybrid, and *P. deltoides* (e.g., Pezeshki and Hinckley 1988, Sperry et al. 1991, Tyree and Ewers 1991, Cochard et al. 1996), all of which are considered prone to cavitation (Tyree and Ewers 1991, Tyree et al. 1992, Cochard et al. 1996). However, other studies on hybrid poplars, including *P. trichocarpa x deltoides* (Gebre et al. 1998, Tschaplinski et al. 1998), showed a range of $\Psi_{\text{md}}$ (-1.6 ~ -2.2 MPa) and $\Psi_{\text{pd}}$ (-0.65 ~ -0.75 MPa) similar to ours. Stomatal conductance of *P. tricocarpa* remains nearly stable to leaf water potential of $\sim 2.0 \text{ MPa}$, while that of *P. deltoides* decreased sharply below $-0.5$
MPa (Scarascia-Mugnozza et al. 1986, Schulte et al. 1987). Hybrids of these species show a variable response, some behave more like *P. trichocarpa* (Scarascia-Mugnozza et al. 1986) whereas others behave more like the *P. deltoides* (Schulte et al. 1987). In other studies, however, both species and their hybrid showed similar sensitivities to soil moisture (Braatne et al. 1992, Allen et al. 1999) and reductions in photosynthetic rates as leaf water potential decreases (Scarascia-Mugnozza et al. 1986). In this study, utilizing \( A_l(z) \) weighted \( \Psi_{pd} \) and \( \Psi_{md} \), we demonstrate that changes in \( K_l \) were largely in response to changes in \( \Psi_{pd} \) that controlled \( g_{sref} \) (Figure 7B and 8B) and reflected canopy level \( G_{sref} \) (Figure 7A).

Height difference between the upper and lower canopy could generated a maximum hydrostatic gradient of 0.1 MPa, yet \( \Psi_{pd} \) was occasionally ~0.5 MPa lower in the upper canopy (Figure 1F). Nighttime stomatal closure is not complete in many species (Oren et al. 1999, Dawson et al. 2007). (Due to nighttime stomatal conductance, the baseline for converting temperature difference to sap flux was set between nights for which \( D \sim 0 \) kPa). Higher \( g_s \) in upper canopy leaves may have caused the vertical gradient in \( \Psi_{pd} \) observed when the nighttime desert air was dry, rendering \( \Psi_{pd} \) measured in the bottom of the canopy a more appropriate surrogate of soil water potential. The residuals between \( G_s \) modeled assuming no soil water limitation and \( G_s \) scaled from measurements were strongly and linearly related to \( \Psi_{pd} \) of the lower canopy (Figure 8B), making the modeled \( G_s \) a good approximation of potential conductance.
4.5.2. Actual and Potential Carbon Assimilation

Although the trees varied in diameter they shared a common vertical space due to the small height differences (~ 1 m) among individuals. Thus, although $A_{net}(z)$ declined from the top of the canopy downwards (based on any of the vertically-explicit light model), estimated tree-level $A_{netC}$ was linearly related to $A_l$. We note that the difference between $A_{netC}$ and GPP is foliar respiration during the day (Table 2), the estimate of which contains additional uncertainty and for stand carbon balance merely represents a quantity that is added and then subtracted. We prefer to use $A_{netC}$ for comparisons to tree level NPP, but revert to GPP for comparison with the more commonly available literature values. The comparison of the vertical light gradients obtained with LM2 (tree-level clumping) with those obtained with LM1 (tree-shoot level clumping) showed little effect due to the minimum amount of clumping in this species (Figure 9 and A3). Thus, LM1 with a more complete account of canopy properties produced only ~ 0.6% difference in GPP (Table 2), and will not be discussed further.

Based on 4C-A with LM2, the daily rates of canopy-level $A_{netC}$, GPP and $E$ were higher in the first period than the second period (Figure 10A) due to the higher $L$ and photosynthetic parameter values, (Table 2 and Figure A.1). Over the entire study, $A_{netC}$ was estimated at 2133 g C m$^{-2}$ ground, and GPP at 2371 g C m$^{-2}$ ground (Table 2). These estimates leave enough carbohydrates for maintenance respiration after accounting for
NPP and its 25% construction respiration cost (1008 + 252 = 1260 g C m\(^{-2}\) ground, after Wullschleger et al. 1997).

When the Beer-Lambert radiative transfer scheme (which accounts for sun angle, vertically variable leaf angle distribution, and thus \(K_{bc}\), and vertically variable clumping at the shoot level and crown level) is simplified by not accounting for clumping (e.g., as in Campbell and Norman 1998), GPP was estimated at 1548 g C m\(^{-2}\) ground (LM3) – too little for a reasonable maintenance respiration (~40% of GPP; after Waring et al. 1998, and accounting for construction respiration). Further simplifying by using a constant \(K_{bc}=0.5\) (i.e. assuming leaf angle distribution is spherical, and the sun remains at zenith during all daytime hours), still keeping light intensity changing over the day, increased GPP to 1901 g C m\(^{-2}\) ground (LM4), leaving nearly enough for respiration. As last simplification we reduced the canopy to a single layer and used daily means of light and temperature, in effect employing BIOME-BGC (Thornton et al. 2002); GPP was again estimated low as 1841 g C m\(^{-2}\) ground (Table 2). We also employed canopy conductance from the sap flux measurements in BIOME-BGC instead of the model’s own estimates, thereby focusing on differences that are caused by the vertical specification of the canopy. This single leaf model produced an estimate of GPP (2066 g C m\(^{-2}\) ground) only 10% lower than the 4C-A/LM2 (Table 2). This indicates that, the simplification of the radiation transfer scheme used in BIOME-BGC (essentially LM4 with daily average light), can produce reasonable estimates of GPP, but issues with its conductance.
estimates may result in unacceptable underestimate. In addition, single-leaf models are incapable reproducing the vertical distribution of GPP.

The most simplified multi-layer approach (4C-A/LM4)— which increases light penetration into the canopy at the expense of realistic solar tracking—underestimated light on the surface of foliage located at the bottom of the canopy: in our stand this would result in the bottom four layers having zero to negative net photosynthesis on a 24-hour basis. The simulation suggested that the bottom 44% of $L$ (averaged over the study) did not contribute carbohydrates to the stand (Figure 10B). Thus, even this unrealistic approach that forces light down the canopy underestimated both GPP and its vertical distribution in the canopy. In contrast, based on estimates from 4C-A/LM2 only foliage in the bottom two layers (averaging 16% of $L$) did not contribute photosynthates to the stand (Figure 10B). This is in agreement with the observed 45% reduction in living branches at the bottom two layers over the study period, with no loss of branches recorded above; at the end of the study the bottom layer had one third of the live branches, and the next layer had one half the live branches found in the layer above. It is thus clear that although reasonable estimates of $A_{netC}$ and GPP can be made with greatly simplified models, a realistic vertical distribution of carbohydrate production can be obtained only if the clumping at the scale of trees (and in some species at the scales of shoots as well; e.g., Schäfer et al., 2003) is incorporated into a radiative transfer model with realistic solar tracking.
Our 4C-A/LM2 produces GPP value that is appreciably higher than NPP. For the stand and over the entire study period, the ratio NPP/GPP is 0.43, similar to the mean of a large number of species (Waring et al. 1998). Using a big leaf approach (as in BIOME-BGC) and solar tracking (as in LM3) recent estimates of NPP/GPP for poplar species and their hybrids ranged 0.58 – 0.72 (Gielen et al. 2005), similar to 4C-A/LM3 (0.64, Table 2) but substantially higher than the 0.49 estimated by the sap-flux constrained BIOME-BGC.

The model estimates allow calculations of water and light use efficiencies. Water use efficiency in forests is expressed in a number of ways. Published values for hybrid poplars on photosynthetic water-use efficiency range 3.6 – 4.2 g C kg\(^{-1}\) H\(_2\)O from leaf gas-exchange measurements (Bassman and Zwier 1991), and production-based water-use efficiency of 2.1 g dry matter C kg\(^{-1}\) H\(_2\)O from studies on potted plants of the same hybrid (Souch and Stephens 1998). These values are similar to those obtained in this study using the 4C-A/LM2 model to estimate \(A_{\text{netC}}\) (4.9 g C kg\(^{-1}\) H\(_2\)O, or 5.3 g for GPP) and growth measurements to estimate NPP (2.3 g C kg\(^{-1}\) H\(_2\)O). Photosynthetic light-use efficiency was estimated at 0.42 g C mol\(^{-1}\) of PAR, or 2.02 g C MJ\(^{-1}\), higher than estimated with other models in forests with slightly lower \(L\) (Whitehead and Walcroft 2005). However, it was similar to other poplar species and deciduous forests of oak and maple (Waring et al. 1995). For example, for dry matter, the light-use efficiency was 1.74 g dry
matter MJ$, similar to other stands of the same genus growing on nutrient rich soils
(Calfapietra et al. 2003, Green et al. 2003).

We used 4C-A/LM2 to estimate GPP if irrigation were sufficient to remove all
limitations to plant available moisture. The estimated potential GPP was 21% higher
than actual, which based on a NPP/GPP of 0.43, would have increased NPP by ~217 g C
m$^{-2}$ ground and associated stand transpiration by 70% increase (Table 2). Assuming further
that this extra carbon would not be used for foliage production because $L$ is already very
high at the stand, and that ~70% would be invested in stem wood production (Scarascia-
Mugnozza et al. 1997, Zabek and Prescott 2006), 162 g C m$^{-2}$ ground would be added to the
stem if there were no soil water limitation to photosynthesis, decreasing yield-based
WUE by 27% (from 1.57 to 1.15 g stem wood C kg$^{-1}$ H$_2$O). Thus, the large increase in
irrigation necessary to remove all water limitation can hardly be justified. The use of
this technique to examine the tradeoffs between production and water limitations offers
opportunities to explore the impacts of increasing or decreasing water use on carbon
gain.
Figure 4.1. Daily daytime average of weather data (A. total incoming radiation, \( R \); B. air temperature \( T_a \); C. vapor pressure deficit, \( D \) (●), and precipitation, \( P \) (bars)), and stand data (D. stand transpiration \( E \); E. leaf area index, \( L \) (●), and quadratic mean diameter at 1.4 m aboveground, \( d_{1.4} \) (○); F. leaf water potential \( \Psi_L \) (predawn (solid) and midday (open) at the top (▲) and bottom of canopy (●); error bars are 1 standard error). In B, C and D, the symbols are measurements and the line is gap-filled data. Two vertical lines represent the beginning of each study period.
Figure 4.2. Average sap flux (bars represent one standard error) of outer (●, 0-20 mm) and inner (○, 20-40 mm) probes of Granier-type heat dissipation sensors on a partially cloudy day.
Figure 4.3. A. Vertical profiles of leaf characteristic length, $d$, leaf area index, $L$, and individual tree leaf area, $A_L$, of the five trees monitored for sap flux in the first period of the study. B. A diurnal pattern of photosynthetic photon flux density, $Q$, on the same cloudy day as in Figure 2, and the modeled average $Q$ on the horizontal surface in each layer.
Figure 4.4. Leaf-level stomatal conductance, $g_s$, responses based on porometer measurements. A. $g_s$ response to vapor pressure deficit, $D$, in leaves from the outer envelope of crowns compared with the inner core, for three levels in the canopy. A boundary line analysis is shown (line) envelope leaves at the top of canopy (large Δ). B. The slope of the response of $g_s$ to $ln(D)$ ($m$ in Equation 7) versus the intercept of the response ($g_{sref}=g_s$ at $D=1$ kPa) for crown envelope (sun) and core (shade) leaves at the three canopy layers. The fitted regression equation was $m = 0.48\cdot g_{sref} - 10.83$ and the dashed lines are 95% confidence intervals. C. $g_s$-light response of leaves from the three levels in the canopy.
Figure 4.5. A. An example of canopy conductance, $G_s$, scaled from sap flux measured in a single tree, versus vapor pressure deficit, $D$. Boundary line analysis is shown for two ($\bullet$, ▲) of the five light categories, the unselected points from the analysis is shown as open symbol (○); the vertical line at $D = 1$ kPa intersects the boundary lines at a value equal to the reference $G_s (G_{sref})$. B. The slope of the response of $G_s$ to $\ln(D)$ ($m$ in Equation 6) versus $G_{sref}$ from analysis of data obtained from 10 trees, partitioned to five light levels in the first (●) and second (○) study periods. C. Stand level $G_{sref}$-light response was similar in the two periods and reached maximum at the fourth light level.
Figure 4.6. Actual $\gamma$, the ratio of the slope of $g_s$ response to the natural logarithm of the vapor pressure deficit, $m$, over the intercept of the response, $G_{sref}$, obtained from analysis of data from 10 trees. The mesh surface shows the $\gamma$ expected based on different ranges in vapor pressure deficit and the ratio of boundary layer conductance to reference stomatal conductance ($G_{bl}/G_{sref}$). Inset shows the relationship between actual and expected $\gamma$, for which the 95% confidence interval encloses unity.
Figure 4.7.A. Comparison between reference conductance (conductance at vapor pressure deficit of 1 kPa) obtained from porometry at the leaf level (gsref) and sap flux at the tree level (Gsref) for days in which leaf-level gas exchange was measured. B. Comparison between gsref and leaf-specific hydraulic conductance, KL, obtained from sapflux and leaf water potential within the same measurement campaign.
Figure 4.8. A. Comparison between modeled canopy stomatal conductance, Gs, assuming no soil water limitation, and the measured Gs that reflects these limitations. B. The relationship between the ratio of modeled and measured reference Gs (Gsref, Gs at D = 1 kPa) and the predawn leaf water potential measured at the lower canopy and used to represent soil water limitation in the first (●) and second (○) study periods.
Figure 4.9. Comparison of relative light on leaf surface from different light models and porometric measurements. Dots represent the average ratio between light on leaf surface and the light above the canopy from eight porometric measurement campaigns. Except Beer and Lambert, three lines (least-square fit, tree and shoot-level clumping and tree clumping) are almost identical.
Figure 4.10. A. Daily actual (black) and potential (grey) stand transpiration, $E$, canopy net assimilation, $A_{\text{netC}}$, gross primary production, GPP, and net primary productivity, NPP, in the two study periods. B. The vertical distribution of $A_{\text{netC}}$ based on three Beer and Lambert radiative transfer formulations: (1) Using correct sun angle, vertically varying leaf angle distribution, and tree-level clumping, LM 2. (2) Using correct sun angle and vertically varying leaf angle distribution, but no clumping, LM 3. (4) Assuming no clumping and constant $K_{\text{be}}$ (i.e. sun is always in zenith and leaf-angle spherically distributed), LM 4. Horizontal dashed line represent the lowest level of branch mortality.
Chapter 5. Conclusions

Light absorption, canopy conductance and the carbon assimilation components of the 4C-A model were evaluated based on field measurements and hydrological models at two sites composed of different species, and highly varying canopy leaf area and environmental conditions.

In my first study, I evaluated the light model by comparing the modeled output of canopy openness and PAR with measurements from a loblolly pine stand at Duke Forest and evaluate the effect of each structural attribute (leaf angle distribution, and clumping at the shoot and the tree level) on the both total APAR and its vertical distribution. The 1-D model estimated well both openness and PAR in the stand that includes, in addition to the dominating pine, a substantial component of broadleaved species in the canopy, and a sub-canopy composed mostly of broadleaves species. Shoot and tree clumping were needed to reproduce openness and PAR measurements down the canopy. However, increased complexity of adding vertically varying architecture had little effect on the vertical distribution of APAR.

My sensitivity analysis on conifer trees showed that ignoring the shoot clumping would result in an overestimation of total APAR, especially where $L$ was low and shoots were highly clumped, with errors decreasing with increasing canopy leaf area. Not accounting for tree density in the model also caused substantial overestimation of
APAR, especially in low density stands. The effect of LAD on total canopy APAR was smaller than either of shoot or tree clumping.

Shoot and tree clumping increases APAR in deeper canopy layers by decreasing absorption in the upper layers. Changing LAD moving from spherically to more horizontally distributed leaves increased APAR at the top, and moving from spherically to more vertically distributed leaves decreased APAR at the top. However, the overall effect of LAD was smaller than that of shoot or tree clumping.

In my second study, I evaluated the accuracy of sap flux scaled mean canopy conductance by scaling measurements from Granier-type sensors to transpiration and assessing in the context of other components of the hydrological balance. My evapotranspiration ($E_T$) estimate, the sum of transpiration and modeled evaporation, where comparable to estimates from eddy covariance, with the differences mostly related to underestimation of eddy covariance values associated with times during and soon after rain events. Moreover, the hydrological budget was balanced well in all four CO$_2 \times$ N treatments throughout the study period, giving confidence in the scaling of sap flux to transpiration and, therefore, in the values of canopy conductance. In addition, measurements and modeled estimates showed that the increase of $L$ by both treatment factors, decreased (although not significantly) throughfall precipitation ($P_T$) leading to higher canopy rainfall interception ($I_C$). Additional results fundamentally agree with those of a three-year study at the site (Schäfer et al. 2002): soil moisture increased under
elevated CO₂. However, I found that the earlier explanation for higher soil moisture under elevated CO₂ that higher leaf litter accumulation on the soil surface (LM) reduced water loss by evaporation, was incorrect. Leaf litter accumulation was the reason for higher soil moisture but through a different process: It reduced overland flow (Fₒ) allowing water more time to infiltrate the soil. Indeed, the effect of increased litter on evaporation from the forest floor was to decrease evaporation from the soils surface (Eₛ) due to increased resistance to vapor transfer, but to increase evaporation from the litter (Eₐ) because the thicker litter layer was able to store more moisture. The opposite responses canceled, and the reason evaporation increased is primarily due to higher Ic. Finally, there was no treatment effect on transpiration.

Having thoroughly assessed both the light model and my ability to scale sap flux to transpiration and, thus, to canopy conductance, I was able to proceed and evaluated the carbon assimilation calculation from a fast growing poplar plantation using 4C-A model. Even though the plantation was intended to achieve maximum biomass production with irrigation and fertilization, water was still limiting at the study site. Therefore, I estimated two measures of canopy stomatal conductance, one with actual soil water limitation and one as the potential without soil water limitation. Actual and soil water-unlimited potential CO₂ uptakes were estimated using actual or potential canopy conductance with the same vertical gradients of light distribution. I found that current irrigation reduced photosynthesis and, assuming a constant ration of NPP/GPP,
growth by ~18% compare to having no water limitation. However, additional 70% of water would be required to achieve water-unlimited growth. Additional irrigation to alleviate all water limitation would have therefore reduced water-use efficiency by 27%.

In addition, similar to my first study, I calculated carbon assimilation based on light models of a range of complexities, but using the same canopy conductance. I found that only light models that incorporate both shoot and tree clumping are able to (1) assimilate enough carbon to support NPP and respirations, showing a ratio of NPP/GPP 0.45, similar to the empirical generated from synthesis of many studies (Waring et al. 1997), (2) produce LUE and WUE values similar to those published for the same or similar species from other sites, and (3) correctly estimate the level at which branches should die due to negative carbon balance as evidence from the record of branch mortality.

In summary, my work improved on previous attempts by delineating the stand conditions under which different specifications of canopy architecture are needed for correct estimation of total light absorption and the vertical distribution of light amount and intensity. I also showed that correct scaling can lead to closure of the hydrological budget in forest ecosystems over a long period of canopy development, punctuated by events such as ice storms and hurricanes that drastically modified the canopy. While doing so, I showed that the major components of the budget are barely affected by CO₂ and nutrient amendments, despite their effect on canopy leaf area. Finally, I utilized the
entire 4C-A framework and showed that, when its light and conductance components are properly configured, it can estimate total GPP well and is accurate enough to pinpoint the layer in the canopy where photosynthesis goes negative.
# Appendix

## Appendix A. Table of Additional Symbols

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>( a(\theta, z) )</td>
<td>the mean gap fraction of the zth layer in a single tree crown at the view angle ( \theta )</td>
<td>dimensionless</td>
</tr>
<tr>
<td>( C_d )</td>
<td>drag coefficient (0.2, Katul and Chung 1999)</td>
<td>dimensionless</td>
</tr>
<tr>
<td>( C_{oa} )</td>
<td>ambient oxygen concentration (210000 ( \mu \text{mol mol}^{-1} ))</td>
<td>( \mu \text{mol mol}^{-1} )</td>
</tr>
<tr>
<td>( e_m )</td>
<td>maximum quantum efficiency (0.08)</td>
<td>( \text{mol mol}^{-1} )</td>
</tr>
<tr>
<td>( h )</td>
<td>canopy height</td>
<td>m</td>
</tr>
<tr>
<td>( ha(n) )</td>
<td>probability of leaf angle in ( n ) degree</td>
<td>dimensionless</td>
</tr>
<tr>
<td>( j )</td>
<td>electron transport rate</td>
<td>( \mu \text{mol m}^{-2} \text{leaf s}^{-1} )</td>
</tr>
<tr>
<td>( j_{\text{max}25} )</td>
<td>light saturated rate of electron transport at 25°C</td>
<td>( \mu \text{mol m}^{-2} \text{leaf s}^{-1} )</td>
</tr>
<tr>
<td>( K_{\text{be}}(z) )</td>
<td>extinction coefficient in the zth layer</td>
<td>dimensionless</td>
</tr>
<tr>
<td>( K_{\text{be, total}}(z) )</td>
<td>average extinction coefficient to the zth layer weighted with leaf area in each layer</td>
<td>dimensionless</td>
</tr>
<tr>
<td>( K_c )</td>
<td>Michaelis constant for ( \text{CO}_2 ) fixation</td>
<td>( \mu \text{mol mol}^{-1} )</td>
</tr>
<tr>
<td>( K_m )</td>
<td>turbulent diffusion coefficient</td>
<td>m² s⁻¹</td>
</tr>
<tr>
<td>( K_o )</td>
<td>Michaelis constant for oxygen inhibition</td>
<td>mmol mol⁻¹</td>
</tr>
<tr>
<td>( k )</td>
<td>von Karman constant (0.41)</td>
<td>dimensionless</td>
</tr>
<tr>
<td>( L_c(z) )</td>
<td>cumulative leaf area index to the zth layer</td>
<td>m² m⁻²</td>
</tr>
<tr>
<td>( N )</td>
<td>stand density</td>
<td>trees m⁻²</td>
</tr>
<tr>
<td>( N_a )</td>
<td>nitrogen concentration per unit leaf area</td>
<td>g m⁻²</td>
</tr>
<tr>
<td>( Q_b )</td>
<td>direct radiation</td>
<td>( \mu \text{mol m}^{-2} \text{ground s}^{-1} )</td>
</tr>
<tr>
<td>( Q_{b}(z) )</td>
<td>direct radiation at the bottom of the zth layer</td>
<td>( \mu \text{mol m}^{-2} \text{ground s}^{-1} )</td>
</tr>
<tr>
<td>( Q_d )</td>
<td>diffuse radiation</td>
<td>( \mu \text{mol m}^{-2} \text{ground s}^{-1} )</td>
</tr>
<tr>
<td>( Q_{d}(z) )</td>
<td>diffuse radiation at the bottom of the zth layer</td>
<td>( \mu \text{mol m}^{-2} \text{ground s}^{-1} )</td>
</tr>
<tr>
<td>( Q_{t.b}(z) )</td>
<td>direct radiation on leaf surface in the zth layer</td>
<td>( \mu \text{mol m}^{-2} \text{leaf s}^{-1} )</td>
</tr>
<tr>
<td>( Q_{t.a}(z) )</td>
<td>diffuse radiation on leaf surface in the zth layer</td>
<td>( \mu \text{mol m}^{-2} \text{leaf s}^{-1} )</td>
</tr>
<tr>
<td>( Q_{t.s}(z) )</td>
<td>scattered radiation on leaf surface in the zth layer</td>
<td>( \mu \text{mol m}^{-2} \text{leaf s}^{-1} )</td>
</tr>
<tr>
<td>( Q_{t.t} )</td>
<td>total radiation on leaf surface</td>
<td>( \mu \text{mol m}^{-2} \text{leaf s}^{-1} )</td>
</tr>
<tr>
<td>( Q_{ob} )</td>
<td>direct radiation at the top of the canopy</td>
<td>( \mu \text{mol m}^{-2} \text{ground s}^{-1} )</td>
</tr>
<tr>
<td>( Q_{od} )</td>
<td>diffuse radiation at the top of the canopy</td>
<td>( \mu \text{mol m}^{-2} \text{ground s}^{-1} )</td>
</tr>
<tr>
<td>( Q_s )</td>
<td>scattered radiation</td>
<td>( \mu \text{mol m}^{-2} \text{ground s}^{-1} )</td>
</tr>
<tr>
<td>( Q_{s}(z) )</td>
<td>scattered radiation at the bottom of the zth layer</td>
<td>( \mu \text{mol m}^{-2} \text{ground s}^{-1} )</td>
</tr>
<tr>
<td>( Q_2 )</td>
<td>maximum fraction of quanta used in electron transport</td>
<td>dimensionless</td>
</tr>
<tr>
<td>( R )</td>
<td>universal gas constant (8.314)</td>
<td>J mol⁻¹ K⁻¹</td>
</tr>
<tr>
<td>( S(z, \theta) )</td>
<td>projected area of tree crown in zth layer at the view angle ( \theta )</td>
<td>m²</td>
</tr>
</tbody>
</table>
Appendix B. Net Assimilation and Gross Primary Production

The 4C-A model (Schäfer et al. 2003) calculates canopy photosynthesis using canopy conductance constrained by sap flux measurement with Farquhar-type photosynthesis model (Farquhar et al. 1980, Farquhar and von Caemmerer 1982). At each layer in the canopy, \( g_s(z) \) of sunlit and shaded leaf were estimated from the stomatal light response curves, generated from porometric measurements (Figure 4C). The \( g_s(z) \) was converted to the \( G_S \) by multiplying with the respective sunlit and shaded leaf area of each layer and summing up for the canopy. This \( G_S \) was constrained by sapflux-measured conductance by linearly adjusting mean of the canopy \( g_s \) (Equation 5).

\[ A_{\text{net}} \] was calculated for the sunlit and shaded leaf area in each layer by solving \( C_i \) from two potential capacities and by taking the minimum (Farquhar and von Caemmerer 1982):
\[ A_{\text{net}} = \min \left( \frac{W_c}{W_j} \right) - R_d = g_c (C_a - C_i) \]  \hspace{1cm} (B.1)

where \( W_c \) is the Rubisco-limited rate and \( W_j \) is the electron transport limited rate of ribulose-1,5-bisphosphate regeneration, \( R_d \) is the daytime respiration rate assumed 0.015\( V_{c\text{max}} \) \cite{Casella2002}, \( g_c \) is converted from water to CO\(_2\) due to different diffusivities, and \( C_a \) is the ambient CO\(_2\) concentration, changing from 364 to 371 \( \mu \)mol mol\(^{-1}\) over the study period \cite{Keeling2005}. The two linear algebra equations for \( C_i \) were solved at half hourly time-steps and the minimum \( A_{\text{net}} \) was selected.

In Equation B.1, \( W_c \) and \( W_j \) were calculated as

\[ W_c = V_{c\text{max}} \frac{C_i - \Gamma_*}{C_i + K_c \left( 1 + \frac{C_i}{K_o} \right)} \]  \hspace{1cm} (B.2)

\[ W_j = J \frac{C_i - \Gamma_*}{4.5 C_i + 10.5 \Gamma_*} \]  \hspace{1cm} (B.3)

where \( \Gamma^*, K_c, K_o \) and \( J \) are calculated according to Bernacchi et al. (2001 and 2003).

\[ J = \frac{Q_2 + J_{\text{max}} - \sqrt{(Q_2 + J_{\text{max}})^2 - 4 \Theta_{\text{PSII}} Q_2 J_{\text{max}}}}{2 \Theta_{\text{PSII}}} \]  \hspace{1cm} (B.4)

\[ \Gamma^* = 42.75 e^{\left( \frac{37830(T_e - 25)}{298(R(T_e + 273))} \right)} \]  \hspace{1cm} (B.5)

\[ K_c = 404.9 e^{\left( \frac{79430(T_e - 25)}{298(R(T_e + 273))} \right)} \]  \hspace{1cm} (B.6)

\[ K_o = 278.4 e^{\left( \frac{36380(T_e - 25)}{298(R(T_e + 273))} \right)} \]  \hspace{1cm} (B.7)

\( V_{c\text{max}}, J_{\text{max}}, Q_2 \) and \( \Theta_{\text{PSII}} \) were calculated as Bernacchi et al. (2001 and 2003).
\[ V_{c,\text{max}} = V_{c,\text{max}25} e^{\left(\frac{26.35 - 65.33}{T_a+273}\right)} \]  
\[ (B.8) \]

\[ J_{\text{max}} = J_{\text{max}25} e^{\left(\frac{43.54}{T_a+273}\right)} \]  
\[ (B.9) \]

\[ Q_2 = 0.5 Q_L(z) \alpha \Phi_{\text{PSII,max}} \]  
\[ (B.10) \]

\[ \Theta_{\text{PSII}} = 0.76 + 0.018 T_a - 0.00037 T_a^2 \]  
\[ (B.11) \]

where \( \Phi_{\text{PSII,max}} \) was calculated as Bernacchi et al. (2003):

\[ \Phi_{\text{PSII,max}} = 0.352 + 0.022 T_a - 0.00034 T_a^2 \]  
\[ (B.12) \]

Finally, \( V_{c,\text{max}25} \) and \( J_{\text{max}25} \) were calculated from the nitrogen concentration measurements based on relationship that include the same species in a similar age (Casella and Ceulemans 2002; \( V_{c,\text{max}}=28.9*N_a \) and \( J_{\text{max}}=67.3*N_a-18.3 \); see Figure A.1).

Our N concentration data were available for top and bottom leaves; there was no difference in concentration between crown envelope and inner core leaves (P=0.11), so data in each of the two levels were pooled. We assumed that the concentration in top leaves remained unchanged until 60% of the light (estimated as the percent of cumulative light above the canopy during the study period) was attenuated, reflecting the saturating portion of the photosynthetic light response curve. Over the lower canopy zone in which light was assumed to affect foliar N concentration (typically ~1/2 of total height), [N] was interpolated between the values measured in top and bottom leaves. The interpolation was linear with the reduction in light intensity estimated with each of the Light models 1 to 4. Top and bottom values were linearly interpolated over
time between consecutive measurements. For BIOME-BGC, the values from the top and bottom were used for sun and shade leaf, respectively.

Gross primary production (GPP) was calculated by adding $R_d$ to $A_{net}$.

**Appendix C. Canopy Radiative transfer**

The above the canopy $Q$ was partitioned into $Q_{ob}$ and $Q_{od}$ components using measured and expected clear day radiation (Spitters et al. 1986). $Q_s$ was assumed zero above the canopy. Then, the interception of $Q_b$, $Q_d$ and $Q_s$ were estimated separately in each 1 m layers inside the canopy. In every layer, $Q_b$ on sunlit horizontal surface is the same as the top of the canopy (C.1). The proportion of sunlit area was calculated as Nilson (1999) (C.2&3).

$$Q_b(z) = Q_{ob}$$  (C.1)

$$\tau_b(z, \theta) = e^{-\frac{N \sum S(z, \theta)(1-a(z, \theta))}{\Pi(z)}}$$  (C.2)

$$a(z, \theta) = e^{-\frac{K_{sh}(z)I(z)z^2}{NS(z, \theta)}}$$  (C.3)

where $N$ is the stand density, $S(z, \theta)$ is the projected area of a conical crown with a radius of 75% of the distance between trees, $a(z, \theta)$ is the mean gap fraction in a single tree crown at the view angle $\theta$ (Nilson 1999). $\Pi(z)$ is defined as the average ratio of shoot silhouette area to the projection area of all leaves with their natural orientation, but spread out so they do not shade each other (Stenberg 1998). In Light models 2 - 4 shoots were assumed to have leaves with no clumping, i.e. $\Pi(z)$ was 1. However, for Light model 1, we assumed an additional shoot-level clumping that varied vertically. Shoot-
level clumping was estimated based on the following approach: (1) based on observations, it was assumed that shoots were not clumped at all at the bottom of the canopy, (2) it was assumed that the average of total clumping (shoot + tree) are as measured at a stand of the same species (Niinemets et al. 2004), (3) the vertical pattern in clumping was similar to the vertical pattern of leaf mass per area in a stand with high LAI (Liberloo et al. 2007), and (4) solving, based on 1-3 for the unique shoot level clumping at the top. Shoot-level clumping at the top was 0.95. In other words, there was little evidence of clumping for this species already at top shoots (Figure. A2.A).

\[ K_{be}(z,\theta) \text{ in Equation C.3 was calculated as} \]
\[ K_{be}(z,\theta) = \frac{\sqrt{\frac{x(z) + \tan^2 \theta}{x(z) + 1.774 (x(z) + 1.182)^{-0.733}}}}{C.4} \]

Values of \( x(z) \) were similar to a oak canopy from Kull et al. (1999) and Wirth et al. (2001) changing between 1.5 to 2.75 from the top to the bottom of canopy (Figure A2.B).

\( Q_d \) and \( Q_s \) at the bottom of each layer was calculated as

\[ Q_d(z) = \tau_d(z)Q_{od} \quad (C.5) \]
\[ Q_s(z) = (\tau_{bt}(z,\theta) - \tau_b(z,\theta))Q_b(z) \quad (C.6) \]

\( \tau_d(z) \) and \( \tau_{bt}(z,\theta) \) was calculated as

\[ \tau_d(z) = 2\int_0^{\frac{\pi}{2}} \tau_{b,\text{total}}(z,\theta) \sin \theta \cos \theta d\theta \quad (C.7) \]
\[ \tau_{bt}(z,\theta) = e^{-\sqrt{2\alpha NS(\theta,z)(1-\alpha(\theta,z))}} \quad (C.8) \]

\( \tau_{b,\text{total}}(z,\theta) \) is calculated with the \( L_{e}(z) \), \( K_{be,\text{total}}(z,\theta) \) and \( \Pi_{\text{canopy}}(z) \) as
\[
\tau_{h,\text{total}}(z, \theta) = e^{-\text{NS}(\theta, z)(1 - u_{\text{total}}(\theta, z))}
\] (C.9)

\[
a_{\text{total}}(z, \theta) = e^{\left(\frac{K_{\text{hc, total}}(z)L(z)\Pi_{\text{canopy}}(z)}{\text{NS}(z, \theta)}\right)}
\] (C.10)

\(K_{\text{hc, total}}(z)\) and \(\Pi_{\text{canopy}}(z)\) were average values weighted with leaf area in each layer from the top of canopy to the layer.

\(Q_{L,b}(z)\) was calculated by multiplying the light on leaf surface with the probability of leaf angle distribution. The light on leaf surface was calculated by multiplying the light on the horizontal surface arriving through the layer above with the cosine of leaf angle and divided by the cosine of sun angle;

\[
Q_{L,b}(z) = \int_{0}^{\pi/2} Q_{b}(z - 1)\cos n \cos \theta \text{ ha}(n)
\] (C.11)

where \(\text{ha}(n)\) is the probability of leaf angle distribution.

\(Q_{L,d}(z)\) and \(Q_{L,s}(z)\) used the average radiation at the top and bottom of each layer.

\[
Q_{L,d}(z) = \frac{Q_{L,d}(z - 1) + Q_{L,d}(z)}{2}
\] (C.12)

\[
Q_{L,s}(z) = \frac{Q_{L,s}(z - 1) + Q_{L,s}(z)}{2}
\] (C.13)

The total light on sunlit leaf was calculated by summing direct, diffuse and scattered and the total light on shade leaf was calculated by summing diffuse and scattered radiation only. \(Q_{\text{avg}}\) was calculated as:

\[
Q_{\text{avg}} = \frac{\sum_{z=1}^{12} L(z)\left[Q_{\text{sc}}(z)(Q_{L,b}(z) + Q_{L,d}(z) + Q_{L,s}(z)) + (1 - Q_{\text{sc}}(z))(Q_{L,d}(z) + Q_{L,s}(z))\right]}{L}
\] (C.14)
We tested the performance of light models with three different canopy specification, the most complicated tree-shoot clumping (Light Model 1), the less complicated tree clumping (LM2), and the simple Beer-Lambert (LM3). We calculated $Q_{\text{L,t}}$ (total light at the surface of leaves) for each time in which a gas exchange measurement (with associated PPFD) was made. Because the porometric measurements are done on a leaf in its natural inclination, we expected a large scatter in the comparison between model output and measurements, and only tested for bias. LM1 and LM2 showed no bias at any of the three measurement heights (Figure. A3), and as expected given the small shoot clumping employed in LM1, there was little difference between their performances. In contrast, LM3 showed some underestimation at the top layer, which became so severe with depth that the model estimates essentially described the lower bound of the data in both the middle and bottom of the canopy.

**Appendix D. Boundary layer conductance**

For $G_{\text{bl}}$ calculations, $U(z)$ was modeled using a first-order closure model for a planar-homogeneous, stationary and high Reynolds number flow based on the half-hourly average $\overline{U}$ above the canopy (Landsberg and James 1971). The boundary layer conductance of each canopy layer was calculated by:

$$G_{\text{bl}}(z) = 0.147 \sqrt{\frac{\overline{U}(z)}{d(z)}}$$  \hspace{1cm} (D.1)
where $G_b(z)$, $\overline{U}(z)$, $d(z)$ are boundary layer conductance, average wind speed and leaf characteristic length of the $z$th layer, respectively.

$\overline{U}(z)$ is calculated by solving differential equations numerically using the Thomas algorithm with 10 iterations and 0.5 relaxation at each iteration (D.2&3, Kreyszig 1988).

\[
\frac{\partial u' w'}{\partial z} = -C_d L(z) \overline{U}(z)^2 \quad \text{(D.2)}
\]

\[
u' w' = -K_m \frac{\partial \overline{U}(z)}{\partial z} \quad \text{(D.3)}
\]

where $K_m$ is assumed to change only with $h$ and calculated as

\[
K_m = k h u_w R \quad \text{(D.4)}
\]
Figure A.1. Seasonal variation of photosynthetic parameters at 25 °C. A. $V_{\text{cmax25}}$ at the top (●) and bottom (○) of canopy. B. $J_{\text{max25}}$ at the top (●) and bottom (○) of canopy.
Figure A.2. Canopy specification. A. Vertical distribution of shoot-level clumping factor used in LM 1. B. Vertical distribution of leaf angle distribution.
Figure A.3. Light comparison between three different light models and porometric measurements from three canopy positions. Open dots represent the average light on leaf surface from porometric measurements (at least 4 measurements). Solid line represents least-square fit through data. Other lines represent the fit through the modeled data from three different light models (Beer and Lambert: dotted, shoot and tree-level clumping: dash, tree-level clumping: dash-dot-dot)
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Biography

Hyun-Seok Kim was born in Seoul, Korea on April 9, 1970. In Feb 1993, he received his B.S. in Agricultural Science from Seoul National University. In Feb 1995, he received his first M.S. in Agricultural Science at Seoul National University with Dr. Kyung Joon Lee. In June 2000, he received his second M.S. in Forest Science from University of Washington with Dr. Thomas M. Hinckley, whether after a month he began his Ph.D. work with Dr. Ram Oren. Currently he has over 10 publications and presentations.