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Modeling Canopy Photosynthesis Of A Scrub-oak Ecosystem Under Elevated Co2

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MODELING CANOPY PHOTOSYNTHESIS OF A SCRUB-OAK ECOSYSTEM UNDER ELEVATED CO$_2$

by

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ABSTRACT

Rising atmospheric CO_2 and the need to understand potential impacts on terrestrial ecosystems has become increasingly recognized. Models can play a beneficial part in this research to enhance understanding of ecosystem responses to changing conditions like elevated CO_2. In this study, data from a long term elevated CO_2 experiment in a native forested ecosystem in east central Florida were employed to assess the utility of a multi-layer canopy photosynthesis model as a tool to better understand the responses to elevated CO_2 in this ecosystem. Model results compared satisfactorily with the canopy gas exchange measurements in this ecosystem for the period modeled. Sensitivity analyses were used to evaluate the robustness of the model and understand the effects that changing model parameters had on model results, i.e. carbon assimilation in the system. The parameters evaluated included canopy height, leaf area density profile, number of canopy layers, maximum rate of carboxylation (V_{cmax}), and canopy species composition. Results of the sensitivity analyses point to structure and species as being important to carbon assimilation in this ecosystem. Although only an initial examination, this model could be a valuable tool to further understanding of the response of this important ecosystem to increasing CO_2 and indicates that further work is certainly warranted.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF ACRONYMS/ABBREVIATIONS

A_{nc}	net canopy photosynthesis
C_a	atmospheric carbon dioxide
CO_2	carbon dioxide
FACE	free-air CO_2 enrichment
FWCC	Florida Fish and Wildlife Conservation Commission
K_e	light extinction coefficient
KSC	John F. Kenney Space Center
LAD	leaf area density
LAI	leaf area index
NASA	National Aeronautics and Space Administration
NEE	net ecosystem exchange
OTC	open top chamber
PAR	photoysynthetically active radiation
SERC	Smithsonian Environmental Research Center
V_{cmax}	maximum rate of carboxylation

INTRODUCTION

The reality of rising atmospheric CO_2 and the potential impacts on terrestrial

ecosystems has become increasingly recognized. Research has commonly focused on

the effects of elevated CO_2 on plant biomass and ecosystem processes (see review

Drake *et al*., 1997; Rasse *et al*., 2005). Others have also looked at the interactions

between elevated CO_2 and other ecosystem properties like plant biodiversity (Owensby

et al., 1999; Reich *et al*., 2001), herbivory (Stiling *et al*., 1999, 2003; Hamilton *et al*.,

2004), and plant reproductive fitness (Stiling *et al*., 2004). Although the subjects of

these studies have spanned from controlled to natural ecosystems in the field, they

have commonly been rather short-term experiments. One of the few long term

experiments focused on the response of a natural, forested ecosystem to elevated CO_2

is located on the east coast of central Florida at the NASA John F. Kennedy Space

Center (KSC) and headed by the Smithsonian Environmental Research Center (SERC).

The SERC elevated CO_2 experiment commenced operations in 1996 and was under

continuous operations until 2007. Among the many attributes that make this ecosystem

an interesting subject for elevated CO_2 studies is that it has a relatively low stature and

all of the components of a forest ecosystem. In addition, it is a declining and

increasingly fragmented habitat (Myers, 1990) critical to the Florida Scrub-Jay

(*Aphelocoma coerulenscens*), listed as threatened by both the United States Fish and

Wildlife Service and the Florida Fish and Wildlife Conservation Commission (FWCC).

The ecosystem is important to other organisms including a keystone species, the

Gopher Tortoise (*Gopherus polyphemus*), listed as a species of special concern by the FWCC, whose burrows are important to other native species (Diemer, 1992).

Models have been used to enhance understanding of the movement of carbon through ecosystems, explore responses to changing environmental conditions including elevated CO_2, and extend the spatial scale of the investigations (Rasse*, et al*., 2003; Schäfer *et* al., 2003). A canopy photosynthesis model that could be useful in exploring aspects of the effects of rising CO_2 on the native ecosystem including the effect of differing species responses, changes in community composition, and other ecoysystem processes was developed by Dr. G. Katul and Dr. S. Palmroth (Duke University) and is similar to the one described in Schäfer *et* al. (2003). The model was developed for use at the Duke Forest free-air CO_2 enrichment (FACE) in a planted stand of *Pinus taeda* L. that includes a number of broadleaf species. It is a multi-layer model that combines models of leaf level sap flux scaled conductance, light, and a biochemical model of photosynthesis into a canopy level assimilation model that incorporates species and ecosystem specific data.

The objective of this study was to assess the utility of applying this model to a native ecosystem to expand the understanding of the ecosystem responses to elevated atmospheric CO_2. The KSC site provides an opportunity to assess the use of this conductance driven model on a native ecosystem under long-term exposure to elevated CO_2 because of the availability of the necessary input data for the model and the CO_2 exchange measurements to assess the results.   I applied the model data collected over

2

the course of this experiment and qualified the photosynthesis estimates using gas exchange measurements from the site. I evaluated the robustness of the basic model structure and explored the model to understand the effect of changing some model parameters (e.g., ecosystem structure and species composition) on carbon assimilation in the system and to determine the level of detail needed to capture photosynthesis under elevated CO_2 conditions. If this initial exploration proved successful, it was believed that this model could be used by the researchers interested in this native system to further their efforts to understand the effects of rising CO_2 levels on natural ecosystems. The model could also be used for cross-site comparisons for other forest systems which would permit regional and, perhaps, global scaling.

METHODS

Model description

Net canopy photosynthesis was modeled using leaf level gas exchange and a multi-layer approach to scale from the leaf to the canopy level. The vegetation canopy was divided into its component species for all of the model elements described in the following.

The effective leaf conductance to H_2O, g_{LW}, was computed using a simplified version of the Penman-Monteith equation (Montieth & Unsworth, 1990)

$$g_{LW} = \frac{(K_G * J)}{D} \qquad (1)$$

where K_G is the conductance coefficient (0.4236 * T_a + 115.8, kPa m^3 kg^{-1}), a function of air temperature (T_a; °C) accounting for temperature effects on the psychrometric constant, latent heat of vaporization, and specific heat of air at constant pressure (Phillips & Oren, 1998; Ewers & Oren, 2000), J is the sap flow (kg H_2O m^{-2} leaf s^{-1}), and D is the vapor pressure deficit (kPa). Errors in estimating stomatal conductance increase with low values of vapor pressure deficit so minimum values were limited to 0.6 kPa (Oren *et al.*, 1999; Ewers & Oren, 2000). Bulk canopy conductance was calculated by scaling the effective leaf conductance using the leaf area index (LAI). The bulk canopy conductance to CO_2 was estimated using the ratio of the diffusivities of H_2O to CO_2.

Light was used to estimate leaf level conductance at the different canopy layer and to scale up to the canopy level to match the calculated bulk canopy conductance. A leaf area density profile of the canopy was generated to partition the LAI through the canopy layers. Photosynthetically active radiation (PAR; μmol m^{-2} s^{-1}) levels at various canopy layers were estimated by multiplying the measured PAR by the fraction of incident radiation, P_{DF}, calculated for each of these levels using

$$P_{DF} = e^{(-K_e * LAD_S * dz)} \qquad (2)$$

where K_e is the extinction coefficient, LAD_S is the cumulative sum of the leaf area density function, and dz is the height of the canopy layers. A shaping function generated from the light response of leaf stomatal conductance was used to estimate leaf conductance at the various canopy layers.

Net photosynthesis, A_n (umol m^{-2} leaf s^{-1}) was estimated by successive uses of two relationships: a biochemical model of photosynthesis (Collatz et $al.$, 1991) and a gas exchange relationship. The biochemical model describes photosynthesis at the leaf level as the minimum of three different rate limiting steps and takes the form

$$A_n \approx \min \begin{Bmatrix} J_E \\ J_C \\ J_S \end{Bmatrix} - R_d \qquad (3)$$

where J_E, J_C, and J_S are the light limited, Rubisco limited, and sucrose limited steps of photosynthesis respectively, and R_d is day respiration (see Collatz et $al.$, 1991 for details). The gas exchange relationship equates net assimilation of CO_2 to the stomatal

conductance to CO_2 multiplied by difference in CO_2 concentration between the atmosphere and the intercellular spaces, i.e.

$$A_n = g_L \left(c_a - c_i \right)$$
(4)

where g_L is the stomatal conductance to CO_2, c_a is the atmospheric CO_2 concentration, and c_i is the intercellular CO_2 concentration. The net photosynthesis for the canopy, A_{nc}, was calculated by summing the product of the net photosynthesis at every canopy layer by the leaf area density and layer height. A diagram of the model elements is shown in Figure 1.
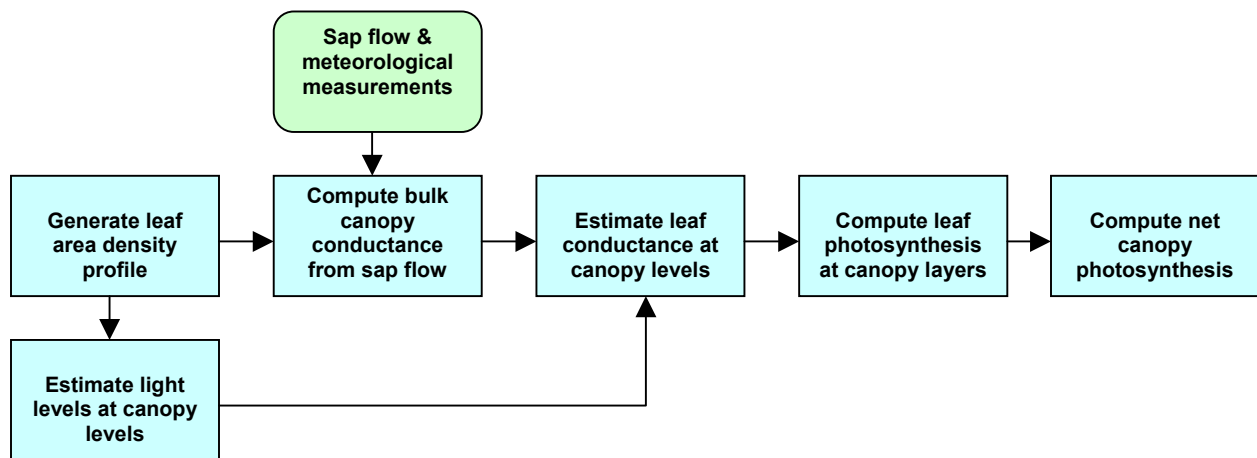
Figure 1. A diagram of the elements of the canopy photosynthesis model.

Field measurements

The experiment site was located at the Smithsonian Environmental Research Center (SERC) CO_2 lab located on KSC on the east coast of central Florida (28°36'N,

80°40'W). The climate is subtropical, warm and humid, with a wet period generally

occurring between June and October. Mean long-term annual precipitation is 1274 ±

278 mm (1984-2003 National Atmospheric Deposition Program annual summary reports

for site at KSC). Soils are sandy, well drained and low in nutrients. The vegetation is a

fire maintained oak-saw palmetto (*Serenoa repens*) scrub community. The specific

natural fire frequency of this oak-saw palmetto scrub, while not specifically known, may

be as frequent as 10 years (Schmalzer & Hinkle, 1992; Schmalzer & Hinkle, 1996). The

experiment site was burned in June 1995 and January 1996, prior to the start of a long-

term study of ecosystem carbon cycling in May 1996. Sixteen octagonal open top

chambers (OTC) with a ground surface area of approximately 9.45 m^2 constructed from

PVC and mylar film were operated on the site with half at ambient CO_2 concentrations

(ambient chambers) and the other half at elevated CO_2 concentrations (ambient + 350

μmol CO_2 m^{-2} s^{-1}; elevated chambers). Pure CO_2 was added to the ambient air blown

into the elevated chambers. Eight unchambered plots served as controls at the site.

See Dijkstra *et al*. (2002) and Hymus *et al*. (2003) for more details on chamber design

and operation.

The vegetation community is dominated by two species of oaks, *Quercus myrtifolia*

Willd*,* and *Q. geminata* Small*,* that accounted for about 76%, and 15% of the

aboveground biomass, respectively, prior to burning the site (Li *et al.*, 1999). Together

with *Q. chapmanii* Sargent, the oaks comprise about 96% of the above ground biomass

(Dijkstra *et al.*, 2002). Although there is much variation in the canopy composition

within the chambers, the modeled canopy composition for this study was confined to *Q.*

7

myrtifolia and *Q. geminata* because they comprise the largest portion of the above ground biomass and most of the species-specific data routinely collected at the experiment site. For this study, canopy height was estimated to be 1.5 m and was divided into 20 layers.

Leaf area index measurements collected during various months at the site between May 1999 and March 2002 were available (Li *et al.*, 2003) for model parameterization. Leaf area index (LAI) measurements from the available data were used if taken in the same month or close to the days for which canopy photosynthesis was modeled. If no measurements were available for the period of interest, then either an average of the measurements from the months before and after the days of interest were used or, in the case of days after February 2002, LAI values that were averages of those from similar periods of the year in 2000 and 2001. The canopy for the model was divided into fractions of leaf area for *Q. myrifolia* (84%) and *Q. geminata* (16%). Measured leaf area density profiles were not available for any of the species on the experiment site, so the leaf area distribution through the canopy was created using the observations of the SERC researchers at the experiment site. The canopy of *Q. myrtifolia* appears to have most of its leaves toward the top of the canopy, while in *Q. geminata* the leaves seem to be more evenly distributed through the canopy. The leaf area density profiles for *Q. myrtifolia* were modeled with 97% of leaf area in the top half of its canopy and in *Q. geminata* it was modeled with the leaf area evenly distributed vertically through the canopy (Figure 2).
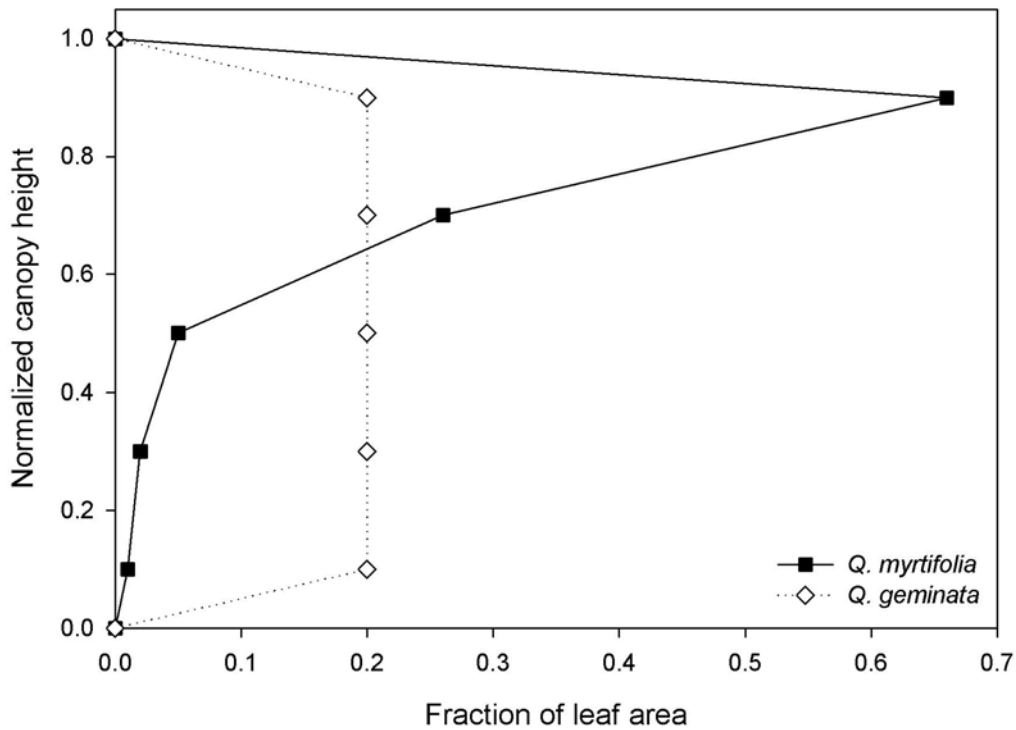
Figure 2. Estimated leaf area density profiles for *Q. myrtifolia* and *Q. geminata*.

Micrometeorological measurements and periodic CO_2 gas exchange measurements were collected inside and outside the chambers since the beginning of the long-term experiment. The chamber air temperature (T_a) used in the model was the arithmetic mean of four thermocouples (Omega Engineering, Stamford, CT) located inside a chamber within the vegetation canopy at the four cardinal directions (i.e. north, south, east, and west). The radiation levels used in the model were measurements from a PAR (400-700 nm) sensor (LI 190; LI-COR, Lincoln, NE) located above the canopy in one of the unchambered control plots adjusted by an attenuation factor of 22% (Hymus *et al.*, 2002a) to reflect the decrease in light level caused by the OTC. The relative humidity data used in the model for days in 2000 and 2001 were derived from absolute

water vapor (LI-6262; LI-COR, Lincoln, NE) and air temperature measurements taken

inside each and averaged over a CO_2 treatment. Starting in 2002, relative humidity

measurements were made using a sensor (CS 500; Campbell Scientific, Logan, UT)

located inside one of the chambers. The atmospheric CO_2 concentration (c_a) data used

in the model were the mean measured CO_2 concentration inside the ambient or

elevated chambers measured during the daytime period in which canopy

photosynthesis was modeled.

Approximately monthly during 2000 through 2002 for a period between 4 and 16 days,

lids were placed on the OTCs so that net ecosystem CO_2 exchange (NEE)

measurements could be performed. Individual measurements inside a chamber were

discarded if the wind speed at the time of the measurement was less than 1 m s^{-1} or

greater than 5 m s^{-1} to reduce potential errors. Experiments have indicated that at night

wind speed below 1 m s^{-1} may not allow adequate mixing of air in the canopy and wind

speeds above 5 m s^{-1} may allow outside air to leak into the chambers (Dore *et al.*, 2003;

Hymus *et al.*, 2003). Measurements from a chamber were also discarded if the

chamber was identified as having incorrect or suspicious values (e.g., due to an

equipment malfunction or otherwise) or if the CO_2 treatments had been altered for any

reason. Mean ambient and elevated daytime NEE values were computed for times

when at least six chambers had measurements that could be included. For times when

there were fewer than six chambers with measurements available, gap fill models were

used based on mean light and NEE measurements for daytime periods occurring 15

days before and after the dates when canopy photosynthesis was modeled. Net

ecosystem exchange measurements during the photoperiod (PAR > 50 µmol m^{-2} s^{-1})
were subjected to the same screening procedure and then mean ambient and elevated
NEE were plotted against the mean PAR level during that measurement period.
Regression analysis was performed using the SigmaPlot 8.0 (SPSS Inc., Chicago, IL)
curve fit function. The results were then used to compute NEE values to fill gaps in the
measurement period.

The data collection interval for the micrometeorological measurements varied during the
period of interest (i.e. 2000 through 2002). Until June 2000, the chamber data were
collected at 11-minute intervals except when lids were placed on the chambers to
perform NEE measurements when the interval was 26 minutes. From June 2000
through July 2001, the sampling interval remained at 11 minutes except when NEE
measurements were performed when the interval was 17.5 minutes. From August 2001
onward, the sampling intervals for all chamber data were changed to 15 minutes.

Values for the light extinction coefficient, K_e, used in the model were derived from
measurements in February and July 2000 (Hymus *et al.*, 2002a) when LAI was at the
annual minimum and maximum. Values for days in spring and summer were the means
of February and July measurements, respectively. Values for fall days were an average
of spring and summer values. The CO_2 compensation points for the *Quercus* spp. were
estimated from Hymus *et al*. (2002b). The maximum rate of carboxylation, V_{cmax}, for all
days was estimated using the mean of available field measurements (Li *et al.,*
unpublished) made at the site since the start of the long-term experiment.

Sap flow data used for this study were collected from both ambient and elevated

chambers three times (generally spring, summer, and fall) during the years 2000

through 2002 in conjunction with another experiment (Li, personal communication). All

sap flow data were collected at 15-minute intervals. Mean sap flow data by CO_2

treatment (i.e. ambient and elevated) for *Q. myrtifolia* were available for all three years,

while sap flow for *Q. geminata* was only available for 2001. To fill in the *Q. geminata*

data for the missing days and times during 2000 and 2002, I calculated an average day

by season and CO_2 treatment from the data available during 2001. For days of interest

where the sap flow data collection interval was different than the other data needed in

the model (i.e. 2000 to mid 2001), I used the interpolation function in MATLAB 6.5 (The

MathWorks, Inc.) on the known points of mean sap flow during the daylight period to

determine sap flow values for the times at which the other data were collected.

The light response of stomatal conductance for *Q. myrtifolia* and *Q. geminata* were

established using a LI-6400 Portable Photosynthesis System (LI 6400; LI-COR, Lincoln,

NE). Measurements were taken in the field at growth CO_2 starting no earlier than 08:40

hours and finishing no later than 12:10 hours during eight days between 17 December

2003 and 5 January 2004.   Randomly selected ambient and elevated OTCs were

sampled on each of the eight measurement days. The first chamber sampled during

each day alternated between the ambient and elevated CO_2 treatments.   In each

chamber, a leaf from each species was sampled *in situ* except for one chamber where a

Q. geminata leaf was not accessible. Stomatal conductance was measured using ten

PAR levels in a sequence similar to Li *et al.* (2003): 1000 µmol m^{-2} s^{-1}, then 1500, 2000, 1000, 700, 400, 200, 100, 50, and 0 µmol m^{-2} s^{-1}. Non-linear regression analysis of the measurements was performed using the curve fit function in SigmaPlot 8.0 (SPSS Inc., Chicago, IL).

Model implementation

Canopy photosynthesis was simulated for daytime periods between 09:00 and 16:00 for selected days during 2000 through 2002. These days reflect dates when both sap flow measurements and NEE measurements were collected and when no more than 25 % of the mean NEE data measurements during the daytime period were discarded and required gap filling measures (see above). Model parameters that did not change for the dates modeled (i.e., static) are shown in Table 1 and those that did change (i.e., dynamic) are shown in Table 2.   The model results were compared to the gas exchange measurements taken in the OTCs.

Sensitivity analyses were performed to explore the impact of changes to model parameters on the net canopy photosynthesis results. These involved changing a single parameter of the model and comparing the resulting mean daytime net canopy photosynthesis estimate to the mean daytime net canopy photosynthesis estimated prior to the parameter change. Parameters that changed in the analysis included canopy height, leaf area density profile, number of canopy layers, V_{cmax}, and canopy species composition. Canopy height was increased to twice the initial height. The leaf

13

area density profiles were changed to reflect a normal distribution of leaf area through

the canopy for both oak species. The number of layers that the canopy was divided into

within the model was increased to 40 layers and decreased to 1 layer (a "big leaf"). The

maximum rate of carboxylation, V_{cmax}, was increased and decreased by 25 % for all

periods. The canopy composition was changed to reflect a monospecific stand

composed entirely of *Q. myrtifolia* and *Q. geminata*.

Table 1. Static parameters used in the model.

Parameter (units)	*Q. myrtifolia*	*Q. geminata*
canopy height (m)	1.5	1.5
V_{cmax} **(µmol m^{-2} s^{-1})**		
ambient treatment	91.3	113
elevated treatment	61.6	69.5
CO$_2$ compensation point (µmol m^{-1})	48.8	34.9
Leaf stomatal conductance light response	See Table 3	
α_p	0.8	
e_m	0.08	
K$_{C25}$ (µmol mol^{-1})	300	
K$_{O25}$ (µmol mol-1)	300	
C$_{oa}$ (µmol mol^{-1})	210	

Table 2. Dynamic parameters used in the model.

Parameter (units)	Mar 2000	May 2000	Oct 2000	Mar 2001	Feb 2002	Jun 2002
LAI (m^2 m^{-2})						
ambient treatment	1.19	1.51	1.26	0.9	1	1.58
elevated treatment	1.58	1.93	1.63	1.21	1.25	2.12
Light extinction coefficient (K_e)	1.05	0.875	0.96	1.05	1.05	0.875
[CO_2] (μmol m^{-2} s^{-1})						
ambient treatment	378	370	369	391	376	381
elevated treatment	738	725	719	745	732	736

RESULTS

Leaf stomatal conductance light response

Leaf stomatal conductance, g_s, increased with increasing levels of PAR at growth C_a for both species of oak with maximum g_s being higher in *Q. geminata* than in *Q. myrtifolia*. In both *Q. myrtifolia* and *Q. geminata*, elevated C_a decreased g_s (Figure 3).
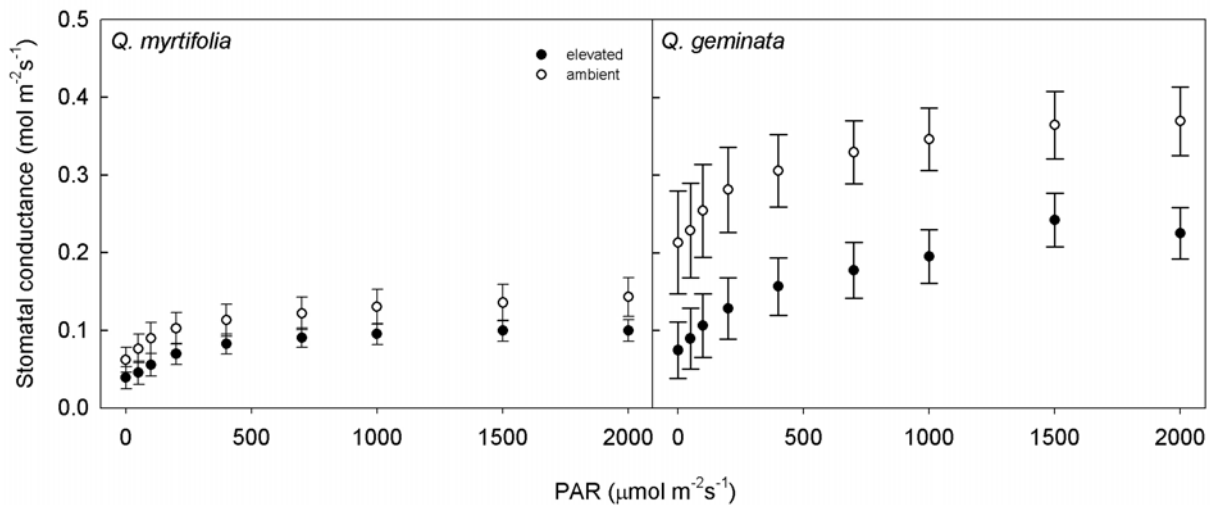

Figure 3. Response of leaf stomatal conductance of dominant *Quercus* spp. to changes in PAR. Extensions are means ± 1 S. E.

Non-linear regression analysis (SPSS Inc., Chicago, IL) on the leaf stomatal conductance response to light data shown in Figure 3 resulted in estimated leaf level stomatal conductance, g_s, curves of the form

$$g_S = g_{S0} + (a*PAR/(b+PAR)) \tag{5}$$

16

where PAR is estimated at canopy layer height z, and g_{S0} is the estimated leaf level stomatal conductance at zero PAR. The regression coefficients and R^2 values are shown in Table 3.

Table 3. Regression coefficients and R^2 values for leaf stomatal conductance response to light data shown in Figure 3.

Species	CO_2 treatment	gs(0)	a	b	R^2
Q. myrtifolia	ambient	0.063	0.086	265.011	0.992
Q. myrtifolia	elevated	0.037	0.073	264.021	0.995
Q. geminata	ambient	0.212	0.187	384.706	0.996
Q. geminata	elevated	0.076	0.211	667.507	0.978

Sapflow and NEE measurements

Sapflow data were available for 58 days between 2000 and 2002. NEE measurements were made during 30 full days out of those 58 days. Analysis of the NEE measurements between the daytime hours of 09:00 to 16:00 in those 30 days resulted in 14 days for modeling canopy photosynthesis. The dates of the days modeled in 2000 were 8 March, 10 March, 3 May, 4 May, 19 October, and 21 October. Only 10 March was modeled in 2001 and in 2002 the dates modeled were 25-26 February, 1 June, 3-5 June, and 11 June. The regression analysis on the NEE and PAR data for all dates resulted in non-linear curves of the form

$$NEE = NEE_0 + (a*PAR/(b+PAR)). \qquad (6)$$

Regression coefficients and R^2 values from the regression analysis are shown in Table 4. The maximum percentage of mean NEE measurements discarded during for the 14 days when canopy photosynthesis was modeled was 24 % for 10 March 2001. No

daytime NEE measurements required gap-filling actions during the daytime hours for five of the 14 days: 25 February 2002, 1 June, and 3-5 June 200. Micrometeorological measurements were available for the 14 days at the various data collections intervals described. The mean daytime PAR, air temperature, and relative humidity for ambient and elevated chambers are shown in Figure 4.

Table 4. Regression coefficients and R^2 values for NEE gap fill regression analysis.

| Month/Year	Treatment	NEE_0	a	b	R^2
March 2000	ambient	-4.86	15.27	174.55	0.81
	elevated	-5.19	25.23	363.92	0.89
May 2000	ambient	-20.39	35.86	60.19	0.51
	elevated	-10.22	45.05	287.01	0.87
October 2000	ambient	-7.08	30.16	288.11	0.95
	elevated	-6.77	50.86	592.51	0.97
March 2001	ambient	-4.06	14.94	255.24	0.78
	elevated	-4.27	24.63	447.21	0.73
February 2002	ambient	-3.51	16.11	420.11	0.91
	elevated	-0.73	27.77	540.42	0.79
June 2002	ambient	-11.07	28.26	170.86	0.60
	elevated	-3.92	49.81	625.95	0.78
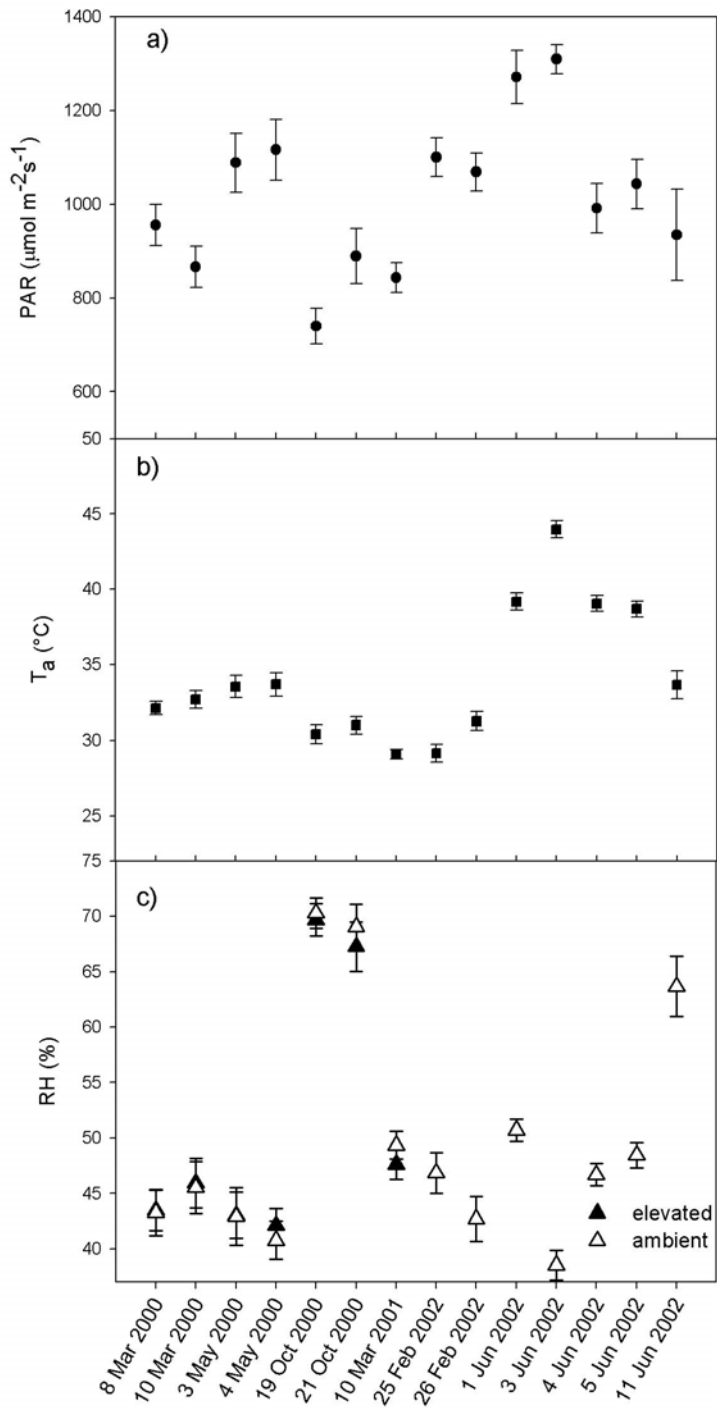
Figure 4. Daytime a) PAR, b) air temperature, and c) relative humidity inside chambers. Extensions are means ± 1 S. E.

Modeled net canopy photosynthesis

The results of the net canopy photosynthesis model are shown in Figure 5. Mean
daytime (i.e. between 09:00 and 16:00) values for the 14 days are shown in Figure 6.
The maximum daytime value of net canopy photosynthesis estimated by the model
during the 14 days was 37.38 and 57.53 µmol CO_2 m^{-2} s^{-1} for ambient and elevated CO_2
treatments, respectively. The maximum daytime value occurred on 11 June 2002 when
maximum PAR was measured. The mean daytime model results are compared to the
mean daytime NEE measurements after gap fill in Figure 6.

Sensitivity analyses

Canopy structure

The change in the canopy height from 1.5 m to 3.0 m had no effect on the estimated net
canopy photosynthesis values at the measurement sampling intervals (data not shown).
Changing the leaf area density profiles for the oak species from the initial distributions
as shown in Figure 2 to a case where both species leaf area density (LAD) profiles were
modeled as normal distributions resulted in only slight differences (< 0.5% increase or
reduction) in mean daytime net canopy photosynthesis (data not shown). For most of
the dates and CO_2 treatments, changing the LAD profiles to normal distributions for both
oak species resulted in higher mean daytime net canopy photosynthesis estimates.
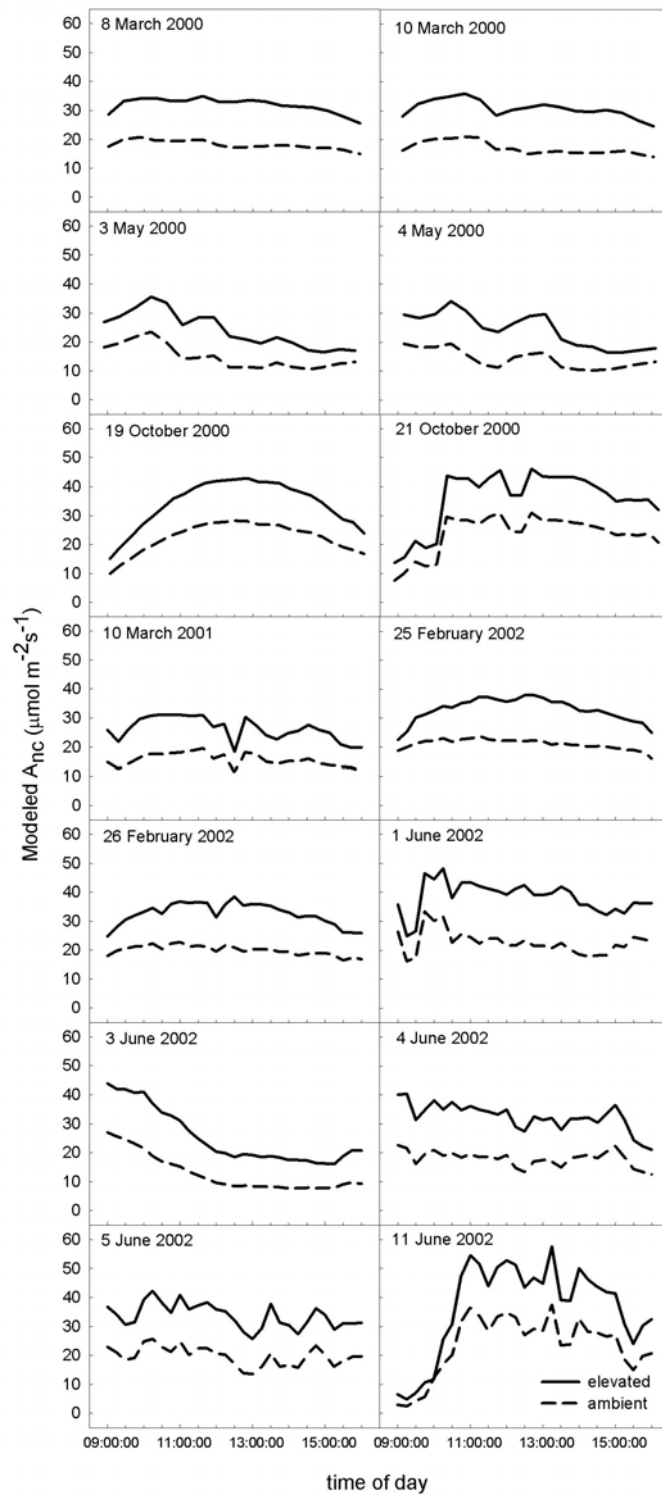Three exceptions were on 10 March 2000 (ambient only), 19 October 2000, and 11
June 2002.

Figure 5. Modeled net canopy photosynthesis estimates for the measured micrometeorological data from 14 days in 2000 to 2002.
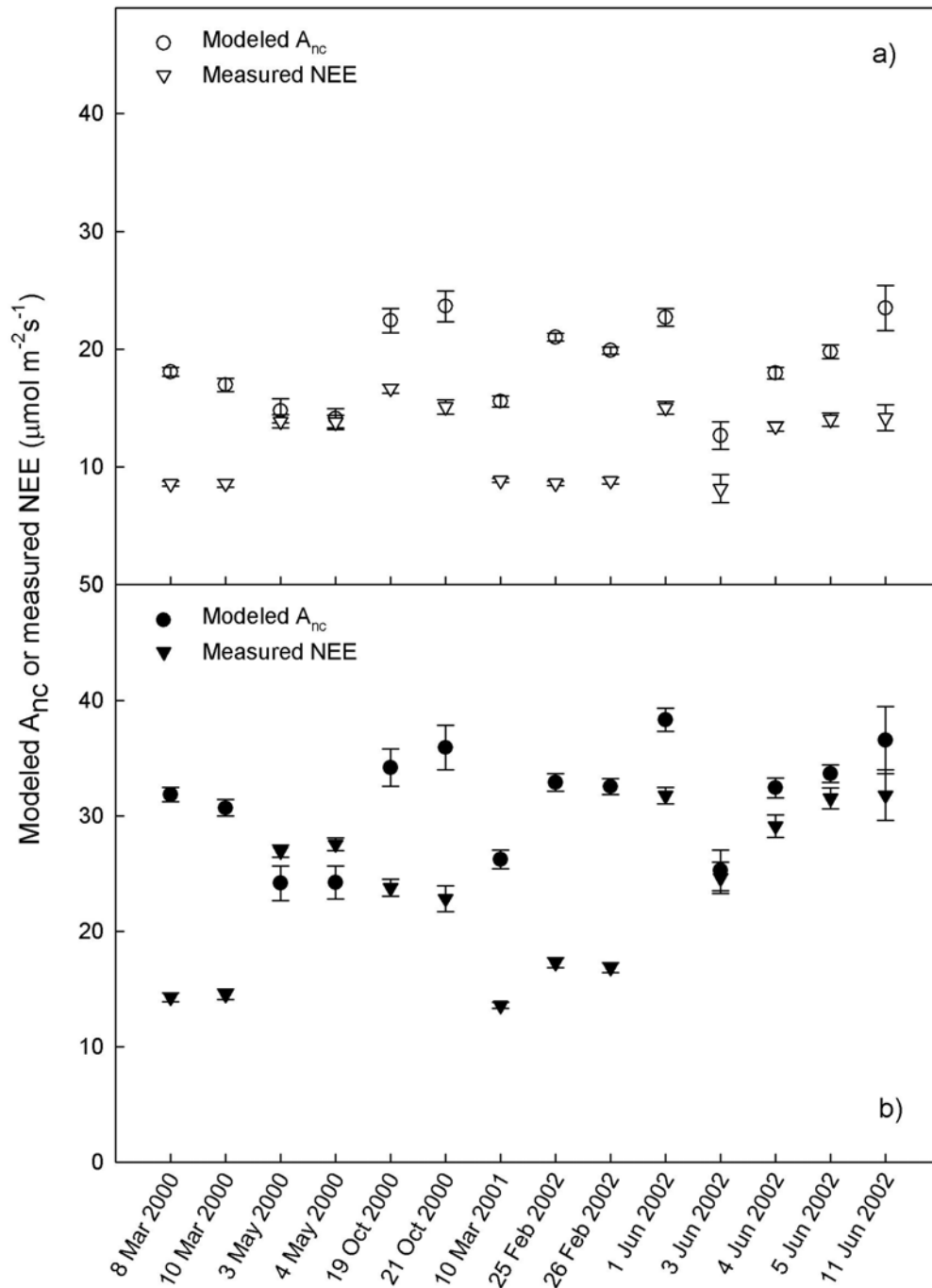
Figure 6. Modeled mean daytime net canopy photosynthesis (A_{nc}, circles) and NEE measurements (triangles) for a) ambient and b) elevated treatments. Extensions are means ± 1 S. E.

In general the largest difference on any date was seen in the elevated treatment, but on 19 October 2000, and 11 June 2002, the greatest difference was seen in the ambient treatment.

Changing the number of canopy layers used in the model had varying degrees of impact on the mean daytime canopy photosynthesis estimates. When the canopy was modeled as a single layer, the estimated mean daytime canopy photosynthesis values increased considerably for all dates compared to the initial case with 20 canopy layers (Figure 7a) with the average increase being 11.54 % and 13.33 % for ambient and elevated treatments, respectively. When the number of canopy layers was doubled (i.e. changed to 40 layers) the change resulted in slightly lower mean daytime canopy photosynthesis estimates with the average decrease for ambient and elevated treatments being 0.94 % and 1.15 %, respectively (Figure 7b). The largest difference in mean daytime canopy photosynthesis estimates for both canopy layer changes and CO_2 treatments occurred on 19 October 2000. On this date the change from a 20-layer canopy to a single layer canopy resulted in an increase in mean daytime net canopy photosynthesis of 29.77 % and 31.60 % for ambient and elevated CO_2 treatments respectively. Doubling the number of canopy layers for this date resulted in a decrease in the estimated mean daytime A_{nc} by 2.27 % and 2.46 % for ambient and elevated treatments respectively. In general, the absolute value of the differences seen for each of the dates were about an order of magnitude greater for the single layer than for the 40 layer case and the difference for the elevated treatment were higher than that for the ambient treatment. However, higher differences were seen in the ambient treatment on

3-4 May 2000 in the case of the single layer model and only in 3 May 2000 in the case of the 40-layer model.

Changing V_{cmax}

When V_{cmax} was increased and decreased by 25 % for each of the dates, results of the comparison of the mean daytime canopy photosynthesis estimates varied between dates and CO_2 treatments (Figure 10 and Figure 11). For all 14 dates, increasing V_{cmax} increased mean daytime estimates in the elevated treatments by an average of 4.00 %. Increasing V_{cmax} in the ambient treatments increased the mean daytime estimates in only 9 of the 14 dates. Mean daytime estimates were decreased for 10 March 2000, 3-4 May 2000, 19 October, and 4 June 2002. When V_{cmax} was decreased by 25 % the mean daytime canopy photosynthesis values estimated by the model decreased for all dates and CO_2 treatments.
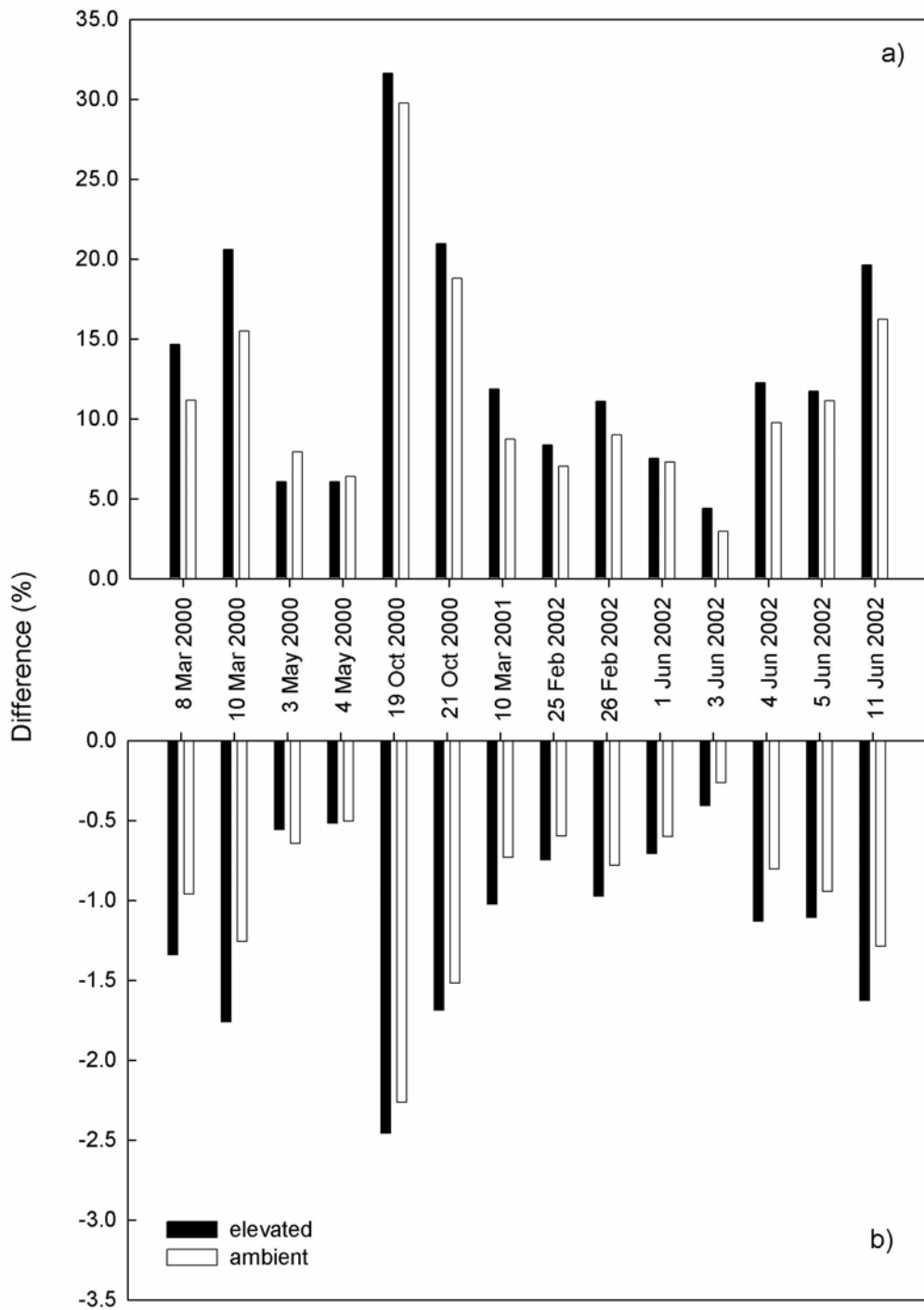
Figure 7. Differences between estimated mean daytime net canopy photosynthesis values when the canopy was changed from 20 layers to a) a single layer and b) 40 layers.
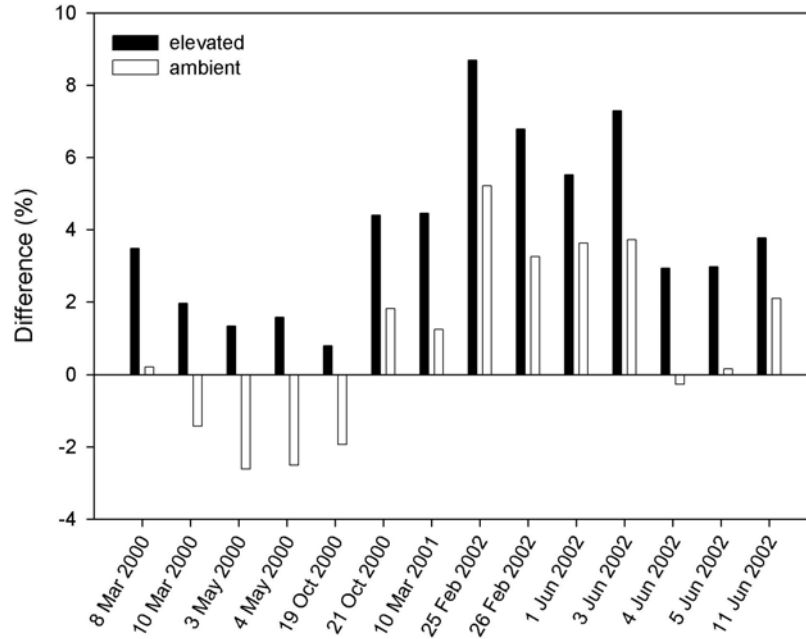
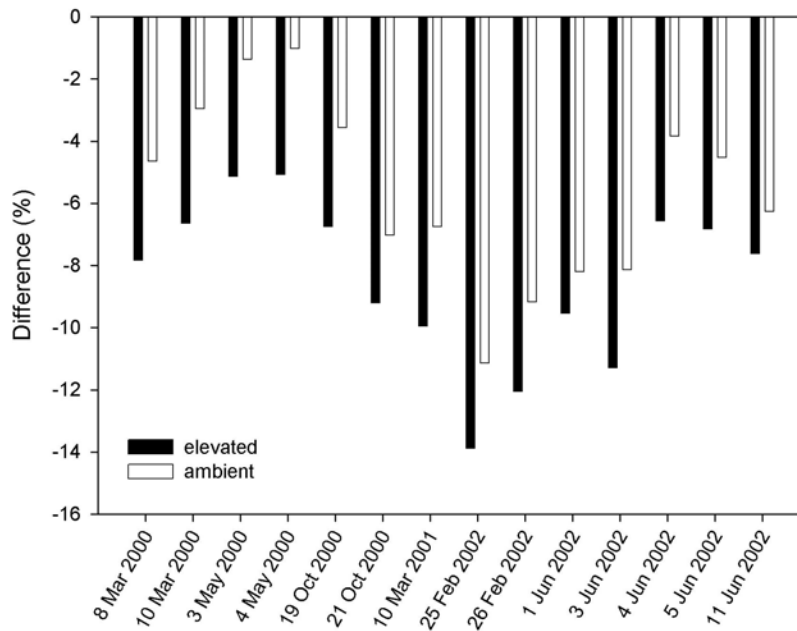Figure 8.   Effect of a 25% increase in V_{cmax} on mean daytime net canopy photosynthesis**.**

Figure 9. Effect of a 25% decrease in V_{cmax} on mean daytime net canopy photosynthesis.

Individual species effect

Changing the canopy from a mixed species canopy composed of *Q. myrtifolia* and *Q. geminata* to a single species canopy composed of only *Q. myrtifolia* or *Q. geminata* had very different effects on the mean daytime net canopy photosynthesis estimates. In the case of a *Q. myrtifolia* canopy, the mean daytime net canopy photosynthesis was decreased for all dates (Figure 10). The largest differences were seen on 3-4 May 2000 for both CO_2 treatments. The change in canopy composition decreased the mean daytime net canopy photosynthesis values for both days by about 23 % for the ambient treatment and 24-25 % for the elevated treatment.   When the canopy was changed to one composed of only *Q. geminata,* the effect was quite different (Figure 11). The effect of the change varied for the 14 days modeled. For the most part the differences were below 15 % increase or decrease with the rather dramatic exception of 3-4 May 2000 and 10 March 2001. On the two days in May both ambient and elevated treatments had a considerable increase in the mean daytime net canopy photosynthesis of 65-74 % with the increase in the ambient treatment being larger than that in the elevated treatment. On the March 2001 date, the ambient treatment saw a dramatic decrease of 77 %, while the elevated treatment mean daytime net canopy photosynthesis increased by a modest 7 %.
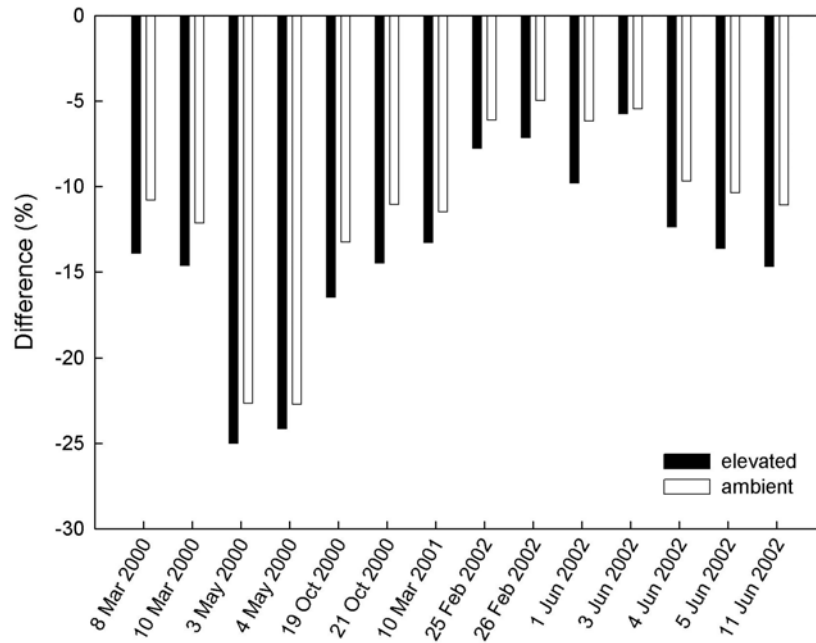
Figure 10. Effect of changing the canopy composition from mixed to single species, *Q. myrtifolia*, on mean daytime net canopy photosynthesis.
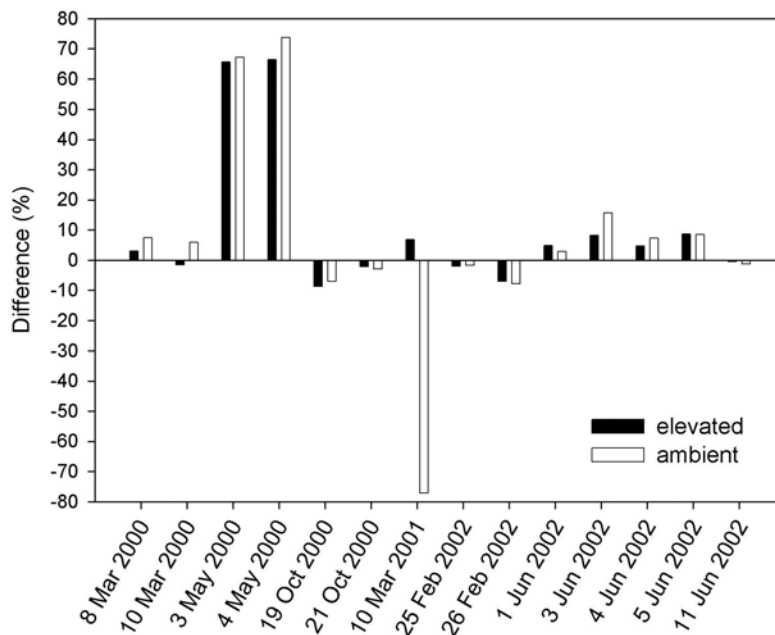

Figure 11. Effect of changing the canopy composition from a mixed to single species, *Q. geminata*, on the mean daytime net canopy photosynthesis.

DISCUSSION

Leaf stomatal conductance

The data collected for the leaf stomatal conductance response to PAR and subsequent fitted curves showed the expected relationships for both species and CO_2 treatments (Figure 3). Stomatal conductance increased with increasing PAR in both species, reaching saturation at about 1000 µmol $m^{-2}s^{-1}$ PAR similar to results seen in Li *et al*. (2003). The elevated c_a reduces stomatal conductance in many species and has been seen in both *Quercus* spp. (Drake *et al*., 1997; Li *et al*., 2003). Maximum g_s in *Q. geminata* was higher than that seen in *Q. myrtifolia* for both treatments. The highest g_s value for *Q. myrtifolia* was lower than the highest value reported by Li *et al*. (2003) by as much as 50 %. I found no similar published data for stomatal conductance of *Q. geminata* from the site to compare.

Modeled net canopy photosynthesis

In general, the model results for ambient and elevated chambers were as expected. Elevated CO_2 stimulated net canopy photosynthesis for all dates in this study (Figure 6). Higher rates of photosynthesis in the elevated treatments have been shown repeatedly in previous studies at this site (Li *et al*., 1999; Ainsworth *et al*., 2002; Hymus *et al*., 2003; Li *et al*., unpublished). The amount of stimulation varies between dates and although only 14 dates are examined, these are consistent with the intra-annual differences seen in other experiments (Ainsworth *et al*., 2002; Hymus *et al*., 2003).

Comparison with NEE measurements

When the model results were compared with the measured NEE however, there are some dates where the comparison was not as predicted. Because the model estimates net canopy photosynthesis and the measurements taken in the chambers are NEE differences would be expected between the values; the difference being autotrophic and heterotrophic respiration. In the case of the ambient treatments, comparison of mean daytime modeled A_{nc} with mean daytime measured NEE showed clearly higher A_{nc} values except on 3-4 May 2000, when there was only a slight difference. During these dates A_{nc} and NEE values overlapped during parts of the daytime hours (data not shown) and the mean PAR was among the highest and RH was among the lowest for the days modeled (Figure 4). In the case of the elevated treatments, comparison of the mean daytime A_{nc} and NEE values showed A_{nc} estimates higher for all dates except 3-4 May 2000.

Sensitivity analyses

The largest effects to mean daytime net canopy photosynthesis were seen in the changing the number of canopy layers, canopy species composition, and V_{cmax}. Changing the leaf area density profile for both species to a normal distribution had little effect when looking at mean daytime A_{nc}. The changes may be more significant if one looked at the changes vertically through the canopy.

Treating this canopy as a single layer had a considerable effect on the estimated net canopy photosynthesis. Although there are no direct measures of net canopy photosynthesis to quantitatively compare with these model results, the single layer approach may overestimate net canopy photosynthesis. The slight decrease in model results seen by doubling the number of canopy layers would seem to point to a multi-layer model yielding better estimates of net canopy photosynthesis in this model. I only looked at three cases of canopy layers (i.e. one, 20 and 40 layers) in this study, but further work looking at numbers of layers between one and 20 should point to a lower threshold were an increase in the number of layers does not effect the results very appreciably.

Changing the species composition from the mixed canopy with the two co-dominant oaks to a canopy with only the single oak species yielded very different results depending on which of the co-dominant oaks was present. The results with the canopy composed entirely of *Q. myrtifolia* consistently showed a decrease in the mean daytime canopy photosynthesis for all dates while the canopy composed only of *Q. geminata* showed increased and decreased mean daytime net canopy photosynthesis values with some unexplained results for the two days in May 2000 and March 2001. Of the two scenarios, a canopy increasingly dominated by *Q. myrtifolia* may be more likely in an atmosphere of increased CO_2. Dijkstra et al. (2002) found that elevated CO_2 increased aboveground biomass for *Q. myrtifolia* and *Q. chapmanii*, but not *Q. geminata*. Stiling et al. (2004) found that acorn density increased for *Q. myrtifolia* and *Q. chapmanii*, but not *Q. geminata* suggesting the potential for future change in community composition.

31

Based on results of the model, the change to an increased percentage of *Q. myrtifolia* may lead to decreased carbon assimilation in this system.

Decreasing the maximum rate of carboxylation, V_{cmax}, by 25 % had a larger effect on net canopy photosynthesis than did increasing V_{cmax}, by 25 %. For all dates the mean daytime net canopy photosynthesis was decreased in both treatments with the largest decreases being in the elevated treatment. This is analogous to the effect of photosynthetic acclimation, which has been seen in both *Quercus* spp. over the course of the chamber experiment (Li et al., 1999; Ainsworth et al., 2002; Hymus et al., 2002b; Li et al., unpublished).

Overall, the model results compare satisfactorily with the measurements in this ecosystem for the 14 days modeled. From this initial exploration of the model, although only a handful of parameters, one at a time, were explored, structure and species are highlighted as important in carbon assimilation in this ecosystem. This model could be a valuable tool to further the understanding of the response to this important system to an increasing CO_2 atmosphere. Further work is certainly warranted to apply this model to the rich data set available for this singular long-term experiment and to help point to additional avenues of inquiry to understand how our natural world will change in the face of anthropogenic enrichment of atmospheric CO_2.

APPENDIX A: SAMPLE MODEL CODE

(Model originally authored by G. Katul and S. Palmroth and modified for this study)

Note: Sample shown is for ambient CO_2 case with oak species differentiated by prefix "m" for *Q. myrtifolia* and prefix "g" for *Q. geminata*

Main Model

```
clear
close

ELEV=4.5

Area_ratio=0.230;
LAI=0.9;
mLAI=0.84*LAI;
gLAI=0.16*LAI;
h=1.5;

Ko=1.05;

Ca=391;

clear DF_DATA;
DF_DATA=load ('aSp01.txt');
DOY=DF_DATA(:,1);
HHMM=DF_DATA(:,2);
Tam=DF_DATA(:,3);
RHm=DF_DATA(:,4)/100;
PARm=DF_DATA(:,5);
mJsm=DF_DATA(:,6)/(1000*3600);
gJsm=DF_DATA(:,7)/(1000*3600);
NN=length (DOY);

z=[0:0.025:1]*h;
dz=z(2)-z(1);
mLAD=amSp01_get_leaf_area_density (mLAI,z,h);
gLAD=agSp01_get_leaf_area_density (gLAI,z,h);

HH=floor(HHMM(i)/100);
MM=HHMM(i)-HH*100;
TIM(i)=DOY(i)+HH/24+MM/60/24;

mJs=mJsm(i)+eps;
gJs=gJsm(i)+eps;
PAR=PARm(i);
RH=RHm(i);
Ta=Tam(i);
```

```
[mgc,mgw,mgl_w]=amSp01_sapflow_conductance(ELEV, Area_ratio,
mLAI,Ta,RH,mJs);
mgwat(i)=mgw;
[ggc,ggw,ggl_w]=agSp01_sapflow_conductance(ELEV, Area_ratio, gLAI,Ta,RH,gJs);
ggwat(i)=ggw;

mPAR_z=amSp01_PAR_MODEL (z,mLAD, Ko, PAR);
gPAR_z=agSp01_PAR_MODEL (z,gLAD, Ko, PAR);
% PAR_zt=[PAR_zt; PAR_z];

mg_leaf=amSp01_leaf_level_guess (z,mPAR_z,mLAD,mgc);
gg_leaf=agSp01_leaf_level_guess (z,gPAR_z,gLAD,ggc);


[mAn, mCi]=amSp01_photosynthesis_model(Ta, Ca, mg_leaf, mPAR_z);
[gAn, gCi]=agSp01_photosynthesis_model(Ta, Ca, gg_leaf, gPAR_z);

mAn_c(i)=sum(mAn.*mLAD*dz);
gAn_c(i)=sum(gAn.*gLAD*dz);
An_c(i)=mAn_c(i)+gAn_c(i);
dlmwrite('aSp01.out',An_c,',');
end
```

Get leaf area density for *Q. myrtifolia*


```
function [mLAD]=amSp01_get_leaf_area_density (mLAI,z,h)

mLADm=[0 0.010 0.020 0.050 0.260 0.660 0];
zm=[0 0.1 0.3 0.5 0.7 0.9 1.0001];
dz=z(2)-z(1);
zm1=zm*h;
mLADi=interp1(zm1, mLADm, z,'cubic');
mLAD=(mLADi/(dz*sum(mLADi)))*mLAI;
dlmwrite('amLAD.out',mLAD,',')
```

Get leaf area density for *Q. geminata*


```
function [gLAD]=agSp01_get_leaf_area_density (gLAI,z,h)

gLADm=[0 0.20 0.20 0.20 0.20 0.20 0];
zm=[0 0.1 0.3 0.5 0.7 0.9 1.0001];
```

```
dz=z(2)-z(1);
zm1=zm*h;
gLADi=interp1(zm1, gLADm, z,'cubic');
gLAD=(gLADi/(dz*sum(gLADi)))*gLAI;
dlmwrite('agLAD.out',gLAD,',')
```

Leaf level guess for *Q. myrtifolia*

```
function mg_leaf=amSp01_leaf_level_guess (z,mPAR_z,mLAD,mgc)
n=length(z);
dz=z(2)-z(1);

myo=0.0632;
ma=0.0856;
mb=265.0112;
mg_leafw=myo+ma*mPAR_z./(mb+mPAR_z);
mg_leafc=0.66*mg_leafw;
CORR=sum(mg_leafc.*mLAD*dz)/(mgc+eps);
mg_leaf=mg_leafc/CORR;
```

Leaf level guess for *Q. geminata*

```
function gg_leaf=agSp01_leaf_level_guess (z,gPAR_z,gLAD,ggc)
n=length(z);
dz=z(2)-z(1);

gyo=0.2122;
ga=0.1871;
gb=384.7064;
gg_leafw=gyo+ga*gPAR_z./(gb+gPAR_z);
gg_leafc=0.66*gg_leafw;
CORR=sum(gg_leafc.*gLAD*dz)/(ggc+eps);
gg_leaf=gg_leafc/CORR;
```

PAR model for *Q. myrtifolia*

```
function mPAR_z=amSp01_PAR_MODEL (z,mLAD, Ko, PAR)
n=length(mLAD);
dz=z(2)-z(1);
```

```
mCUM_LADa=cumsum(mLAD);
mCUM_LADb=mCUM_LADa(n)-mCUM_LADa;
mPDF=exp(-Ko*mCUM_LADb*dz);
mPAR_z=PAR*mPDF;
```

PAR model for *Q. geminata*

```
function gPAR_z=agSp01_PAR_MODEL (z,gLAD, Ko, PAR)
n=length(gLAD);
dz=z(2)-z(1);
gCUM_LADa=cumsum(gLAD);
gCUM_LADb=gCUM_LADa(n)-gCUM_LADa;
gPDF=exp(-Ko*gCUM_LADb*dz);
gPAR_z=PAR*gPDF;
```

Sapflow conductance for *Q. myrtifolia*

```
function [mgc,mgw,mgl_w]=amSp01_sapflow_conductance(ELEV, Area_ratio,
mLAI,Ta,RH,mJs)
P=101.3*exp(-ELEV/8200);
Cp=1005;
Lv=2502000-2.308*1000*Ta;
a=0.611; b=17.502; c=240.97;
Tc=Ta;
Ta_K=Ta+273.15;
estar=a.*exp(b.*Tc./(Tc+c));
ea=RH*estar;
VPDa=estar-ea;
VPD=max(VPDa,0.6);
rho=1.3079-0.0045*Ta;
Kg=0.4236*Ta+115.8;
Area_ratio_m2_m2=Area_ratio*10000;
mgl_w=(Kg*mJs/VPD)*(rho)*(1000000/18);
mgw=mgl_w*mLAI;
mgc=0.66*mgw/1000;
```

Sapflow conductance for *Q. myrtifolia*

```
function [ggc,ggw,ggl_w]=agSp01_sapflow_conductance(ELEV, Area_ratio,
gLAI,Ta,RH,gJs)

P=101.3*exp(-ELEV/8200);
Cp=1005;
Lv=2502000-2.308*1000*Ta;
a=0.611; b=17.502; c=240.97;
Tc=Ta;
Ta_K=Ta+273.15;
estar=a.*exp(b.*Tc./(Tc+c));
ea=RH*estar;
VPDa=estar-ea;
VPD=max(VPDa,0.6);
rho=1.3079-0.0045*Ta;
Kg=0.4236*Ta+115.8;
Area_ratio_m2_m2=Area_ratio*10000;
ggl_w=(Kg*gJs/VPD)*(rho)*(1000000/18);
ggw=ggl_w*gLAI;
ggc=0.66*ggw/1000;
```

Physiological constants for *Q. myrtifolia*

```
function [amVcmax, alpha_p, e_m, mTau_star,Kc, Ko,
Coa]=amSp01_Physiological_constants(T1);
amVcmax25=91.3;
mTau_star = 48.8;
alpha_p=0.8;
e_m=0.08;
Kc25=300 ;
Ko25=300 ;
Coa=210;
amVcmax=amVcmax25*exp(0.088*(T1-25))./(1+exp(0.29*(T1-41)));  %umol/(m^2 s)
Kc=Kc25*exp(0.074*(T1-25));
Ko=Ko25*exp(0.018*(T1-25));
```

Physiological constants for *Q. geminata*

```
agVcmax25=113;
gTau_star=34.9;
alpha_p=0.8;
e_m=0.08;
```

```
Kc25=300 ;
Ko25=300 ;
Coa=210;
agVcmax=agVcmax25*exp(0.088*(T1-25))./(1+exp(0.29*(T1-41)));
Kc=Kc25*exp(0.074*(T1-25));
Ko=Ko25*exp(0.018*(T1-25));
```

Photosynthesis model for *Q. myrtifolia*

```
function [mAn, mCi]=amSp01_photosynthesis_model(Ta, Ca, mg_leaf, mPAR_leaf)
[amVcmax, alpha_p, e_m, mTau_star,Kc, Ko,
Coa]=amSp01_Physiological_constants(Ta);

alpha1=alpha_p*e_m*mPAR_leaf;
alpha2=2*mTau_star;
AA=-mg_leaf+eps;
BB=mg_leaf.*(Ca-alpha2)-alpha1;
CC=alpha2.*mg_leaf*Ca+alpha1*mTau_star;
mCi1=(-BB-(BB.^2-4*AA.*CC).^0.5)./AA/2;
mAn1=mg_leaf.*(Ca-mCi1);

alpha1=amVcmax;
alpha2=Kc*(1+Coa/Ko);
AA=-mg_leaf+eps;
BB=mg_leaf.*(Ca-alpha2)-alpha1;
CC=alpha2.*mg_leaf*Ca+alpha1*mTau_star;
mCi2=(-BB-(BB.^2-4*AA.*CC).^0.5)./AA/2;
mAn2=mg_leaf.*(Ca-mCi2);

mAn=min(min(mAn1,mAn2),mAn3)-0.015*amVcmax;
mCi=Ca-mAn./mg_leaf;
```

Photosynthesis model for *Q. geminata*

```
function [gAn, gCi]=agSp01_photosynthesis_model(Ta, Ca, gg_leaf, gPAR_leaf)
[agVcmax, alpha_p, e_m, gTau_star,Kc, Ko,
Coa]=agSp01_Physiological_constants(Ta);

alpha1=alpha_p*e_m*gPAR_leaf;
alpha2=2*gTau_star;
AA=-gg_leaf+eps;
```

```
BB=gg_leaf.*(Ca-alpha2)-alpha1;
CC=alpha2.*gg_leaf*Ca+alpha1*gTau_star;
gCi1=(-BB-(BB.^2-4*AA.*CC).^0.5)./AA/2;
gAn1=gg_leaf.*(Ca-gCi1);

alpha1=agVcmax;
alpha2=Kc*(1+Coa/Ko);
AA=-gg_leaf+eps;
BB=gg_leaf.*(Ca-alpha2)-alpha1;
CC=alpha2.*gg_leaf*Ca+alpha1*gTau_star;
gCi2=(-BB-(BB.^2-4*AA.*CC).^0.5)./AA/2;
gAn2=gg_leaf.*(Ca-gCi2);

gAn3=agVcmax/2;
gAn=min(min(gAn1,gAn2),gAn3)-0.015*agVcmax;
gCi=Ca-gAn./gg_leaf;
```

APPENDIX B: SAMPLE MODEL INPUT VARIABLES

Model parameter	Units	Description
h	m	canopy height
LAI	m^2 leaf m^{-2} ground	leaf area index
K_e		Light extinction coefficient
C_a	$\mu mol\ m^{-2}\ s^{-1}$	atmospheric CO_2 concentration
ELEV	m	site elevation
V_{cmax}	$\mu mol\ m^{-2}\ s^{-1}$	maximum rate of carboxylation
α_p		leaf absorptivity for PAR
e_m	$mol\ mol^{-1}$	maximum quantum efficiency
K_{C25}	$\mu mol\ mol^{-1}$	Michaelis constant for CO_2
K_{O25}	$\mu mol\ mol^{-1}$	inhibition constant for O_2
C_{oa}	$mmol\ mol^{-1}$	oxygen mole fraction
DOY		day of year
HHMM		hours and minutes
Ta	degree Celsius	air temperature
RH	percentage	relative humidity
PAR	$\mu mol\ m^{-2}\ s^{-1}$	photosynthetically active radiation
Jsm	$g\ m^{-2}\ sap\ s^{-1}$	sapflow
z	m	canopy height at which leaf area density is interpolated
Area ratio	$m^2\ cm^2$	leaf area to cross sectional stem area
Tau star		compensation point

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    respiration to elevated atmospheric CO_2 in two scrub oaks. *Global Change*

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    atmospheric CO_2 concentration in the Florida scrub-oak species *Quercus*

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