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MAESTRA2: A MODEL FOR SIMULATING SPATIALLY EXPLICIT CARBON DIOXIDE EXCHANGE RATES AMONG SPECIES' WATER STRESS RESPONSE

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MAESTRA2: A MODEL FOR SIMULATING SPATIALLY EXPLICIT CARBON DIOXIDE EXCHANGE RATES AMONG SPECIES' WATER STRESS RESPONSE

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Accepted by:
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ABSTRACT

MAESTRA2, a species specific mechanistic model, was parameterized to estimate water use, carbon accumulation and organ specific respiration of five deciduous tree species under both irrigated and water stressed conditions. The model was validated using temporally and spatially explicit ecophysiological data to account for seasonal changes in species physiology. The following tree species: *Acer rubrum L. 'Summer Red'* (*A. rubrum*), *Betula nigra* (*B. nigra*), *Paulownia elongata* (*P. elongata*), *Quercus nuttallii* (*Q. nuttallii*), and *Quercus phellos* (*Q. phellos*) were intensively measured and organ specific destructively harvested samples were compared to modeled estimates of carbon accumulation. Among species, we observed variability in carbon dioxide exchange rates under well watered and water stressed conditions. *A. rubrum* carbon sequestration under water deficit was 29% less than the well watered treatment. The species other than *A. rubrum* were similar to each other (56%-63% less carbon sequestered as compared to the well watered). *A. rubrum* root biomass was higher in the drought treatment as compared to the well watered control, possibly explaining its carbon sequestration characteristics. Modeling validation results indicated that the model does have the capability to down regulate photosynthetic capacity on a per species basis. Differences between measured values and modeled estimates were within 6% for *A. rubrum*, 12% for *B. nigra*, 8% for *P. elongata*, 2% for *Q. nuttallii,* and 7% for *Q. phellos*. Therefore,

seasonal carbon accumulation estimates adequately represented field observations in both well watered and drought treatments. Moreover, sap flux measurements confirmed the models ability to estimate diurnal gas exchange under both well watered and water stressed conditions. The work provides evidence that MAESTRA2 is a process-based model capable of accurately quantifying spatially explicit carbon dioxide exchange rates at the species level and in response to water stress.

DEDICATION

I would like to sincerely thank Dr. William Bauerle for providing me with the opportunity and the support that made completing this work possible. His incredible generosity and patient mentoring extend beyond the scope of this research and will always be remembered.

I would like to thank Dr. Victor Shelburne and Dr. Geoff Wang for contributing their insights and expertise throughout the course of this research.

Finally, I would like to thank my fiancée Cathy for her continuous support as well as for being a source of encouragement in my life.

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INTRODUCTION

Models of carbon exchange between vegetation and the atmosphere are important for integrating physiological information across scales of biological and physical organization (e.g., Harley & Baldocchi 1995). Several three-dimensional models that simulate carbon exchange at the intracanopy scale have been proposed (e.g., Thorpe et al. 1978; Wang and Jarvis 1990a; Myneni 1991; Chen et al. 1994; Desmarez et al. 2000; Sinoquet et al. 2001). Although application of these models involves the same underlying processes, a major uncertainty in modeling tree growth is the lack of understanding of whole-plant allocation (Reynolds et al. 1996). As a result, growth estimates have traditionally been tested against data sets that are temporally sparse (e.g., McMurtrie & Landsberg 1992). In most cases, models are forced to rely on major simplifications due to the paucity of data. Moreover, we know of no intratree model that encompasses all organs in the process of calculating tree carbon exchange. Although there has been considerable research on carbon exchange of individual trees and forest ecosystems, we call into question the use of over simplified carbon exchange models that allege to predict whole tree climate change response.

In the context of climate change, simulation models have proven to be an important tool in predicting the carbon sequestration response to environmental stress. Unfortunately, few models incorporate soil moisture as a constraint and this has been identified as a weakness in their predictive ability under drought

stress conditions (Hanson et al. 2004). Subsequently, the three attributes of precipitation (low, variable, unpredictable) manifest as unencapsulated dynamics of primary productivity predictions (Whitford 2002; Reynolds et al. 2004). Over the last four decades, global hydrologic studies have reported that the majority of the Earth's terrestrial component is significantly affected by drought and the amount of water stressed land area has more than doubled in that time span (Dai et al. 2004). Given the anticipated rate of climate change and the incurred atmospheric and terrestrial influence on flora, more comprehensive models must be developed and evaluated to ascertain the effects of water stress on the global terrestrial carbon budget.

Trees are genetically diverse and highly complex organisms that must endure long-term consequences of climatic variations. In light of these complexities, a models' ability to predict tree growth among a genetically diverse population growing across a temporally and spatially diverse environment would depend on the models ability to capture both genetic and environmental influences. Although ecophysiological modeling has successfully accomplished the quantification of phenotypic traits (e.g., biomass accumulation and transpiration rate) via genotype specific parameter sets in annual crop species (Hoogenboom et al. 1997; Hoogenboom and White 2003; Reymond et al. 2003; for a review see White and Hoogenboom, 2003); parameterizing the genetic influences on tree growth among species through physiological processes is still atypical (Martin et al. 2005). To capture the variation in environmental drivers and

biotic response to this forcing, process-based models offer a means to predict the growth of a system as complex as a tree (e.g., Weinstein et al. 1991; Valentine et al. 1998; Baldwin et al. 1998; Landsberg 2003; Bauerle et al. 2007).

In this study, we focus on a species specific method of biological process model parameterization at the tree organ-level because changes in climate will influence specific physiological pathways that then can manifest themselves at higher scales (e.g. whole tree). We use clonal plants to make the separation of genetic variability less difficult. Furthermore, the use of clonal plants allows the exact replication of a given species genotype to environmental stress, which makes it possible to differentiate between influences of genetic variability on the response of a tree to a given stress. In so doing, we investigate the feasibility and validity of using the detailed simulation model MAESTRA2 to predict species specific water stress responses in five deciduous tree species. MAESTRA2 is an updated version of MAESTRO (Wang and Jarvis 1990a) and MAESTRA (Medlyn 2004). Recently, Medlyn et al. (2005) demonstrated MAESTRA's ability to predict CO_2 exchange in the dominant species of a coniferous forest plantation. We expand on her work by parameterizing our version (MAESTRA2) to account for photosynthetic and respiration responses to drought stress in several species of deciduous trees under precise irrigation control. In so doing, we are able to describe the important long term biotic response responsible for variation in forest atmosphere carbon exchange (Richardson et al. 2007).

The species in this study originate from similar climatic conditions. Thus,

any species differences in carbon exchange under the same environmental conditions can be attributed to the effects of quantitative physiological variation brought about by genetic differences and/or variation in gene expression. Using specific species parameter sets developed from measurements, we examine genetically inherent differences among species. Our specific objectives were to: 1) investigate whether experimentally derived parameter sets could account for the biomass accumulation of individual species, 2) validate the model simulations under a range of soil moisture conditions, 3) examine the species variation in response to water stress, 4) provide insight into the possibility to parameterize species responses from basic organ-level processes, and 5) validate a whole tree carbon budget model for deciduous tree species using estimated net carbon accumulation versus organ dry weights. The main hypothesis driving this research is that genetic constraints among species, brought about by evolutionary adaptation, underlie a species response to climate change.

Although numerous studies have described morphological and physiological differences in tree species and the subsequent affect of soil moisture stress, we focus on species specific physiological constraints and their water stress induced CO_2 flux limitations. Therefore, by incorporating species specific physiological constraints within a restructured version of the process based MAESTRA2 model, we determine the source of biotic variation and/or inadequacies in simpler models.

MATERIALS AND METHODS

Study Area:

The duration of the study was from May 15, 2006 to October 15, 2006 (first signs of leaf senescence), capturing the majority of the 2006 growing season. The field site was located at the Clemson University Calhoun Field Laboratory in Clemson, South Carolina, USA (latitude 34° 40′ 8′′; longitude 82° 50′ 40′′). Site attributes involve a gravel pad receiving full sun exposure, outfitted with a pressure-regulated micro emitter irrigation system (ML Irrigation Inc., Laurens, SC.). A full site description is provided in Bauerle et al. (2002).

Plant Material:

In a common garden, South Carolina grown saplings of *Acer rubrum L. 'Summer Red'* (*A. rubrum*), *Betula nigra* (*B. nigra*), *Quercus nuttallii* (*Q. nuttallii*), *Quercus phellos* (*Q. phellos*), and root cuttings of *Paulownia elongata* (*P. elongata*), 40 of each, were planted in 57 L plastic containers containing Fafard 2B custom mix potting substrate (Fafard Inc., Anderson, SC) and fertilized with 9 Kg m^{-3} of Osmocoat Pro® 19-5-8 slow release fertilizer (Scotts Inc., Marysville, OH). Plants were randomly distributed throughout the plot in a grid pattern (1.5 m spacing), initially watered to container capacity, and allowed to drain for 24 h. 360° micro-emitter irrigation was applied at the base of each tree stem, delivering 1 L of water three times daily to each of the 200 trees. All trees were kept well

watered and allowed to acclimate to the site for 45 d before drought treatments began.

Drought Treatment:

     After monitoring trees under well watered conditions for 45 d, a randomized drought treatment was applied. Twenty trees per species were randomly assigned to a drought treatment and 20 trees to a well watered treatment. Water stress treatment trees were outfitted with 360° micro-emitters that emit 70% less water than well-watered control emitters. Irrigation times and duration were adjusted per tree species and treatment to insure that the soil volumetric water content (VWC) in the drought treatment was < 0.3 m^3 • m^3 and the well watered treatment remained > 0.3 m^3 • m^3 VWC (a predetermined value shown to not induce water stress). In addition, all of the containers were wrapped in Al foil to reduce the radiation load and outfitted with 3 mil plastic sheeting skirts to exclude precipitation recharge.

Substrate Water Measurements:

     Bulk VWC was recorded every 48 h at two locations in the soil profile of each container using a Theta Probe type ML2 (Delta-T Devices, Cambridge, England) at 10 cm and 20 cm below the potting medium surface. Readings were taken by inserting the probe into predrilled holes at two depths, and taking the average of the readings to estimate bulk VWC for each container (Bauerle et al.

2003). In addition to Theta Probe values, ECH_2O probes, type EC-20 (Decagon Devices, Pullman, Washington, USA) were installed at a 45° angle in the soil of four randomly selected trees per species per treatment and bulk VWC was recorded every min and hourly averages output to a CR7X data logger (Campbell Scientific, Logan, UT).

Sap-flux Measurements:

Sap flow gauges (Dynamax Inc., Houston, TX) were installed on four randomly selected trees per species (two per treatment). The gauges encircled the stem with a flexible heating element equipped with a thermocouple above and below the element to measure vertical heat loss as water carries heat up the stem in the sap flow process. Saran Wrap® and a thin layer of silicon based grease was placed between the stem and the heating element to insure adequate contact with the stem as well as to exclude moisture. Weather resistant insulation covered the gauges to approximately 15 cm above and below the heating element and Al foil covered the foam to further exclude solar radiation. Data was colleted by a CR10X data logger (Campbell Scientific, Logan, UT) coupled with a multiplexer (AM416, Campbell Scientific, Logan, UT) every 30 sec, and 15 min averages were stored (SM4M, Campbell Scientific, Logan, UT).

Leaf Gas Exchange Measurements:

Leaf gas exchange measurements were taken at three week intervals on recently fully expanded leaves of four replicate trees per species. Measurements were taken with a portable gas exchange system (CIRAS-1, PP Systems, Haverhill, MA) outfitted with a light and temperature controlled cuvette (Model PLC(B), PP Systems). The temperature inside the cuvette was controlled at 25° C and humidity was held constant at 19 mb to create a moderate vapor pressure deficit of 1.27 kPa. Leaf net photosynthesis (A_{net}) versus CO_2 (A_{net}-C_i curves, were A_{net} is in umol m^{-2} s^{-1} and C_i is the internal CO_2 concentration expressed as the mol fraction of CO_2) were constructed as described in Bauerle et al. (2007). In addition to A-C_i curves, light response curves were constructed with the same system as described in Bauerle et al. (2003).

Organ Specific Respiration:

Organ respiration was collected on excised stem, coarse root, and fine root tissues immediately at harvest with a portable gas exchange system (CIRAS-1, PP Systems) connected to a respiration chamber (SRC-1, PP Systems). The chamber was modified with a lid to seal and enclose the organ. Respiration was logged after reaching a steady state. Organ chamber volume consumption was determined volumetrically after gas exchange measurement.

Relative Growth Rate Destructive Sampling:

Three trees of each species per treatment (30 total) were randomly selected and destructively harvested on a three-week interval during the study (7 total harvests). Leaves were removed and total leaf area was obtained with a leaf area scanner (LiCor 3100, Lincoln, NE). The soil was gently washed from the roots and fine roots (diameter < 3mm) were separated from the coarse root material (diameter > 3mm). Individual organs (leaves, stem, coarse roots, and fine roots) were then placed in paper bags, dried at 70 $^{\circ}$C for approximately 21 d, and dry weights were measured to the nearest 0.1 g. After each harvest, the remaining trees in the plot were randomly repositioned to a solid block in order to avoid gap effects in the canopy.

Allometric Measurements:

Three dimensional tree canopy characteristics were measured one day prior to each destructive harvest throughout the season. Measurements included total tree height, trunk diameter, trunk length, and three dimensional live crown size (x, y, and z direction in m). Tree mensuration data, along with site parameters such as slope and aspect, were used to parameterize the model MAESTRA2 (details below).

MAESTRA2 Parameterization:

The essence of this study is a species specific modeling analysis that aims to quantify the differences in growth among species and their subsequent response to water stress. The analysis consists of a series of simulations in which species specific parameters encapsulated a species response. In this study, MAESTRA2 (see Medlyn 2004 for a retrospective of the process model MAESTRA), a three-dimensional model for calculating photosynthesis, transpiration, and absorbed radiation was parameterized for the experimental site with a suite of measurements taken during the course of the study. MAESTRO, a prior version of MAESTRA2, was originally developed and validated on coniferous trees (Wang and Jarvis 1990a,b). More recently, Bauerle et al., (2002; 2004a) updated the model to run on a 15 minute time step, incorporated a soil moisture response function, and parameterized and validated the model on deciduous trees using measurements of leaf-level g_s, photosynthetic rates, crown transpiration, and crown light interception. A detailed description of MAESTRA2, however, is beyond the scope of this article. Specific to our version of "MAESTRA2", we updated the g_s response by incorporating physical and hormonal drought response functions (Bauerle et al., 2002; 2004c), maximum rate of Rubisco activity (Vc_{max}), mesophyll conductance, and maximum electron transport rate (J_{max}) leaf temperature response functions (Bernacchi et al., 2001; 2002; and 2003; Bauerle et al. 2007), and deciduous tree light transfer (Bauerle et al., 2004b). The application of MAESTRA2 in this study is grounded in the

work of others where prior versions of the model have been validated and used to estimate species specific photosynthesis and transpiration; interested readers are referred to Wang and Jarvis (1990a,b), Kruijt et al., 1999; Luo et al. (2001); Medlyn (1998; 2004), Bauerle et al. (2002; 2004b; 2006; 2007), and Medlyn et al. (2005) for detailed descriptions of applications.

Specific to this study, the models spatial explicitness was critical, where MAESTRA2 allows canopy parameterization at the individual crown and sub crown level. The photosynthetic radiation response of a "target crown", therefore, depends on the structure of the crown and the distribution of irradiance over the crown. Spatial characteristics are accounted for with a Cartesian coordinate system. To integrate PAR absorption over temporal and spatial distributions of irradiance, each crown layer is treated as unifacial and the assimilating leaf area is defined as one-sided. The positions and dimensions of the trees surrounding the target crown are used to calculate the sunlit and shaded fractions of leaf area after passing through the neighboring tree canopies, where the canopy is represented by an array of ellipsoidal tree crowns. In our study, the intercepted and absorbed radiation was calculated for each crown, with each crown divided into 3 layers, resulting in 12 sectors of 30° with each layer forming 36 equal sub-volumes.

Another critical aspect of the model is the ability to parameterize the physiological genetics on a species by species basis. Thus, our sampling structure and measurements allowed us to describe each species genetic

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difference with clonal-specific parameters and control equations using process-based physiological models such as the Ball-Berry (Ball et al. 1987) and the Farquhar and von Caemmerer (1982). The response of a species to an environmental condition was thus represented by 'meta-mechanisms' that represent quantitative variation in species differences via species specific experimental response curve parameters (e.g., Reymond et al., 2003; Tardieu, 2003).

Model inputs included spatially explicit plot and tree measurements and organ specific physiology data. Meteorological data to drive the model was collected by an on site weather station on a 15 min time step with a CR10X data logger (Campbell Scientific, Logan UT). Soil moisture data were input into a physical drought response equation described in Bauerle et al. (2002). Model output in g of carbon exchange was estimated on a 15 min, hourly and daily time step and estimates were validated with field collected measurements.

RESULTS

Species Specific Variation:

        The model was parameterized slightly different for each species and treatment based on differences in physiology, leaf area, and soil moisture (Table 1). At the end of the season, water stress was observed to have caused significant reductions in height, leaf area, and dry weight among species, although seasonal carbon fluxes and the severity of carbon reduction due to water stress at specific time points throughout the season also differed among species. Figure 1 illustrates the seasonal changes in carbon reduction as a percentage of the well watered control. After the drought treatment was initiated, carbon sequestration constraints responded relatively quickly with a dry weight decline in the range of 20%- 48% over a 17 day period when compared to the well watered control trees. All species except for *A. rubrum* reached a peak carbon accumulation in the range of 56%- 63% lower than that of the well watered controls by Julian day 253, while at the same time, *A. rubrum's* maximum drought effect was only 29% lower by dry weight when compared to the well watered treatment. In addition, a slight decrease in percent dry weight reduction was observed for all species except *Q. nuttallii* from Julian day 253 to 283, at which time an increase in root carbon storage offset the large carbon reductions observed in the previous month.

Species exhibited specific differences in organ specific carbon partitioning in response to drought stress. Figure 2 illustrates the organ specific carbon partitioning in response to well watered and water stressed conditions. Although all species showed a marked decrease in leaf carbon accumulation under drought stress, *Q. nuttallii* responded to water stress with the overall greatest decline in leaf carbon, 84%, while *P. elongata* retained the highest leaf carbon under drought, 46% reduction. *B. nigra* reduced carbon allocated to stem growth by 75%, while maintaining relatively equal carbon allocation to coarse root growth when compared to the well watered control. In addition to having the lowest overall carbon decrease in response to drought stress, *A. rubrum* increased fine root production by 46% relative to the well watered treatment.

Modeling Results:

Measured sap flux reveals species diurnal transpiration differences (Figure 3). Furthermore, Figure 3 illustrates sap flow of well watered trees compared to MAESTRA2 model estimates of transpiration during seven representative days of the study period, Julian day 206 to 213. The results indicate that *P. elongata* transpires approximately twice as much water, a weekly sum of 26.73 Kg m^{-2}, as compared to the other four species, where their water use ranged from a weekly sum of 12.09 to 14.09 Kg m^{-2} (Figure 3). Sap flow under water deficit conditions shows a lower water use for all species that range from 33% (*Q. nuttalli)* to 79% (Q. *phellos)* decrease in weekly water use*.* Most

importantly, the comparison of model estimates of transpiration to sap flow under both the well watered and drought treatment validate MAESTRA2's ability to diurnally estimate gas exchange on a species specific basis and respond to a range of water deficit conditions (Figure 3 and 4).

The dry weight data from each of the seven harvests were used to compare to model carbon estimates (Figure 5). Multiple comparisons between the measured and modeled data under both well watered and drought were made at each harvest. Comparisons were also made between the carbon accumulated in the well watered and drought treatments to indicate the time that a significant treatment effect was observed. Figure 5 illustrates that the model has the ability to predict both intraseasonal and seasonal net carbon gain in well watered deciduous tree species and also has the capability to down-regulate net carbon assimilation in response to drought on a species specific basis. Thus, we found no significant differences in modeled versus measured net primary production under water stress conditions (Figure 5).

The percent of carbon allocated to each organ was used to partition total tree carbon estimates among organs (Figure 6). Figure 6 further illustrates organ-specific carbon of well watered trees in comparison to model estimates. Modeled estimates slightly under predicted leaf carbon for *B. nigra* by 7% and *Q. phellos* by 20%, and over predicted coarse root carbon for *Q. phellos* by 13% and *P. elongata* by 27%. Modeled estimates of fine root production accounted for actual fine root carbon accumulation in all species and estimated stem carbon

was not significantly different from the measured data for *A. rubrum, B. nigra,* and *Q. nuttallii.*

Measured organ-specific dry weight data were compared with model estimates for the drought treatment on Julian day 283 (Figure 7). Model estimates overestimated actual stem and leaf carbon in *P. elongata* by 34% and 35% respectively, stem carbon in *Q. phellos* by 36%, and fine root and leaf carbon in *A. rubrum* by 24% and 25%. Model predictions of carbon accumulation compared to measured values showed no significant difference for all other organ specific comparisons.

Respiration Results:

Woody respiration was analyzed as the average of three trees per species per treatment and compared to the average of three model simulations per species per treatment. Figure 8 illustrates respiration (g CO_2 d^{-1}). In all cases but one, measured respiration was higher in the well watered treatments as compared to the drought treatments. The exception was the root respiration of *A. rubrum*. Due to the increase in fine root production in response to drought, *A. rubrum* was observed to have higher total root respiration in the drought treatments than in the well watered control. In general, the model responded to increased soil moisture deficit with a decrease in total woody respiration. Figure 9 illustrates the seasonal respiration rates of the five study species compared with model estimates of foliar respiration. Measured values indicate a

decrease in foliar respiration as the season progressed beyond Julian day 253.

Model estimates, on the other hand, do not show the same decrease after Julian

day 253.

Species	P_s	R_{day}	A_{max}	J_{max}	VC_{max}	G_o	G_1	L_{comp}	L_{sat}
A. rubrum	16.2^{CD}	2.1^{AB}	14.8^{AB}	196.6^{AB}	67.7^{BC}	0.14^{A}	1.7^{D}	21.1^{AB}	157.3^{A}
B. nigra	26.3^{A}	2.1^{AB}	20.6^{BC}	251.6^{A}	83.2^{A}	0.69^{B}	2.5^{CD}	11.7^{A}	321.9^{BC}
P. elongata	19.9^{BC}	3.5^{C}	27.5^{C}	242.8^{A}	73.7^{AB}	0.14^{A}	5.8^{AB}	29.2^{B}	467.8^{C}
Q. nuttallii	18.5^{BC}	1.7^{B}	12.1^{AB}	142.8^{BC}	58.4^{CD}	0.15^{A}	3.3^{BC}	17.8^{AB}	201.3^{AB}
Q. phellos	12.8^{D}	1.8^{B}	10.2^{A}	127.4^{C}	52.0^{D}	0.11^{A}	2.4^{CD}	16.1^{AB}	192.0^{AB}

Table 1. Leaf level photosynthetic parameters. (A) photosynthetic rate (μmol m^{-2} s^{-1}) , (R_d) foliage maintenance respiration (μmol m^{-2} s^{-1}), (J_{max}) maximum rate of electron transport (μmol m^{-2} s^{-1}), (Vc_{max}) maximum rate of Rubisco activity (μmol m^{-2} s^{-1}), (g_o) minimum stomatal conductance (μmol m^{-2} s^{-1}), (g_1) stomatal opening slope coefficient, (L_c) light compensation point (μmol m^{-2} s^{-1}), (L_{sat}) light saturation point. Different letters within a parameter indicate differences among species ($P < 0.05$).

Species	Watered (g)	Drought (g)	% Reduction
A. rubrum	2817	1989	29%
B. nigra	1615	590	63%
P. elongata	3173	1338	58%
Q. nuttallii	2163	796	63%
Q. phellos	1921	849	58%

Table 2. Dry weight reduction of droughted trees as compared to well-watered over the coarse of the experiment (Julian day 283). Data represent the average of three replicates per species and treatment (n = 3).
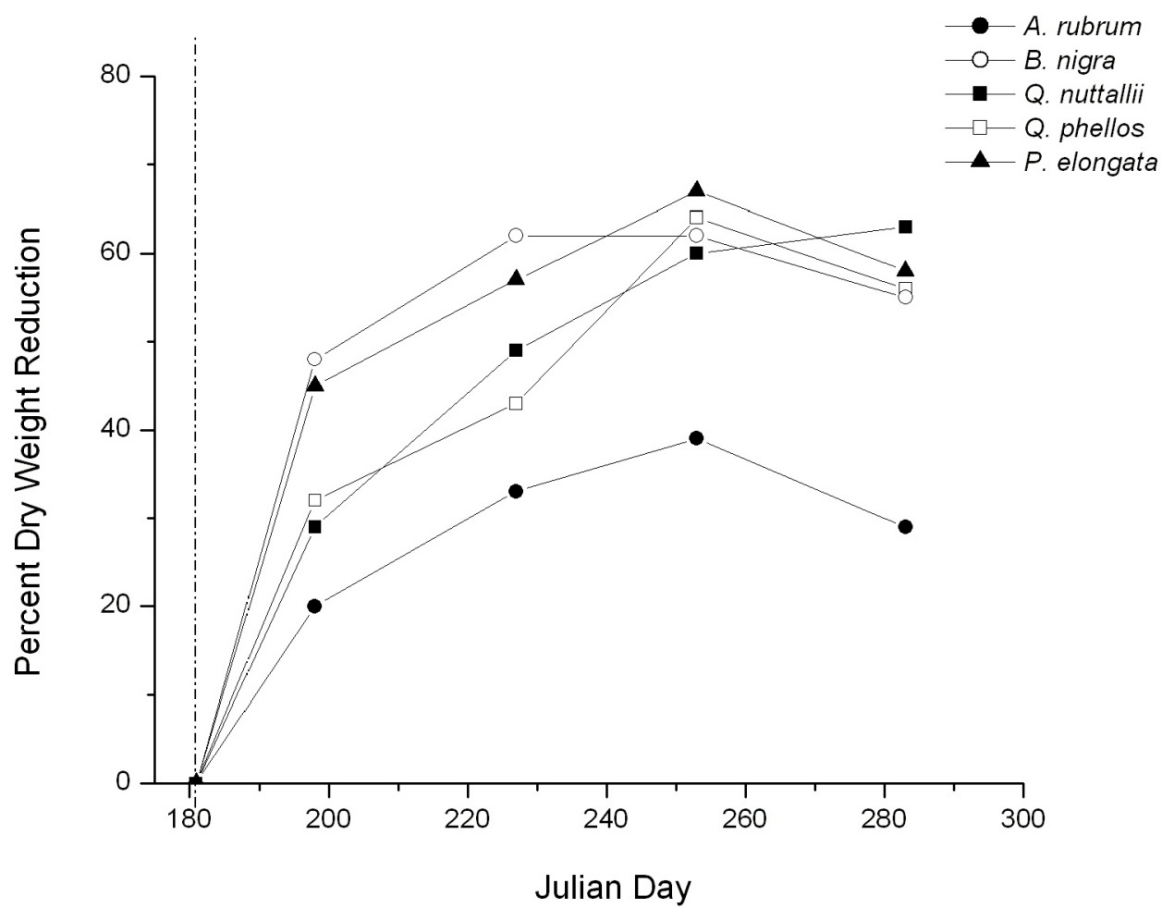
Fig. 1. The percent of carbon sequestration below that of the well watered control after the drought treatment was initiated. The dashed line indicates the start of the drought treatment (Julian day 181).
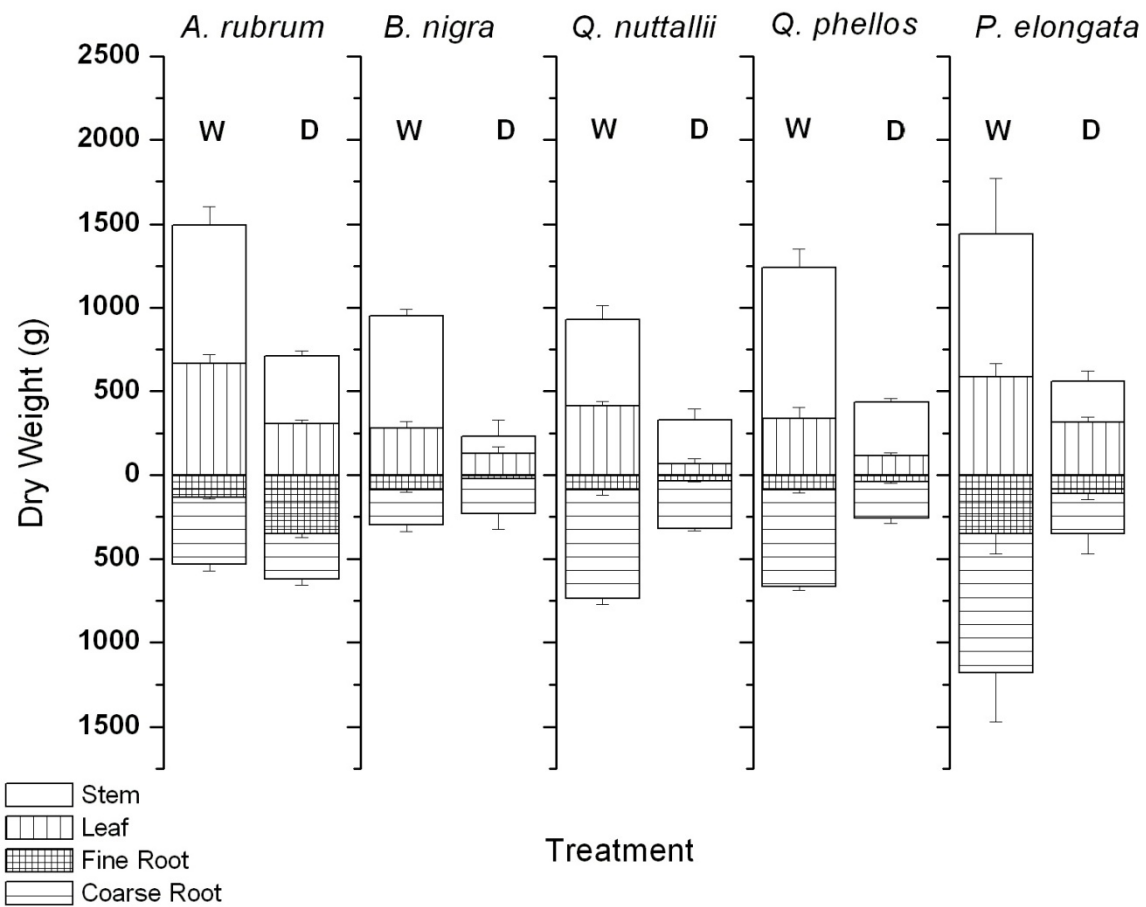
Fig. 2. Organ specific carbon partitioning in response to well watered and drought treatments on Julian day 283. Symbol (W) represents the well watered treatment and symbol (D) represents the drought treatment.
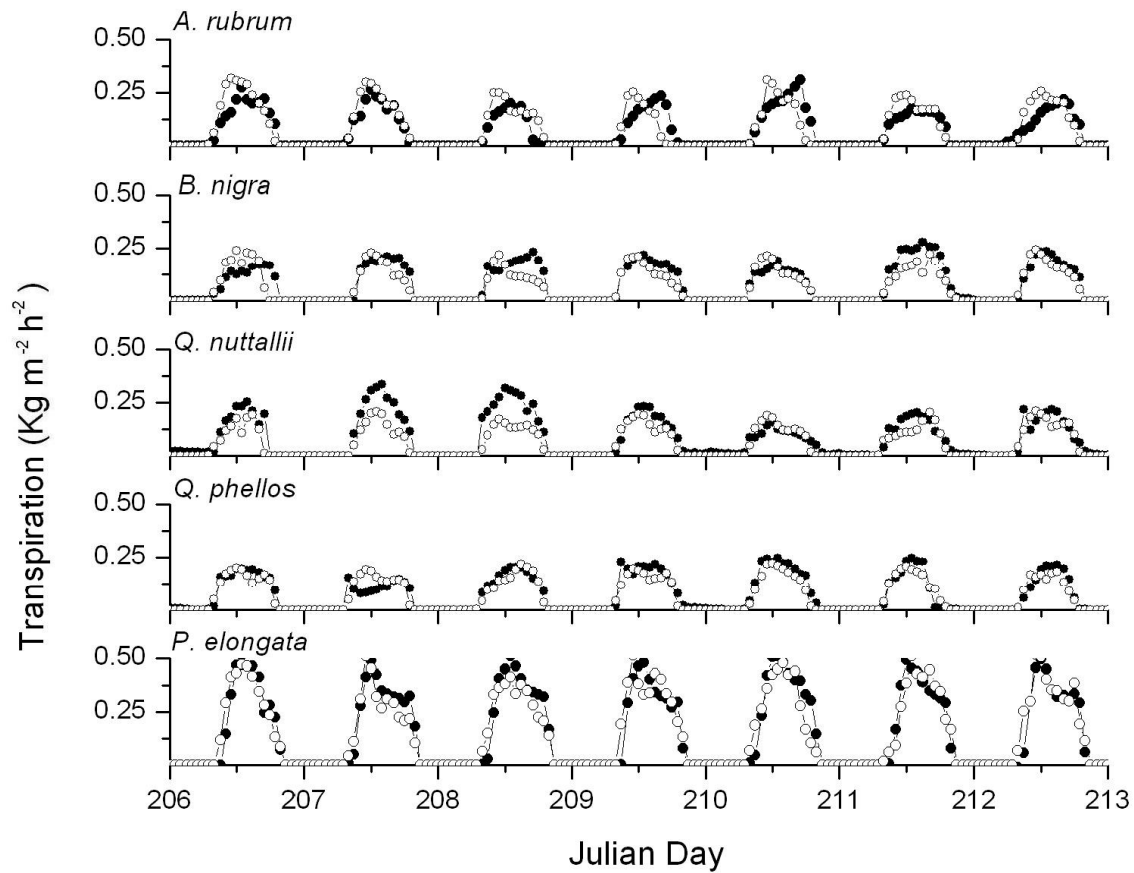
Fig. 3. Diurnally measured versus modeled sap flux under well watered conditions. Data illustrate mean hourly transpiration during a representative seven day time period. Closed circles (●) represent measured data and open circles (○) represent model predictions.
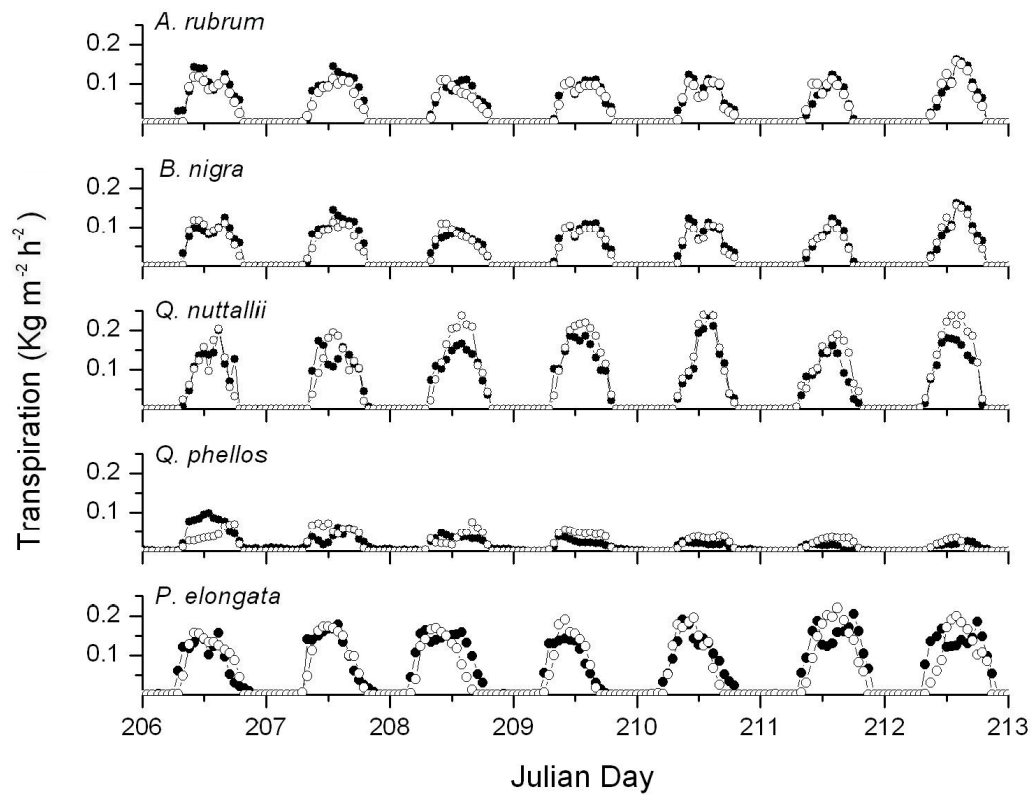
Fig. 4. Diurnally measured versus modeled sap flux under drought stress conditions. Data illustrate mean hourly transpiration during a representative seven day time period. Closed circles (●) represent measured data and open circles (○) represent model predictions.
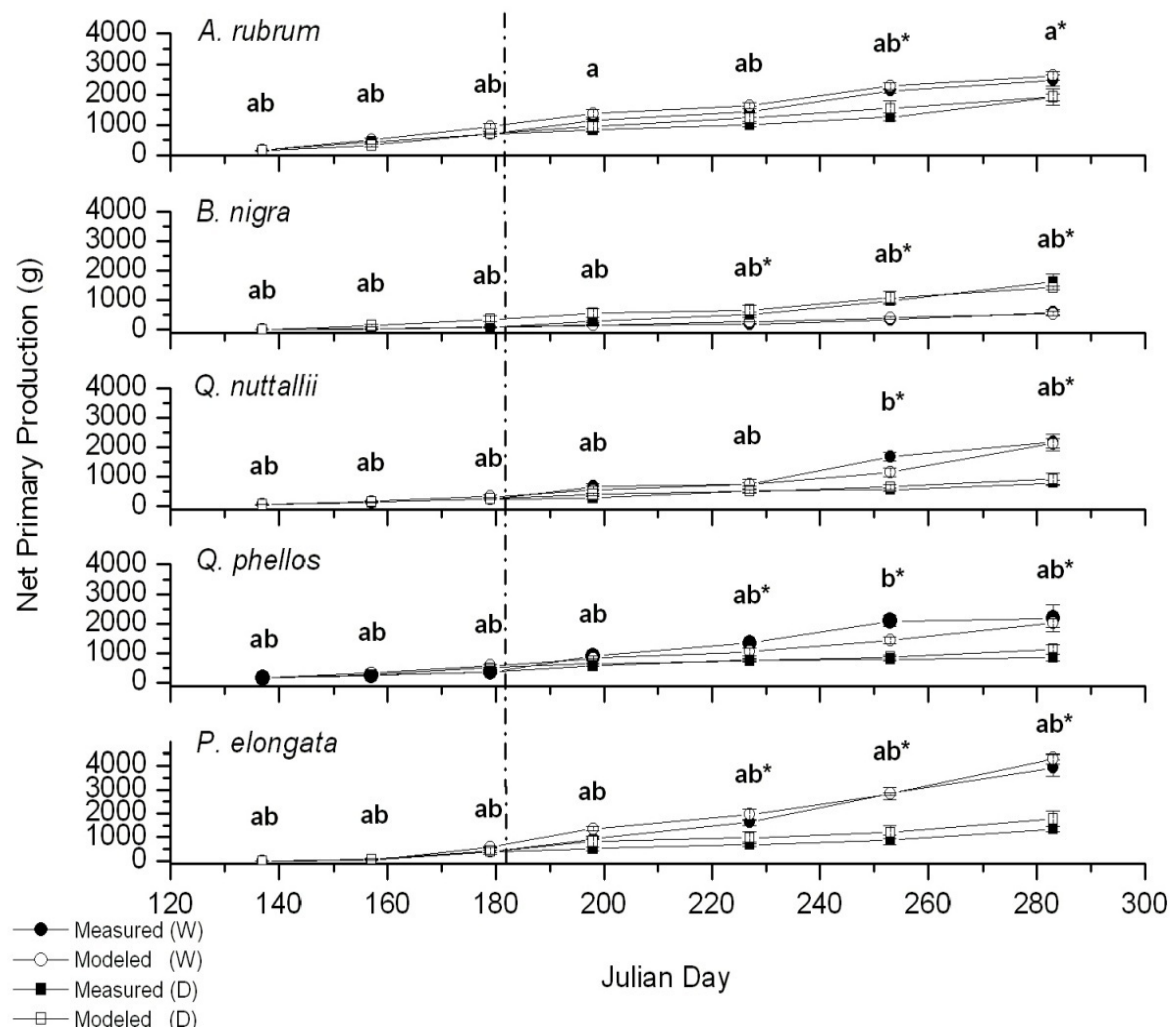
Fig. 5. Measured versus modeled net carbon accumulation throughout the study period. Data are the mean of three trees per harvest date. Symbol (a) indicates no significant difference between measured and modeled data in the well watered treatment at α= 0.05. Symbol (b) indicates no significant difference between modeled and measured data in the drought treatment at α= 0.05 and (*) indicates a significant treatment effect between measured data at α= 0.05. The dashed line indicates the time at which the drought treatment was initiated.
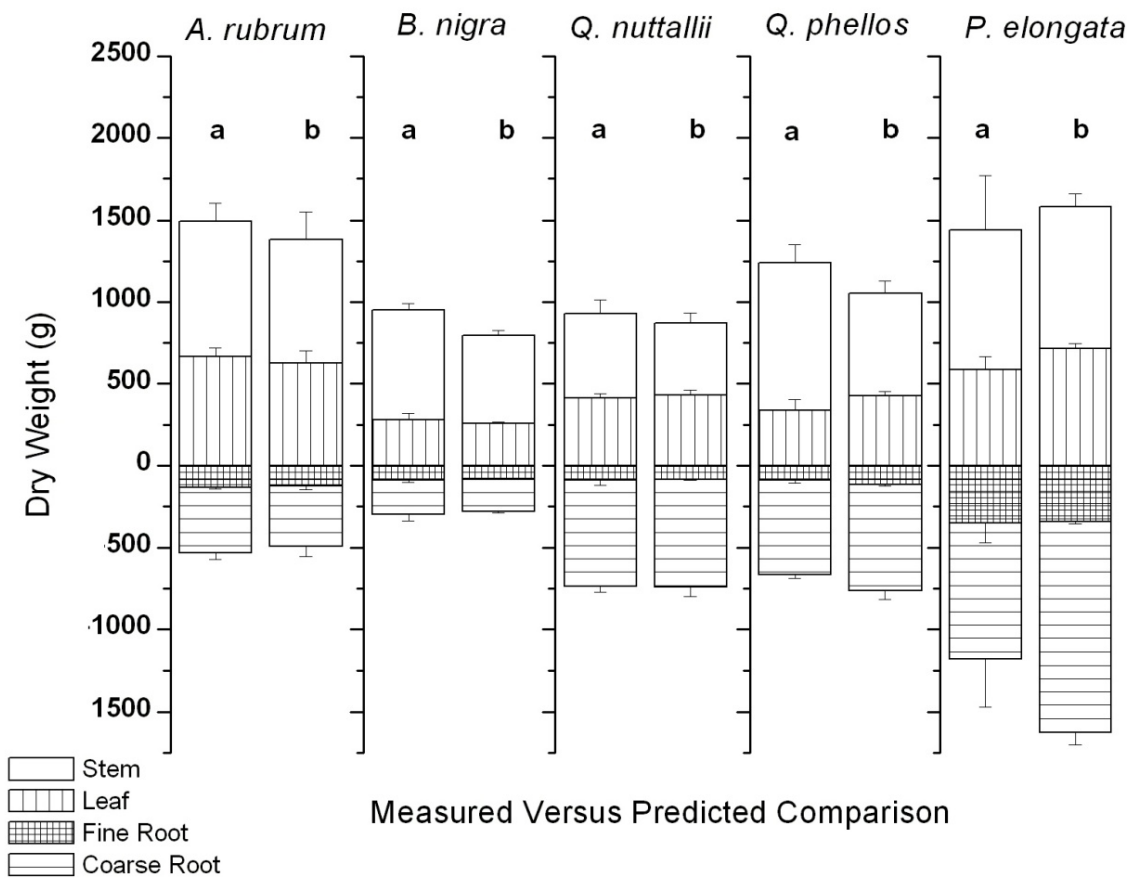
Fig. 6. Organ specific carbon accumulation under well watered conditions. Within a species, bars below the letter (a) represent measured data and (b) represent modeled data.
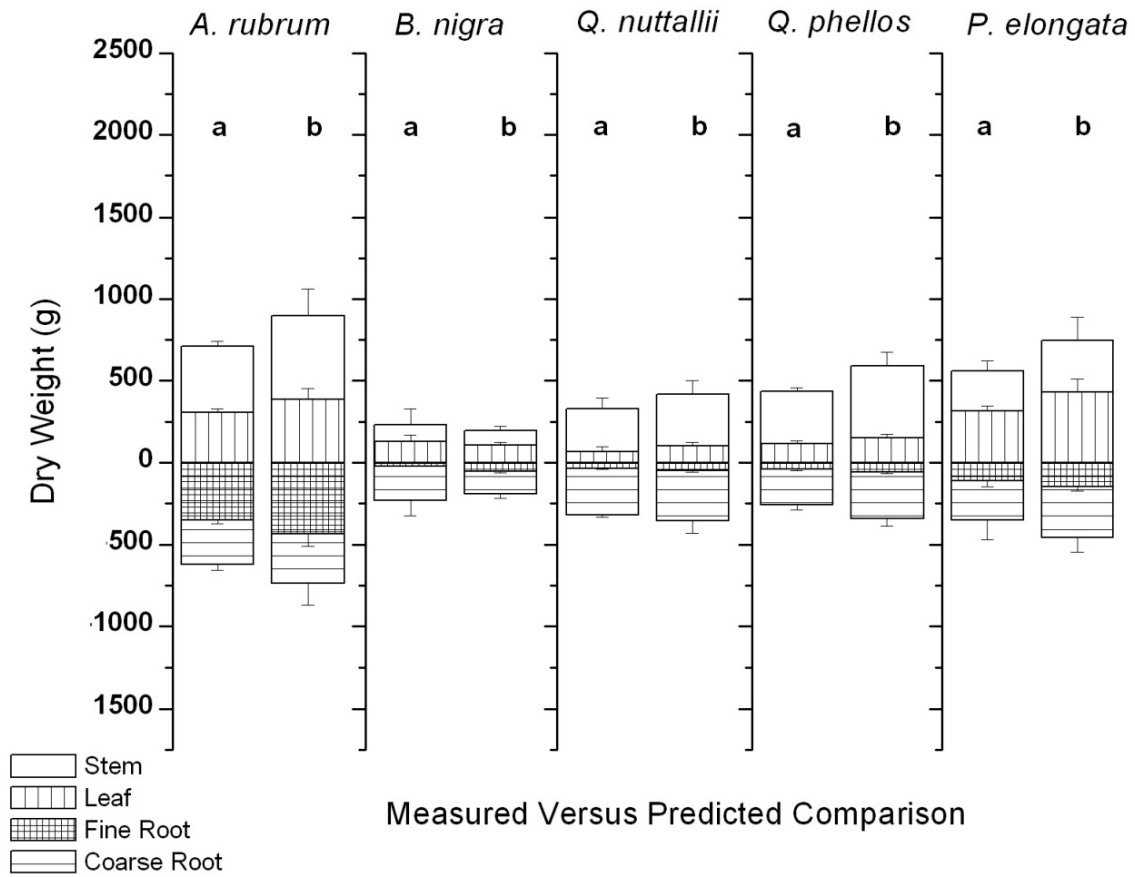
Fig. 7. Organ specific carbon accumulation under drought stress conditions. Within a species, bars below the letter (a) represent measured data and (b) represent modeled data.
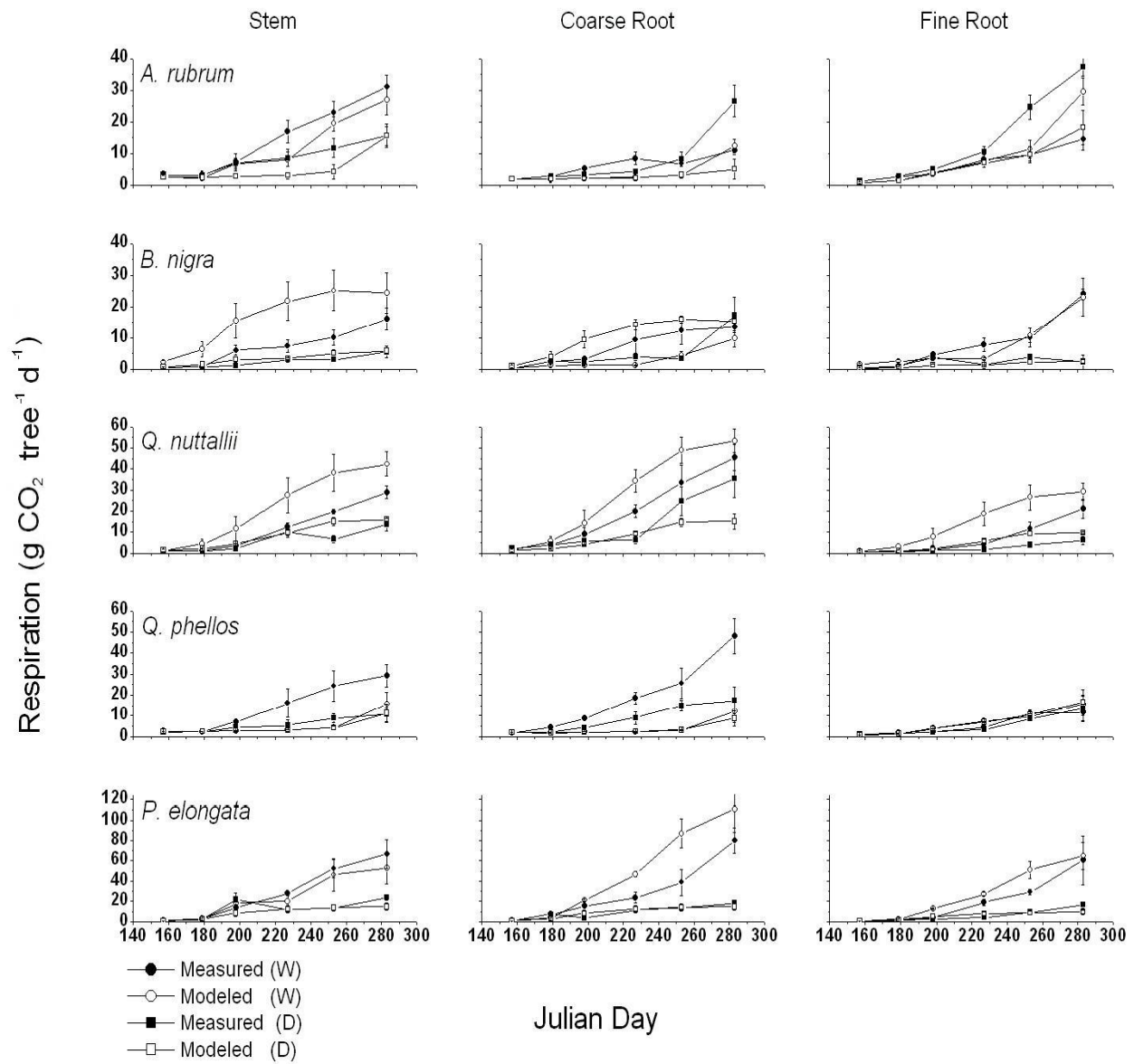
Fig. 8. Measured versus modeled stem, coarse root and fine root
respiration in well watered and drought treatments for the five tree species.
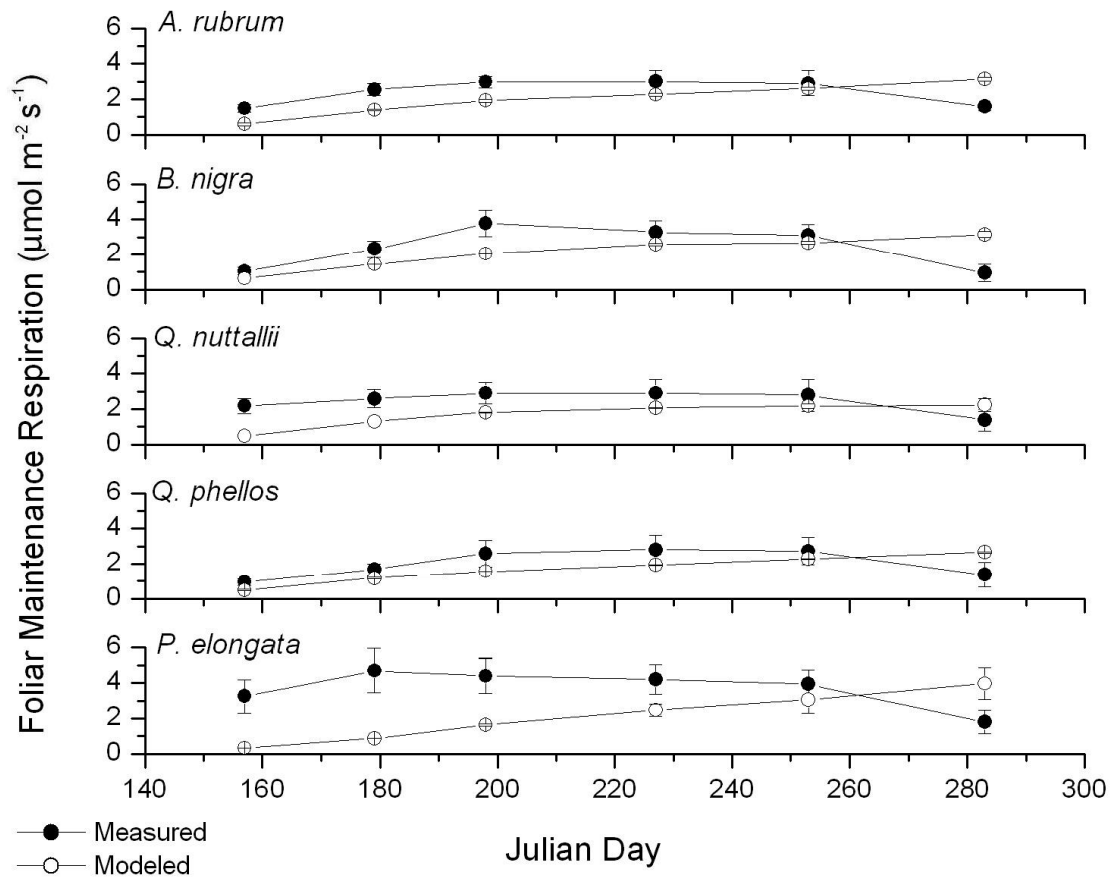
Fig. 9. Measured vs. modeled seasonal foliar maintenance respiration rate. Dashed line indicates the time at which the drought treatment was initiated.

DISCUSSION

Numerous plant simulation models have been used to model net primary production of forests and ecosystems. However, the majority of the models fall short in that they do not account for species specific contributions to net ecosystem carbon fluxes (e.g., Sinoquet et al. 2001; Badeck 2001 et al.; Baldocchi et al. 2002). The results of our study indicate that significant physiological distinctions can be made among species and that the incorporation of species specific physiology is important in modeling carbon fluxes and response to environmental stresses. In addition, a large portion of process models do not allow for spatially explicit physiological parameterization and instead use meteorological inputs to drive physiology sub-models in their attempt to estimate canopy CO_2 and water vapor flux. Although the use of such methodology has a variety of applications in monocultures, models that use generalized physiological responses fall short in estimating species specific carbon fluxes at the organ and species stress response level, thereby oversimplifying the detail required to capture the dynamics of a mixed forest response to environmental stimuli. The MAESTRA2 model has the capability to be parameterized using individual species physiology and the prior version, MAESTRA, has been demonstrated to meet the criteria of predicting carbon fluxes in several species (Medlyn et al. 2005; Janssens et al. 2005; Ibrom et al. 2006). In our study, significant physiological differences measured in the field

provided the opportunity to parameterize MAESTRA2 among species, test the

responsiveness of model output to changes in physiology inputs, and test the

ability of MAESTRA2 to estimate carbon and water fluxes an a species specific

basis. The modeling validation results indicate that the model was responsive to

changes in physiological parameterization and adequately estimated carbon and

water vapor fluxes amongst five deciduous species.

Apart from individual species' inherent physiology being an important

component for accurate model predictions at the species level, we found it

necessary to account for seasonal changes in species physiological activity. The

seasonal variation of physiological parameters such as apparent quantum yield,

maximum photosynthetic capacity and respiration has been shown to be

especially critical in characterizing seasonality of temperate broad leaved

deciduous as opposed to evergreen forests (Zhang 2006). Model predictions of

carbon accumulation have also been shown to be more accurate when

deciduous models are parameterized to account for seasonal fluctuations in leaf

physiological response (Kosugi et al. 2003 & 2006). We too found this to be

evident and therefore, parameterized MAESTRA2 at seven different time points

over the course of the growing season. Thus, MAESTRA2 interpolated between

seasonally distributed physiological responses per species to account for

seasonal changes in physiological activity. Due to the significant variance in both

seasonal fluctuations and species specific physiological model parameters, our

findings reinforce those of Kosugi et al. (2003) and Kosugi et al. (2006) in that the

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incorporation of species seasonal response models into larger ecosystem carbon models is warranted.

Studies that deployed MAESTRA or other similar process models have acknowledged the deficiency of a soil moisture response (Hanson et al. 2004). Most process models, MAESTRA included, either assume that soil moisture availability is non-limiting or are incapable of accounting for stomatal regulatory feedback effects on carbon dioxide exchange rates in response to soil water deficits. Therefore, process models such as MAESTRA have had a tendency to over predict carbon sequestration under water stress conditions (Hanson et al. 2004). The results of our study are novel in that we not only present and validate a modified version of MAESTRA that can capture species carbon sequestration on both an organ and whole plant scale, but additionally validate it in response to alterations in soil moisture. Furthermore, the ability of our version of MAESTRA (MAESTRA2) to simulate individual species carbon assimilation values as a function of inherent species specific attributes (e.g., photosynthetic capacity and respiration) is substantiated under both well watered and water stressed conditions.

At the individual organ or whole tree, variation in soil moisture status plays an important role in regulating the carbon exchange rate between the vegetation and the atmosphere. In fact, drought has been shown to be a major constraint of net ecosystem exchange among species as well as a significant limitation to carbon sequestration in forest systems (Granier et al. 2006). Furthermore, the

response to decreasing water availability is not homogeneous among species and is associated with inherent physiological and genetic constraints. Similar to Manes et al. (2006), who investigated the differences in oak species drought tolerance via their morphological and physiological response; we observed morphological changes that permitted *A. rubrum* to tolerate water stress conditions. However, the morphological root growth response was not observed in any of our other study species. For example, under well watered conditions, *P. elongata* was the fastest growing species in this study and accumulated the most carbon when water was not limiting. In contrast, the changes in *A. rubrum* shoot to root carbon partitioning allowed it to accumulate the greatest amount of carbon under water stress conditions. Specifically, *A. rubrum* deployed a drought avoidance strategy where it shifted carbon allocation to root production under water deficits. Furthermore, we observed a coarse to fine root ratio shift in the drought treatment when compared to the well watered control that is supported by a previous study by Canham et al. (1996). *A. rubrum* was observed to preferentially allocate carbon to above ground biomass in productive soils and to below ground biomass in soils deficient in water and nutrients.

Overall, the carbon sequestration due to water stress varied from 29% (*A. rubrum*) to 56-63% (*Q. phellos, P. elongata, B. nigra, and Q. nuttallii*) lower than the respective well watered control. Most importantly, MAESTRA2 was able to capture the large variation in drought, which further substantiates the use of MAESTRA2 as a species specific model for predicting ecosystem carbon

dynamics in response to environmental stresses such as precipitation deficits. The MAESTRA model has been demonstrated to be capable of estimating transpiration on a per species basis (Bowden et al. unpublished data), we expand on this work by testing the capability of MAESTRA2 to model carbon exchange for several species under a variety of soil moisture conditions. Model validation results illustrate that the model was able to adjust species specific carbon exchange in response to drought.

Previous studies have demonstrated that ecosystem respiration is drastically reduced by drought (e.g., Reichstein et al. 2007). Specific to root organs, Burton et al. (1998) reported a decline in sugar maple root respiration as soil moisture became more limited. Measured values and modeled estimates of photosynthesis and woody respiration rates in our study concur with this observation and indicate that the soil moisture response incorporated in the model is effective in down regulating root system respiration rates under soil water deficits. Moreover, MAESTRA2 has the capability to budget whole tree and organ specific carbon across a range of soil moisture conditions. Although Janssens et al. (2005) compared MAESTRA estimates of net carbon accumulation and woody respiration to dry weight data from a single destructive harvest of *P. sylvestris* exposed to elevated atmospheric CO_2, our study is the first to predict drought stress responses of multiple deciduous tree species within and over the course of an entire growing season.

Numerous carbon flux studies use eddy covariance to validate model estimates of seasonal carbon flux (Baldocchi et al. 2002 & 2003; Medlyn et al. 2005). Though the method is prone to uncertainty due to site topography, a further drawback is the inability to differentiate individual species responses in heterogeneous forest ecosystems (Hollinger and Richardson 2005). An investigation into the validation of carbon models by eddy covariance reveals that uncertainty in the eddy covariance data accuracy originates from a variety of sources that include random natural fluctuations in an ecosystem, instrumentation error, and the lack of sufficient replicate eddy covariance data to quantify measurement error (Medlyn et al. 2005). Aside from these eddy covariance shot comings that make model validation at the ecosystem scale problematic, eddy covariance cannot quantify carbon fluxes at the tree or organ level. Therefore, an alternative method to quantify tree level flux would be to calibrate whole canopy gas exchange chambers with sap flow (Dragoni et al. 2005). However, canopies enclosed in the chambers alter the environment and the instrumentation is not trivial to deploy under outdoor conditions. Our destructive harvest method, therefore, aimed to reduce or eliminate these factors, as well as enable us to simultaneously examine multiple species and organ responses under the same environmental conditions.

CONCLUSIONS

MAESTRA2 is the latest rendering of the MAESTRO/MAESTRA model evolution. The predicted versus measured comparison indicates that the species specific detail in model parameterization allowed MAESTRA2 to adequately predict net carbon accumulation among species. The merit of detailed model parameterization, especially with the aim to scale up to the stand or ecosystem level, has been expressed by others (e.g., Baldocchi et al. 2002; Janssens et al. 2005). Thus, MAESTRA2's ability to predict at the species and organ level and in response to soil water deficits could be useful in deciphering the dynamics of deciduous forest response to precipitation.

LITERATURE CITED

Badeck F.W., Lischke H., Bugmann H., Hickler T., Honninger K., Lasch P., Lexer M.J., Mouillot F., Schaber J. & Smith B. (2001) Tree species composition in European pristine forests: comparison of stand data to model predictions. *Climatic Change* **51,** 307-347.

Baldocchi, D.D., Wilson, K.B., & Gu, L. (2002) How the environment, canopy structure and canopy physiological functioning influence carbon, water and energy fluxes of a temperate broad-leaved deciduous forest - An assessment with the biophysical model CANOAK. *Tree Physiology* **22,** 1065-1077.

Baldwin V.C., Dougherty P.M. & Burkhart H.E. (1998) A linked model for simulating stand development and growth processes of loblolly pine. In The productivity and sustainability of Southern forest ecosystems in a changing environment, pp. 305-326. Eds. Mickley R.A. & Fox S.A. Springer-Verlag, New York, NY.

Ball J.T., Woodrow I.E., & Berry JA. (1987) A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. *In Progress in Photosynthesis Research,* pp. 221-224. Ed. J. Biggens. Martinus Nijhoff Publishers, Dordrecht.

Bauerle W.L., Post C.J., McLeod M.F., Dudley, J.B. & Toler J.E. (2002) Measurement and modeling of the transpiration of a temperate red maple container nursery. *Agriculture and Forest Meteorology* **114,** 45 – 57.

Bauerle W.L., Timlin D.J., Pachepsky Y.A. & Anantharamu S. (2006) Adaptation of the biological simulation model MAESTRA for use in a generic user interface. *Agronomy Journal* **98,** 220-228.

Bauerle W.L., Bowden J.D., McLeod M.F. & Toler J.E. (2004a) Modeling intra-crown and intra-canopy interactions in red maple: assessment of light transfer on carbon dioxide and water vapor exchange. *Tree Physiology* **24,** 589-597.

Bauerle W.L., Toler J.E. & Wang G.G. (2004b). The stomatal conductance of Acer rubrum L. ecotypes under varying soil and atmospheric water conditions: Predicting stomatal responses with an abscisic acid-based model. *Tree Physiology* **24,** 805-811.

Bauerle W.L., Weston, D.J., Bowden, J.D., Dudley, J.B. & Toler, J.E. (2004c). Leaf absorptance of photosynthetically active radiation in relation to chlorophyll meter estimates among woody plant species. *Scientia Horticulturae* **101,** 169-178.

Bauerle, W.L.,Whitlow T.H., Setter, T.L., Bauerle T.L. & Vermeylen F.M. (2003) Ecophysiology of Acer rubrum L. seedlings from contrasting hydrologic habitats: growth, gas exchange, tissue water relations, abscisic acid, and carbon isotope discrimination. *Tree Physiology* **23,** 841-850.

Bauerle W.L., Bowden, J.D., & Wang G.G. (2007). The influence of temperature on within-canopy acclimation and variation in leaf photosynthesis and respiration: Spatial acclimation to microclimate gradients among thermally divergent Acer rubrum L. genotypes. *Journal of Experimental Botany* online early, doi:10.1093/jxb/erm177.

Bernacchi, C.J., Pimentel C. & Long S.P. (2003) In vivo temperature response functions of parameters required to model RuBP-limited photosynthesis. *Plant, Cell & Environment* **26,** 1419-1430.

Bernacchi, C.J., Portis A.R. Nakano H. v. Caemmerer S. & Long S.P. (2002) Temperature response of mesophyll conductance; implications for the determination of Rubisco enzyme kinetics and for limitations to photosynthesis in vivo. *Plant Physiology* **130,** 1992-1998.

Bernacchi, C.J., Singsass E.L., Pimentel C., Portis A.R., & Long S.P. (2001) Improved temperature response functions for models of Rubisco-limited photosynthesis*. Plant, Cell & Environment* **24,** 253-259.

Canham, C.D., Berkowitz, A.R., Kelly, V.R., Lovett, G.M., Ollinger, S.V. and Schnurr, J. (1996) Biomass Allocation and Multiple Resource Limitation in Tree Seedlings. *Canadian Journal of Forest Research* **26,** 1521–1530.

Chen S.G., Fuchs M., Moreshet S. & Cohen Y. (1987) Effects of plant canopy structure on light interception and photosynthesis. *Journal of Quantitative Spectroscopy and Radiative Transfer* **52,** 115-123.

Dai A., Trenberth K. E., Taotao Q. (2004) A global dataset of palmer drought severity index for 1870-2002: Relationships with soil moisture and effects of surface warming. *Journal of Hydrometeorology* **5,** 1117-1130

Dezmarez V., Gastellu-Etchegorry J.P., Mordelet P., Tosca C., Marty G. & Guillevic P. (2000) Modeling of the radiation regime and photosynthesis of a finite canopy using the DART model. Influence of canopy architecture assumptions and border effects. *Agronomie* **20,** 259-270.

Dragoni D., Lakso, A.N. & Piccioni, R.M. (2005) Measuring transpiration in apple trees using heat pulse sap flow gauges calibrated with whole-canopy gas exchange chambers. *Agricultural and Forest Meteorology* **130,** 85-94.

Evans, G.C. (1972) *The Quantitative Analysis of Plant Growth.* Blackwell Scientific Publications, Oxford

Farquhar G.D. & Caemmerer S.v. (1982) Modeling of photosynthetic response to environmental conditions. *In Encyclopedia of Plant Physiology,* pp. 549-588. Eds. O. Lange, B. PS Nobel, C. Osmond and H. Ziegler. Springer-Verlag, Berlin.

Granier, A., Reichstein, M., Bréda, N., Janssens, I.A., Falge, E., Ciais, P., Grünwald, T., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Facini, O., Grassi, G., Heinesch, B., Ilvesniemi, H., Keronen, P., Knohl, A., Köstner, B., Lagergren, F., Lindroth, A., Longdoz, B., Loustau, D., Mateus, J., Montagnani, L., Nys, C., Moors, E., Papale, D., Peiffer, M., Pilegaard, K., Pita, G., Pumpanen, J., Rambal, S., Rebmann, C., Rodrigues, A., Seufert, G., Tenhunen, J., Vesala, T., & Wang, Q. (2006) Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology* **143,** 123-145.

Hanson P.J., Amthor J.S., Wullschleger S.D., Wilson K.B., Grant R.F., Hartley A., Hui D., Hunt Jr. E.R., Johnson D.W., Kimball J.S., King A.W., Luo Y., McNulty S.G., Sun G., Thornton P.E., Wang S., Williams M., Baldocchi D.D., & Cushman R.M. (2004) Oak forest carbon and water simulations: Model intercomparison and evaluations against independent data. *Ecological Monographs* **74,** 443-489.

Harley P.C. & Baldocchi D.D. (1995) Scaling carbon dioxide and water vapor exchange from leaf to canopy in a deciduous forest. I. Leaf model parameterization. *Plant, Cell & Environment* **18,** 1146–1156.

Hollinger D.Y. and Richardson A.D. (2005) Uncertainty in eddy covariance measurements and its application to physiologic models. *Tree Physiology* **25,** 873-885.

Hoogenboom G. & White J.W. (2003) Improving physiological assumptions of simulation models by using gene-based approaches. *Agronomy Journal* **95,** 82-89.

Hoogenboom, G., White J.W., Acosta-Gallegos J., Gaudiel R.G. & Myers J.R. (1997) Evaluation of a crop simulation model that incorporates gene action. *Agronomy Journal* **89,** 613-620.

Hunt, R. (1978) Plant growth analysis. *Studies in Biology*, **96**. Arnold, London.

Hunt, R., Causton, D.R., Shipley, B., & Askew, A.P. (2002). A modern tool for classical plant growth analysis. *Annals of Botany* **90,** 485-488.

Ibrom, A., Jarvis, P.G., Clement, R., Morgenstern, K., Oltchev, A., Medlyn, B.E., Ying, P.W., Wingate, L., Moncrieff, J.B.& Gravenhorst, G. (2006) A comparative analysis of simulated and observed photosynthetic CO_2 uptake in two coniferous forest canopies. *Tree Physiology* **26,** 845-864.

Janssens, I.A., Medlyn, B., Gielen, B., Laureysens, I., Jack, M.E., Van Hove, D., & Ceulemans, R. (2005) Carbon budget of Pinus sylvestris saplings after four years of exposure to elevated atmospheric carbon dioxide concentration. *Tree Physiology* **25,** 325-337.

Kosugi Y., Shibata S., & Kobashi S. (2003) Parameterization of the CO_2 and H_2O gas exchange of several temperate deciduous broad-leaved trees at the leaf scale considering seasonal changes. *Plant, Cell and Environment* **26,** 285-301.

Kosugi, Y., & Matsuo, N. (2006) Seasonal fluctuations and temperature dependence of leaf gas exchange parameters of co-occurring evergreen and deciduous trees in a temperate broad-leaved forest. *Tree Physiology* **26,** 1173-1184.

Kruijt, B., Barton C., Rey A. & Jarvis P.G. (1999) The sensitivity of stand-scale photosynthesis and transpiration to changes in atmospheric CO_2 concentration and climate. *Hydrology & Earth Systems Science* **3,** 55-69.

Landsberg J.J. (2003) Modeling forest ecosystems: state of the art, challenges, and future directions. *Canadian Journal of Forest Research* **33,** 385-397.

Luo Y., Medlyn B., Hui D., Ellsworth D., Reynolds J. & Katul G. (2001) Gross primary productivity in Duke Forest: Modeling synthesis of CO_2 experiment and eddy-flux data. *Ecological Applications* **11,** 239-252.

Manes F., Vitale M., Donato E., Giannini M. & Puppi G. (2005) Different ability of three Mediterranean oak species to tolerate progressive water stress. *Photosynthetica* **44,** 387-393.

Martin T.A., Dougherty P.M., Topa M.A. & McKeand S.E. (2005) Strategies and case studies for incorporating ecophysiology into southern pine tree improvement programs. *Southern Journal of Applied Forestry* **29,** 70-79.

McMurtrie R.E. & Landsberg J.J. (1992) Using a simulation model to evaluate the effects of water and nutrients on the growth and carbon partitioning of *Pinus radiata. Forest Ecology & Management* **52,** 243-260.

Medlyn B.E. (1998) Physiological basis of the light use efficiency model. *Tree Physiology* **18,** 167-176.

Medlyn B.E. (2004) A MAESTRO retrospective. *In* Forests at the Land-Atmosphere Interface, pp. 105-121. Ed. K. McNaughton. CAB International

Medlyn, B.E., Berbigier P., Clement R., Grelle A., Loustau D., Linder S., Wingate L., Jarvis P.G., Sigurdsson B.D. & McMurtrie R.E. (2005) Carbon balance of coniferous forests growing in contrasting climates: Model-based analysis. *Agricultural and Forest Meteorology* **131,** 97-124.

Myneni R.B. (1991) Modeling radiative transfer and photosynthesis in three-dimensional vegetation canopies. *Agricultural and Forest Meteorology* **55,** 323-344.

Reichstein, M., Ciais, P., Papale, D., Valentini, R., Running, S., Viovv, N., Cramer, W., Grainier, A,. Ogee, J., Allard, V., Aubinet, M., Bernhofer, C., Buchmann, N., Carrara, A., Grunwale, T., Heimann, M., Heinesch, B., Knohl, A., Kutsch, W., Loustau, D., Manaca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Pilegaard. K., Pumpanen, J., Rambal, S., Schaphoff, S., Seufert, G., Soussana, J.F., Sanz, M.J., Vesala, T., & Zhao, M. (2007) Redyction of ecosystem productivity and respiration during the European summer 2003 climat anomaly: A joint flux tower, remote sensing and modeling analysis. *Global Change Biology* **13,** 634-651.

Reymond M., Muller B., Leonardi A., Charcosset A. & Tardieu F. (2003) Combining quantitative trait loci analysis and an ecophysiological model to analyze the genetic variability of the responses of maize leaf growth to temperature and water deficit. *Plant Physiology* **131,** 664-675.

Reynolds J.F., & Chen, J. (1996) Modeling whole-plant allocation in relation to carbon and nitrogen supply: Coordination versus optimization: Opinion. *Plant and Soil* **185,** 65-74.

Reynolds J.F., Kemp P.R., Ogle K. & Fernandez R.J. (2004) Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* **141,** 194-210.

Richardson A.D., Hollinger D.Y., Aber J.D., Ollinger S.V. & Braswell B.H. (2007) Environmental variation is directly responsible for short- but not long-term variation in forest-atmosphere carbon exchange. *Global Change Biology* **13,** 1-16.

Sinoquet H., Le Roux X., Adam B., Ameglio T. & Daudet F.A. (2001) RATP: a model for simulating the spatial distribution of radiation absorption, transpiration and photosynthesis within canopies: application to an isolated tree crown. *Plant, Cell & Environment* **24,** 395-406.

Tardieu F. (2003). Virtual plants: modeling as a tool for the genomics of tolerance to water deficit. *Trends in Plant Science* **8,** 9-14.

Thorpe M.R., Saugier B., Auger S., Berger A. & Methy M. (1978) Photosynthesis and transpiration of an isolated tree: model and validation. *Plant, Cell & Environment* **1,** 321-330.

Valentine H.T., Gregoire T.G., Burkhart H.E., & Hollinger D.T. (1998) Predicting growth of loblolly pine stands under elevated temperatures and carbon dioxide. In The productivity and sustainability of Southern forest ecosystems in a changing environment, pp. 341-352. Eds. Mickley R.A. & Fox S.A. Springer-Verlag, New York, NY.

Wang Y.P. & Jarvis P.G. (1990a) Description and validation of an array model-MAESTRO. *Agricultural and Forest Meteorology* **51,** 257-280.

Wang Y.P. & Jarvis P.G. (1990b) Influence of crown structural properties on PAR absorption, photosynthesis, and transpiration in Sitka spruce: application of a model (MAESTRO). *Tree Physiology* **7,** 297-316.

Weinstein D.A., Beloin R. & Yanai R. (1991) Modeling changes in red spruce carbon balance and allocation in response to interacting ozone and nutrient stress. *Tree Physiology* **9,** 127-146.

White J.W. & Hoogenboom G. (2003) Gene-based approaches to crop simulation: Past experiences and future opportunities. *Agronomy Journal* **95,** 52-64.

Whitford W.G. (2002) Ecology of desert systems. Cambridge University Press, Cambridge.

Zhang G.R., Yu G.R., Sun X.F., Wen X.F., Ren C.U., Fu Y.L., Li Q.K., Li Z.Q. Liu Y.F., Guan D.X., Yan J.H. (2006) Seasonal variations of ecosystem apparent quantum yield (α) and maximum photosynthesis rate (P_{max}) of different forest ecosystems in China. *Agricultural and Forest Meteorology* **137,** 178-187.