

Simulating carbon dioxide exchange rates of deciduous tree species: evidence for a general pattern in biochemical changes and water stress response

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- **Background and Aims** Deciduous trees have a seasonal carbon dioxide exchange pattern that is attributed to changes in leaf biochemical properties. However, it is not known if the pattern in leaf biochemical properties – maximum Rubisco carboxylation (V_{cmax}) and electron transport (J_{max}) – differ between species. This study explored whether a general pattern of changes in V_{cmax} , J_{max} , and a standardized soil moisture response accounted for carbon dioxide exchange of deciduous trees throughout the growing season.
- **Methods** The model MAESTRA was used to examine V_{cmax} and J_{max} of leaves of five deciduous trees, *Acer rubrum* ‘Summer Red’, *Betula nigra*, *Quercus nuttallii*, *Quercus phellos* and *Paulownia elongata*, and their response to soil moisture. MAESTRA was parameterized using data from *in situ* measurements on organs. Linking the changes in biochemical properties of leaves to the whole tree, MAESTRA integrated the general pattern in V_{cmax} and J_{max} from gas exchange parameters of leaves with a standardized soil moisture response to describe carbon dioxide exchange throughout the growing season. The model estimates were tested against measurements made on the five species under both irrigated and water-stressed conditions.
- **Key Results** Measurements and modelling demonstrate that the seasonal pattern of biochemical activity in leaves and soil moisture response can be parameterized with straightforward general relationships. Over the course of the season, differences in carbon exchange between measured and modelled values were within 6–12 % under well-watered conditions and 2–25 % under water stress conditions. Hence, a generalized seasonal pattern in the leaf-level physiological change of V_{cmax} and J_{max} , and a standardized response to soil moisture was sufficient to parameterize carbon dioxide exchange for large-scale evaluations.
- **Conclusions** Simplification in parameterization of the seasonal pattern of leaf biochemical activity and soil moisture response of deciduous forest species is demonstrated. This allows reliable modelling of carbon exchange for deciduous trees, thus circumventing the need for extensive gas exchange experiments on different species.

Key words: Carbon budget, deciduous trees, modelling, MAESTRA, soil moisture, species response, transpiration, *Acer rubrum*, *Betula nigra*, *Quercus nuttallii*, *Q. phellos*, *Paulownia elongata*.

INTRODUCTION

Trees are a primary component of terrestrial carbon sinks. The carbon budget of deciduous tree plantations is of particular interest because they sequester carbon, particularly in the juvenile, most productive phase of a tree’s life cycle (e.g. Ryan *et al.*, 2004). Modelling carbon accumulation accurately is most important for obtaining carbon budgets over many spatial and temporal scales. However, growing season patterns in basic biochemical properties of leaves, maximum Rubisco carboxylation (V_{cmax}) and electron transport (J_{max}), affect assimilate production and thus simulation accuracy (Wilson *et al.*, 2001; Kosugi *et al.*, 2003; Xu and Baldocchi, 2003). To complicate matters further, trees are genetically diverse and highly complex organisms that adjust to changes in environmental conditions, including water availability. Recently, studies have highlighted both the inadequacy with which models simulate carbon exchange over the course of a growing season (e.g. Sasai *et al.*, 2007; Harrison *et al.*, 2008; Ricciuto *et al.*, 2008) and the lack of a generic set of parameters to predict soil water constraints (e.g. Van Wijk *et al.*, 2001; Baldocchi *et al.*, 2002; Bauerle *et al.*, 2004;

Verbeek *et al.*, 2007). As a result, development of forest management models still faces the challenge of integrating knowledge that describes the carbon exchange response at different temporal and spatial scales (Pretzsch *et al.*, 2008).

Simulation of forest ecosystem carbon exchange calls for proficient models that capture the physiological behaviour of trees at the ecosystem scale (e.g. Running and Coughlan, 1988; Wang *et al.*, 1998; Pretzsch *et al.*, 2008). A consistent difficulty, therefore, is to determine experimentally the parameters and define the acceptable degree of equation simplification (Tardieu *et al.*, 2005). The goal of the present study, therefore, is to report on a general V_{cmax} and J_{max} seasonal pattern along with a standardized water stress response that describes deciduous tree carbon exchange dynamics throughout the growing season.

A process-based model (MAESTRO; Wang and Jarvis, 1990), which is spatially explicit for individual trees, was used here to simulate seasonal carbon dioxide exchange for different species using a simple leaf biochemical and soil moisture response function. The study is unique in that seasonal variation among deciduous species was controlled for. The specific objectives were to (1) examine the relationship differences between

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species' seasonal physiological changes of leaves, (2) investigate the use of a general soil moisture response model among five temperate deciduous tree species and (3) compare measurements made on pot-grown plants under field conditions with model estimates, made using independently derived parameters, to test a generalized growing season V_{cmax} and J_{max} pattern and a standardized soil moisture response function. Thus, we hypothesized that deciduous species V_{cmax} , J_{max} and soil moisture response parameters could be simplified for predicting the seasonal dynamics of deciduous species' carbon dioxide exchange.

MATERIALS AND METHODS

Site description and plant material

The duration of the study was from 15 May 2006 to 15 October 2006, most of the 2006 growing season. The field site was located at the Clemson University Calhoun Field Laboratory in Clemson, SC, USA (34°40'8"N, 82°50'40"W). A full site description is provided in Bauerle *et al.* (2002). Clonal 1-year-old pot-grown saplings of *Acer rubrum* 'Summer Red', *Betula nigra*, *Quercus nuttallii*, *Quercus phellos* and *Paulownia elongata*, 40 per species, were transplanted from 11-L into 114-L plastic containers of 0.67 m depth on 7 March 2006. To minimize root restrictions, the containers used were three times the size of those used for commercial production of equal dimension deciduous trees throughout a growing season (P. Parsons, Parsons Nursery, Georgetown, SC, pers. comm.). Plants were grown in a potting compost (Fafard Inc., Anderson, SC, USA), a 1:1:1:1 (v/v) mixture of peat, perlite, vermiculite and silt loam fertilized with 9 kg m⁻³ of Osmocoat Pro® 19-5-8 (Scotts Inc., Marysville, OH, USA). To create a common garden, plants were randomly distributed throughout a plot in a grid pattern (1.5-m spacing), initially watered to container capacity and allowed to drain for 24 h.

Soil water measurements

Micro-emitter (360° spray pattern) irrigation was applied at the base of each tree stem, delivering water three times daily. The root zone volumetric water content (VWC) was monitored and maintained within a previously determined well-watered range (0.3–0.5 m³ m⁻³) (Bauerle *et al.*, 2003). To link the soil moisture to the individual trees, ECH₂O probes, type EC-20 (Decagon Devices, Pullman, WA, USA) were installed at a 45° angle in the soil of eight randomly selected trees per species. The probes recorded bulk VWC every minute and hourly averages were saved in a CR7X data logger (Campbell Scientific, Logan, UT, USA). All trees were allowed to acclimate for 45 d.

Drought treatment

At the start of the experiment (after 45 d of growth), 20 trees per species were randomly assigned to the drought treatment and 20 trees to the well-watered control. Drought was achieved by restricting the water supply to 70 % less than the controls. Soil moisture measurements continued with equal numbers of ECH₂O probes between the two treatments randomly distributed. Irrigation times and duration were adjusted per tree

species and treatment to ensure that the VWC in the drought treatment was <0.3 m³ m⁻³ and the control treatment VWC remained >0.3 m³ m⁻³ (a predetermined value shown not to depress gas exchange of the species). In addition, container radiation load was minimized and precipitation excluded as described in Bauerle *et al.* (2002).

Sap-flux measurements

Sap flow gauges (Dynamax Inc., Houston, TX, USA) were installed on four or five randomly selected trees per species (two or three per treatment; models SGB13-WS, SGB16-WS, SGB19-WS, SGB25-WS and SGB35-WS). Installation and operation followed Bauerle *et al.* (2002).

Leaf gas exchange and light absorption measurements

Gas exchange was measured at 3-week intervals on recently fully expanded leaves of four replicate trees per species, using a portable gas exchange system (CIRAS-1, PP Systems, Haverhill, MA, USA) fitted with a light- and temperature-controlled cuvette (Model PLC (B), PP Systems). The temperature inside the cuvette was controlled at 25 ± 0.7 °C and vapour pressure deficit of 1.27 ± 0.12 kPa. Leaf net photosynthesis (A_{net}) versus CO₂ (A_{net}/C_i curves, where A_{net} is in units of μmol m⁻² s⁻¹ and C_i is the internal CO₂ concentration expressed as the molar fraction of CO₂) were constructed as described in Bauerle *et al.* (2007). In addition, light response curves were constructed and quantum yield calculations were corrected for the percentage photosynthetically active radiation absorbed by each leaf from paired SPAD meter (model 502B, Minolta Inc., Ramsey, NJ, USA) measurements as described in Bauerle *et al.* (2006).

Growth and maintenance respiration measurements

Three trees of each species per treatment (30 total) were randomly selected and harvested at 3-week intervals (seven harvests in total). All leaves were removed and measured for total area (LiCor 3100, Lincoln, NE, USA). The soil was gently hand washed from the roots, blotted dry, and fine roots (diameter <3 mm) were separated from the coarse roots (diameter >3 mm). Respiration measurements were made simultaneously on each individual replicate from a separate plant. Each organ was taken, placed inside a 25 °C temperature-controlled room and allowed to equilibrate for 30 min. Stem, coarse root and fine root tissue respiration was measured (CIRAS-1 connected to a model SRC-1 respiration chamber, PP Systems). The chamber was modified with a lid to seal and enclose the organ. Respiration was logged after reaching a steady state and organ volume was determined by water displacement in a graduated cylinder. Individual organs were then dried at 70 °C for approx. 21 d and weighed. After each harvest, the remaining trees in the plot were randomly repositioned at the same spacing.

Model description

We developed a modified version of the three-dimensional photosynthesis, transpiration and absorbed radiation model

MAESTRO (Wang and Jarvis, 1990). Recently, MAESTRO has been renamed MAESTRA and described and applied in several studies, for example Wang and Polglase (1995), Kruijt *et al.* (1999), Bauerle *et al.* (2007), Emhart *et al.* (2007) and Medlyn *et al.* (2007). Readers are referred to an online bibliography of model components, development and application at www.bio.mq.edu.au/maestra. We only detail the changes that applied to the present study. Bauerle *et al.* (2002, 2004) updated the model to run on a 15-min time step, incorporated a soil moisture response function, and parameterized and validated the model on the deciduous tree species *Acer rubrum*. Our version includes the V_{cmax} and J_{max} temperature response functions of Bernacchi *et al.* (2001, 2003) and was parameterized and validated for estimating light transfer and interception (Bauerle *et al.*, 2004) and transpiration (Bowden and Bauerle, 2008) within the crowns of deciduous trees.

Leaf model parameterization

Changes in J_{max} and V_{cmax} over the season were assessed by analysis of covariance among species differences after values were log transformed. As there were no differences between species in the seasonal trends in J_{max} and V_{cmax} a general third-order polynomial was fitted to the seasonal change in the log-transformed values (Fig. 1), to generalize the response among species. The non-linear equations of Fig. 1 were used to parameterize the seasonal pattern of V_{cmax} and J_{max} in the Farquhar and von Caemmerer (1982) biochemical submodel of photosynthesis. The kinetic parameters used to estimate the temperature response of V_{cmax} , J_{max} and leaf dark respiration are described in Bauerle *et al.* (2007).

Differences between species were quantified by parameters within the coupled CO_2 and H_2O models of Farquhar and von Caemmerer (1982) and Ball *et al.* (1987). The linkage between the models is described in Ball *et al.* (1987) and Kim and Lieth (2003). MAESTRA scaled up the leaf-level properties to the whole-tree scale.

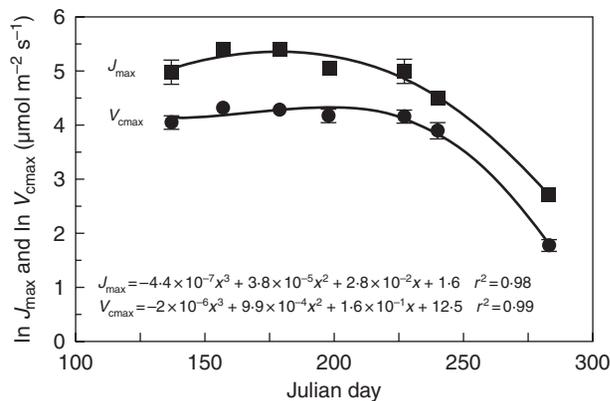


FIG. 1. Seasonal change in the log-transformed mean maximum electron transport rate (J_{max}) and the log-transformed mean maximum carboxylation rate (V_{cmax}) for five species of deciduous trees grown under optimal conditions. The solid lines are non-linear third-order polynomial regression curves fitted to the seasonal data set ($r^2 = 0.98$, J_{max} ; $r^2 = 0.99$, V_{cmax}), where the spread within a day is the natural log of species variation \pm s.e.

The equations and parameters of Granier and Loustau (1994) are followed to scale leaf stomatal conductance (g_s) and model the whole-tree conductance response to soil moisture, with the following changes: the mean value of soil moisture deficit was substituted for the leaf water potential (Schulze *et al.*, 1987) and photosynthetic photon flux density (PPFD) was substituted into the g_s equation, shown to be of primary importance in modelling the response of g_s (Massman and Kaufmann, 1991). The final form of the response model was:

$$g_s = k_1 \left[\frac{P_s}{P_s + k_r} \right] \left[\frac{1 - k_{d1} \delta q}{1 + k_{d2} \delta q} \right] [1 - k_{s1} \exp(k_{s2} \delta M)] \quad (1)$$

where k_1 , k_r , k_{d1} , k_{d2} , k_{s1} and k_{s2} are estimated parameters, P_s is the PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$), δq is the water vapour deficit (g kg^{-1}), and δM is the soil moisture deficit. Note that the parameters are not species-specific. Soil moisture deficit (δM) was estimated by

$$\delta M = (M_{\text{max}} - M) / (M_{\text{max}} - M_{\text{min}}) \quad (2)$$

where M_{max} , M_{min} and M are the maximum, minimum and actual root zone VWC for the specific soil (Cosh *et al.*, 2005). Other functions of the variables were tested (Ogink-Hendriks, 1995), but the estimates derived by Granier and Loustau (1994) gave the best fit (Table 1).

Transpiration of each sub-volume of the crown was calculated by applying an inverse form of the Penman–Monteith equation (Granier and Loustau 1994). A detailed description of how MAESTRA links transpiration of individual leaves to the whole crown and the subsequent leaf energy balance calculations can be found in Medlyn *et al.* (2007).

Meteorological data to drive MAESTRA were collected on a 15-min time step by a weather station at the site, linked to a CR10X data logger (Campbell Scientific) and the data together with soil moisture data were input into the drought response equation (eqn 2).

Stem and root parameterization

Seven times during the growing season (1 d before each harvest), total tree height (H_T), trunk diameter (D_T), trunk length and three-dimensional live crown size (x , y and z direction, in m) were measured. MAESTRA used the D_T and H_T data to interpolate incremental woody biomass across the season, where the total woody stem and root biomass are calculated from the general allometric relation

$$W_B = kH_T D_T^{\text{exp}} + W_I \quad (3)$$

TABLE 1. Estimates of the model parameters from Granier and Loustau (1994)

Parameter	Estimates	Units
k_1	0.02017	mm s^{-1}
k_r	497.791	W m^{-2}
k_{d1}	0.0360	kg g^{-1}
k_{d2}	0.389	kg g^{-1}
k_{s1}	0.0156	–
k_{s2}	4.269	–

where k , D^{exp} and W_1 are organ-specific parameters calculated from H_T and D_T and fine root biomass is assumed to be a constant fraction of total root biomass. To subtract carbon lost via respiration, individual organ respiration (R_o) was calculated on a 15-min time step from dry mass (DM), respiration rate at 25 °C and temperature:

$$R_o = R_{\text{mw}} \exp[Q_{10} (T_a - R_{\text{ot}})] W_B \quad (4)$$

where T_a is air temperature (°C), R_{ot} is organ temperature (°C), Q_{10} is the temperature response factor, and W_B is the woody biomass (kg) calculated from H_T and D_T . Respiration rates of organs from each species (R_{mw}) were calculated from the stem surface area:dry mass ratio according to Valentini *et al.* (1996). In addition, linear interpolation of leaf area development was applied. The online MAESTRA manual (<http://www.bio.mq.edu.au/maestra/>) provides greater detail.

Model simulations and functional group analysis

Net primary production (NPP) was estimated for each species every 15 min from 15 May 2006 to 15 October 2006. Output consisted of 15-min, hourly, and daily carbon and water exchange. Although our main focus was on the simulation of physiological processes between species and scaling up leaf behaviour to the whole plant, convergence in the response of the physiology of leaves was also investigated. Species were lumped into functional groups based on their physiological responses and the mean physiological parameters were calculated. Individual species' estimates were compared with that of the functional group. *Quercus* species were lumped as a potential functional group and *B. nigra* and *P. elongata* as a second functional group. On a physiological basis, *A. rubrum* was significantly different from the other species and/or functional groups and therefore was not included in the functional group analysis.

Validation tests

Estimates of carbon balance under well-watered and drought conditions from MAESTRA were compared with the independently observed values every 3 weeks. In addition, estimates of diurnal patterns of transpiration were compared with independent measured values.

Performance of the model was evaluated by comparing observed values with predicted values, where a paired sample *t*-test for differences in carbon exchange between (1) measured and modelled control 'well-watered' trees of each species, (2) measured and modelled water-stressed trees of each species, and (3) watered and water-stressed trees (treatment effect) at each harvest time was used to test the null hypothesis that the average of the differences between measured and modelled paired observations is zero at $\alpha = 0.05$ (SAS Institute, Cary, NC, USA). In addition, a *t*-test was performed to compare the organ-specific estimates versus measurements in carbon differences among species at the end of the season, again at $\alpha = 0.05$.

RESULTS

Testing the species response against a generalized seasonal response function for predicting leaf-level V_{cmax} and J_{max}

The seasonal trend in V_{cmax} and J_{max} rates was non-linear for all species (Fig. 1), and there were no differences between the responses between species when the log-transformed values were compared ($P = 0.99$; Fig. 1). In fact, a general seasonal pattern of J_{max} and V_{cmax} was observed for all species (Fig. 1) and was represented by a third-order polynomial with an $r^2 = 0.98$ and 0.99 for J_{max} and V_{cmax} , respectively (Fig. 1).

Impact of water stress on dry matter production and partitioning

Over the course of the season, dry matter production differed significantly between the irrigation treatments ($P < 0.05$; Fig. 2). After 17 d of irrigation deficit, carbon sequestration decreased by 20–48 % compared with the well-watered controls. Except for *A. rubrum*, dry matter accumulation over the season was on average 37–46 % less than well-watered values. *A. rubrum* produced more dry matter under water deficit than the other species, 71 % of the well-watered control. Dry matter allocation to organs differed among species; however, the general percentage of allocation to organs within a species was not significantly different across the season and in response to water stress. One notable exception was *A. rubrum*, where water stress caused fine root dry matter to increase by 46 % relative to the well-watered control.

Comparison between observed and simulated estimates of carbon exchange under well-watered and water stress conditions

Parameter values for species' seasonally variable and invariable physiology are given in Tables 2 and 3, respectively. Carbon sequestration was compared over 3 weeks of growth related to the destructive harvests. Figure 3 illustrates species-

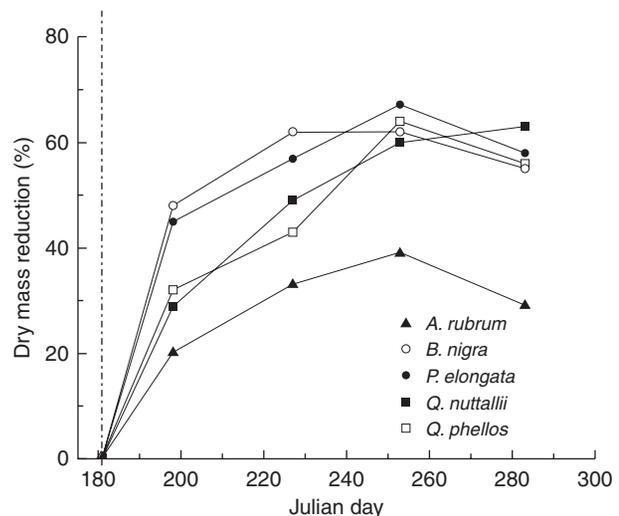


FIG. 2. Decrease in carbon sequestration by trees caused by drought treatment compared with the well-watered controls: *Acer rubrum*, *Betula nigra*, *Paulownia elongata*, *Quercus nuttallii* and *Q. phellos*, as indicated. The dashed line indicates the start of the drought treatment (Julian day 181).

TABLE 2. Control treatment seasonal variation in J_{max} maximum rate of electron transport ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and V_{cmax} maximum rate of Rubisco activity ($\mu\text{mol m}^{-2} \text{s}^{-1}$).

	Julian day						
	137	157	179	198	227	240	283
<i>Acer rubrum</i>							
J_{max}	186.3	257.8	192.8	192.3	154.0	85.0	13.6
V_{cmax}	62.4	75.4	72.6	62.3	66.1	57.5	5.2
<i>Betula nigra</i>							
J_{max}	223.8	244.8	342.3	201.5	245.5	131.2	11.4
V_{cmax}	69.5	87.6	74.7	86.5	97.7	76.2	4.3
<i>Paulownia elongata</i>							
J_{max}	215.0	301.5	262.0	181.5	245.8	91.9	13.8
V_{cmax}	71.5	78.6	88.7	65.1	77.2	46.0	5.9
<i>Quercus nuttallii</i>							
J_{max}	79.2	175.8	195.5	149.0	114.6	70.6	16.0
V_{cmax}	42.1	69.7	65.7	64.2	50.5	41.5	7.5
<i>Quercus phellos</i>							
J_{max}	96.2	165.8	160.0	119.0	123.1	75.8	22.1
V_{cmax}	45.9	66.2	63.9	47.7	51.2	42.1	7.2

specific measured and modelled NPP under both well-watered and drought conditions across the season. Comparisons were made between the carbon accumulated in the well-watered and drought treatments to indicate when a significant treatment effect was observed and the model predicted intra-seasonal NPP in well-watered and water-stressed deciduous tree species (Fig. 3). Validation of the carbon accumulation over the growing season showed that the model predicted carbon sequestration compared with measured values within 6 % for *A. rubrum*, 12 % for *B. nigra*, 8 % for *P. elongata*, 2 % for *Q. nuttallii* and 7 % for *Q. phellos* in the well-watered control treatment and within 2 % for *A. rubrum*, 9 % for *B. nigra*, 24 % for *P. elongata*, 13 % for *Q. nuttallii* and 25 % for *Q. phellos* in the drought treatment.

Although MAESTRA only calculates NPP for the whole tree, carbon partitioning averaged over the season was not significantly different from that during the season, and therefore seasonal averages of organ carbon allocation were used to partition the estimates of whole-tree NPP among organs. Figure 4 illustrates the organ-specific accumulation of carbon in control and drought trees, as compared with model estimates. In the well-watered control, the model predictions under-estimated carbon in leaves of *B. nigra* by 7 % and of *Q. phellos* by 20 % and over-estimated carbon in coarse roots of *Q. phellos* by 13 % and of *P. elongata* by 27%. Modelled estimates of fine root production were within 0.13 kg of actual accumulation of carbon in fine roots in all species and estimated carbon in stems was not significantly different from the measured data for *A. rubrum*, *B. nigra* and *Q. nuttallii*. The measured versus modelled carbon accumulated in organs under drought (Fig. 4) from seasonal NPP estimates over-estimated carbon in stems and leaves in *P. elongata* by 34 and 35 %, respectively, and carbon in stems of *Q. phellos* by 36 %. Carbon in fine roots and leaves in *A. rubrum* were also over-estimated by 24 and 25 %, respectively. However, model predictions of carbon accumulation compared with measured values showed no significant difference for other organs under drought stress.

TABLE 3. Organ-level photosynthetic and respiration parameters

Species	A_{net}	R_d	g_0	g_1	L_{comp}	L_{sat}	r_{Stem}	$r_{Coarse\ root}$	$r_{Fine\ root}$
<i>Acer rubrum</i>	16.2 ± 2.4 ^{CD}	3 ± 0.5 ^A	0.14 ± 0.0 ^A	1.7 ± 0.3 ^D	21.1 ± 4.2 ^{AB}	157.3 ± 20.4 ^A	44.4 ± 7.6 ^A	92.2 ± 12.2 ^{AB}	217.6 ± 31.8
<i>Betula nigra</i>	26.3 ± 3.5 ^A	3.1 ± 0.5 ^A	0.69 ± 0.1 ^B	2.5 ± 0.7 ^{CD}	11.7 ± 3.8 ^A	321.9 ± 41.8 ^{BC}	59.8 ± 13.9 ^A	65.1 ± 7.2 ^{AB}	215.7 ± 19.7 ^A
<i>Paulownia elongata</i>	19.9 ± 2.9 ^{BC}	3.5 ± 0.6 ^A	0.14 ± 0.0 ^A	5.8 ± 1.1 ^{AB}	29.2 ± 5.3 ^B	467.8 ± 34.7 ^C	46.7 ± 11.1 ^A	101.8 ± 13.7 ^{AB}	223.3 ± 38.9 ^{AB}
<i>Quercus nuttallii</i>	18.5 ± 1.7 ^{BC}	2.6 ± 0.4 ^A	0.15 ± 0.0 ^A	3.3 ± 0.9 ^{BC}	17.8 ± 4.6 ^{AB}	201.3 ± 21.9 ^{AB}	41.7 ± 4.1 ^A	80.1 ± 10.2 ^{AB}	135.9 ± 13.7 ^A
<i>Quercus phellos</i>	12.8 ± 1.4 ^D	2.7 ± 0.4 ^A	0.11 ± 0.0 ^A	2.4 ± 0.7 ^{CD}	16.1 ± 4.1 ^{AB}	192.0 ± 18.4 ^{AB}	48.2 ± 9.5 ^A	45.9 ± 4.3 ^{AB}	182.7 ± 25.5 ^{AB}

Average seasonal photosynthetic rate (A_{avg} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), dark respiration rate (R_d , $\mu\text{mol m}^{-2} \text{s}^{-1}$), minimum stomatal conductance (g_0 , $\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal opening slope coefficient (g_1), light compensation point (L_{comp} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), light saturation point (L_{sat} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), stem respiration rate (r_{Stem} , $\text{nmol g}^{-1} \text{s}^{-1}$), coarse root respiration rate ($r_{Coarse\ root}$, $\text{nmol g}^{-1} \text{s}^{-1}$) and fine root respiration rate ($r_{Fine\ root}$, $\text{nmol g}^{-1} \text{s}^{-1}$). Different letters within a parameter indicate differences among species ($P < 0.05$). Note: parameters were used to model both the control and drought treatment response.

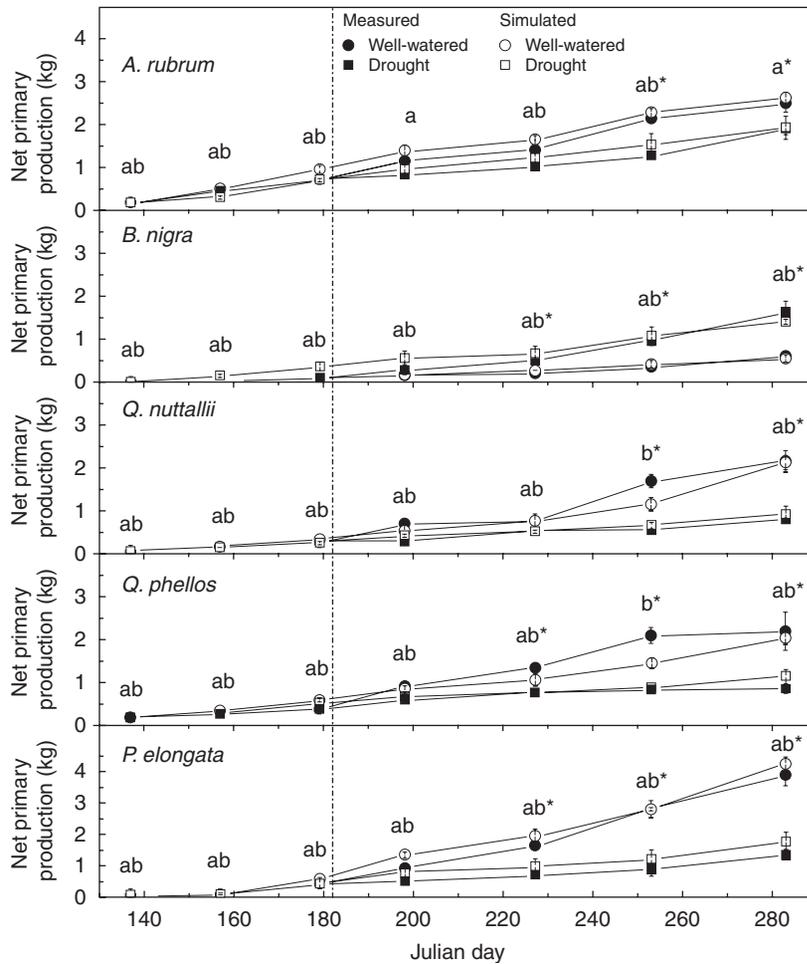


FIG. 3. Measured versus modelled net carbon accumulation throughout the study period. Solid symbols represent well-watered (circles) and drought treatment (squares) measured values and open symbols represent simulated well-watered (circles) and drought treatment (squares) net carbon accumulation. Data are the mean of three trees per harvest date \pm s.e. 'a', no significant difference between modelled and measured data in the well-watered treatment at $\alpha = 0.05$; b, no significant difference between modelled and measured data in the drought treatment at $\alpha = 0.05$; *, a significant treatment effect between measured data at $\alpha = 0.05$. The dashed line indicates the start of the drought treatment (Julian day 181).

Comparison between observed and simulated estimates of transpiration under well-watered and water stress conditions

Predictions of transpiration under well-watered conditions compared with measured values from sap flux during a representative diurnal time course (Julian day 212) are shown in Fig. 5A. *P. elongata* transpired approximately twice as much water as the other four species, 26.7 kg m^{-2} leaf area compared with $12.0\text{--}14.0 \text{ kg m}^{-2} \text{ week}^{-1}$. Figure 5B shows the differences in species' diurnal transpiration under irrigation deficit, which decreased water use for all species, compared with well-watered controls. The reduction in transpiration under water-stress conditions was species specific (cf. Fig. 5A vs. 5B). Differences among species were confirmed by independent measurements made with the sap flow system (data not shown). Species-specific transpiration decreases under irrigation deficit were 33% (*Q. nuttallii*), 43% (*A. rubrum*), 51% (*B. nigra*), 58% (*P. elongata*) and 79% (*Q. phellos*). Among all species, there was a 53% reduction in transpiration compared with well-watered controls. Although there was a good agreement between the seasonal evolution of transpiration and carbon exchange, an

approx. 35% reduction in total daily transpiration occurred in September as compared with July. The decrease corresponded with the decline in V_{cmax} and J_{max} toward the end of the season (Fig. 1).

Functional group predictions

Species differed physiologically (Tables 2 and 3). When *Quercus* sp. were grouped based on physiological characteristics of leaves, simulations under well-watered conditions over-estimated carbon exchange by 6% compared with separate estimates for *Q. phellos* and *Q. nuttallii*. In response to drought, *Quercus* sp. as a functional group under-estimated carbon exchange by approx. 7% compared with separate estimates. Estimates for the second functional group (*B. nigra* and *P. elongata*) were significantly different from those of the individual species, under-estimating carbon exchange by 13% as compared with *B. nigra* and *P. elongata* separately. With drought the discrepancy increased, with a 15% under-estimate.

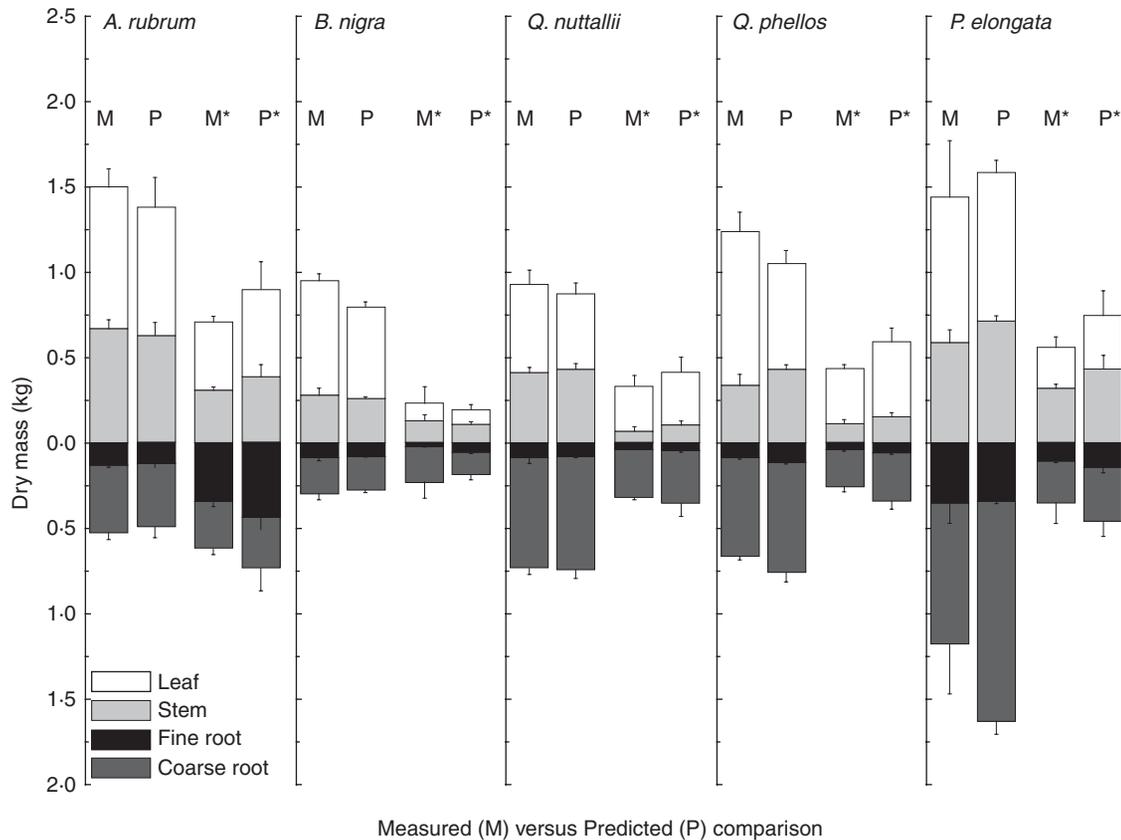


FIG. 4. Carbon accumulation in organs of well-watered and drought trees. Within a species, bars below the letter M and P represent measured and predicted data \pm s.e., respectively. Bars below M* and P* represent measured and predicted data in the drought treatment \pm s.e., respectively.

DISCUSSION

Typically, carbon dioxide exchange of temperate deciduous trees varies over the growing season as a result of changes in the biochemical parameters that influence photosynthetic capacity (Wilson *et al.*, 2001; Kosugi *et al.*, 2003; Ito *et al.*, 2006). The complexity of such changes and difficulties of measurement on the numerous species in forests has precluded analysis of the seasonal differences within and between species (Wilson *et al.*, 2001; Kosugi *et al.*, 2003). We found changes in biochemical parameters over the season consistent with other studies on deciduous trees and were able to test for differences between species. The seasonal change in biochemical parameters was not different between the species tested. The NPP measured and simulated in this study was adequately described with a seasonal trend in biochemical activity that was universal for the species. This finding allows simulation models to be simplified and so describe temporal trends in leaf physiological activity within heterogeneous, deciduous ecosystems. Furthermore, we agree with the conclusions of Wilson *et al.* (2001), Kosugi *et al.* (2003) and Ito *et al.* (2006) that it is critical to include the biochemical fluctuation in simulations of deciduous tree gas exchange.

Carbon exchange and transpiration estimates improved when parameters that characterized the seasonal change in biochemical parameters were used. To regulate g_s , the direct influence of photosynthetic capacity on transpiration was a consequence of the close relationship between g_s and photosynthesis

(Wong *et al.*, 1979). Describing the loss of capacity toward the end of the growing season further suggests that systematic model error can be circumvented if efforts are concentrated on improving the representation of vegetation parameters that are sensitive to seasonal changes. This finding has direct implications for efforts to improve global vegetation models that attempt to scale-up leaf-level carbon exchange and transpiration, in that global models do not usually account for adjustments of photosynthesis parameters (Thum *et al.*, 2008).

Similar to the changes in photosynthetic capacity over the season and the effects on carbon dioxide exchange, fluctuation in soil moisture plays an important role in regulating the carbon exchange rate between vegetation and the atmosphere. In fact, drought has been shown to be a major constraint of net carbon exchange of many species (e.g. Oren and Pataki, 2001), as well as a significant limitation to carbon sequestration in both natural and managed ecosystems (e.g. Granier *et al.*, 2006; Passioura, 2007). With regard to modelling a species' response to soil moisture deficit, studies using earlier versions of MAESTRA or similar process models applied to deciduous species have acknowledged the absence of a soil moisture response function (for a review see Hanson *et al.*, 2004). In fact, most process models (earlier versions of MAESTRA included – Medlyn *et al.*, 2005; Janssens *et al.*, 2005; Ibrom *et al.*, 2006) either assumed that soil moisture was non-limiting or did not account for the differences between species in stomatal regulation of carbon dioxide exchange rates in response

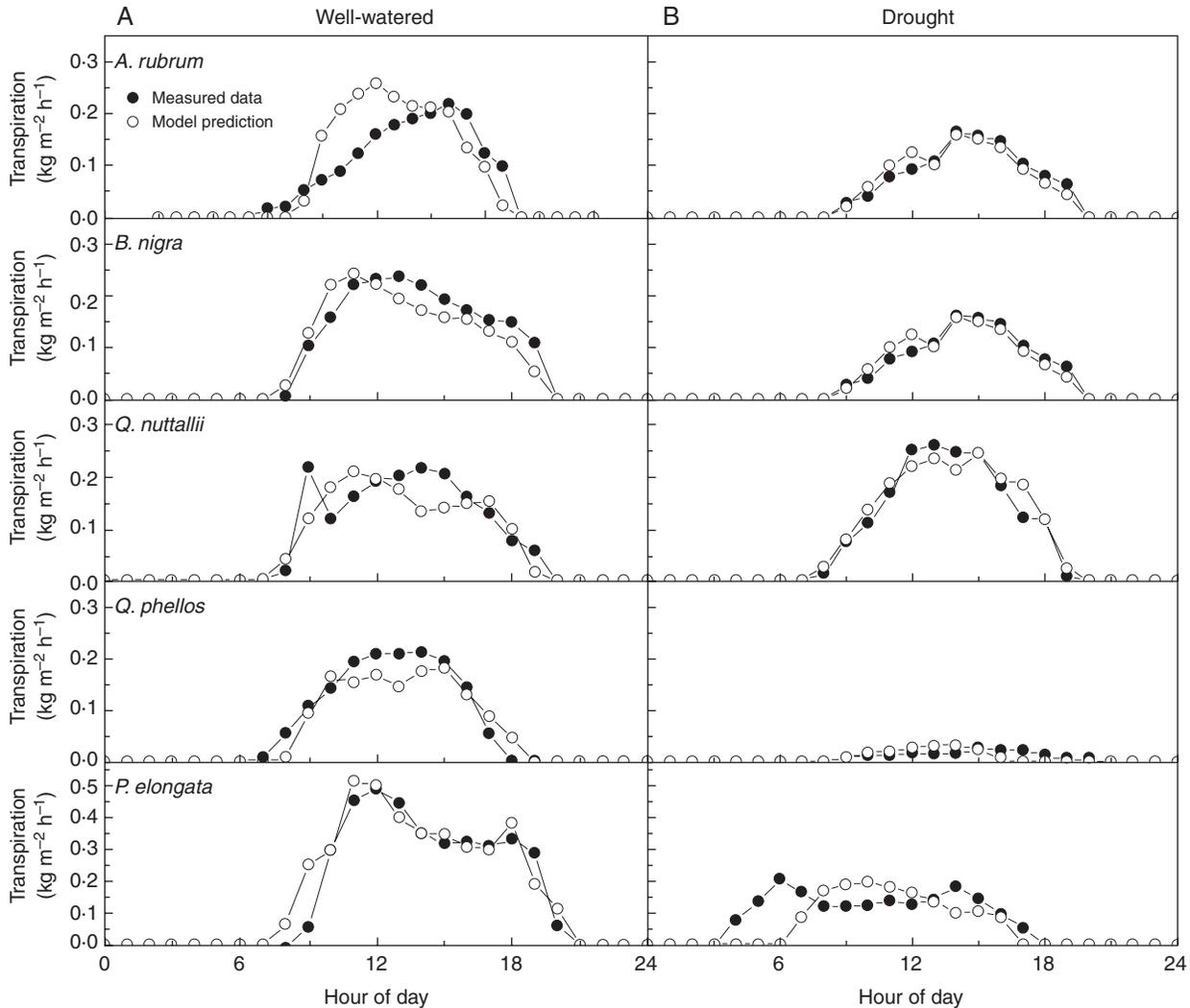


FIG. 5. Measured versus modelled sap flux of five species of deciduous trees during the day under well-watered (A) and drought stress (B) conditions. Data illustrate mean hourly transpiration during a representative diurnal period (Julian day 212).

to soil water deficits. Therefore, models have had a tendency to over-estimate carbon sequestration under water stress (Hanson *et al.*, 2004). In addition, most process models are inadequate in one or more other categories too; for example, they do not describe the contributions of individual species to net ecosystem carbon fluxes (e.g. Badeck *et al.*, 2001; Sinoquet *et al.*, 2001; Baldocchi *et al.*, 2002), do not allow physiological parameterization in space within canopies (Bauerle *et al.*, 2007) and are either not responsive to water stress (e.g. Sinoquet *et al.*, 2001; Hanson *et al.*, 2004) or fail to accurately quantify the soil moisture response among forest species (Wullschlegel *et al.*, 2001). The results of the present study are novel in that we were able to incorporate all of the above. Notably, the study showed that a version of MAESTRA incorporating response to soil moisture that can describe carbon exchange of complete plants of individual species can estimate carbon exchange under both well-watered and water-stressed conditions. The model is appropriate to study differences in carbon exchange among species and to estimate their carbon fluxes in response to water stress with a general soil moisture response sub-model,

which was originally developed to estimate the transpiration of a maritime pine forest (Granier and Loustou, 1994). Despite its origin, the model performed well on all of the deciduous species. However, future studies should investigate if it is also suited to other conifer and deciduous species.

Water stress can decrease NPP by a direct effect on photosynthetic capacity of the mesophyll or by a CO_2 limitation resulting from a decrease in stomatal aperture. Although the stomatal limitation brought about by a decrease in soil moisture was central to constrain both carbon exchange and transpiration under water stress, the discrepancy between measured and modelled values increased with water-stress severity. The parameters V_{cmax} and J_{max} might explain the discrepancy that NPP estimates became increasingly erratic and erroneous along a gradient toward severe water stress. Under these conditions, the parameter changes in V_{cmax} and J_{max} , however, primarily influenced carbon as opposed to transpiration predictions. This observation is in agreement with the physiological parameter sensitivity analysis reported in Bowden and Bauerle (2008). Regardless of water stress, however, the

importance of accounting for V_{cmax} and J_{max} over the course of the growing season was highest when the parameter values changed toward the end of the growing season.

Two gas exchange factors that are unaccounted for may explain the increased discrepancies in model estimates and measured plant water loss under irrigation deficit. First, we constructed our A_{net}/C_i curves under well-watered soil moisture conditions and a moderate VPD to minimize patchy stomatal closure caused by the onset of water (e.g. Downton *et al.*, 1988) and humidity stress (Cardon *et al.*, 1994). Patchy stomatal closure due to either stress could lead to an over-estimation of leaf internal CO_2 levels that would invalidate our calculated C_i values (e.g. Sharkey and Seemann, 1989; Terashima, 1992). Alternatively, cuticular properties may affect gas exchange (e.g. Boyer *et al.*, 1997). The present V_{cmax} and J_{max} calculations do not include cuticular attributes, which could result in a miscalculation of C_i if the diffusion properties of the cuticle differ from those in the stomata. Although the experimental protocol was not designed to permanently impair plant metabolism through prolonged and/or severe water stress, patchy stomatal closure and/or cuticular conductance may explain the increased separation in model estimates and actual plant water loss under water stress conditions.

The present study demonstrates that general biochemical parameters related to season and the response to soil moisture are important: when incorporated into a whole-tree model, they permit simulation of carbon exchange and transpiration for individual deciduous tree species. This conclusion builds on previous research using the MAESTRA model showing that the seasonal photosynthesis and transpiration parameters expressed intraseasonal changes (Bowden and Bauerle, 2008). The present study highlights the need to incorporate seasonal patterns in parameters that control carbon and water exchange, and provides a simple and general method to describe seasonal changes in biochemistry and response to soil moisture when simulating deciduous species carbon dioxide and water exchange.

CONCLUSIONS

Modelling the carbon and water balances of forests generally requires many parameters and a proficient means to incorporate the biochemical activity of species during the season, and the response to soil moisture is important for understanding such ecosystems. This study shows that the seasonal pattern of leaf biochemical activity and its response to soil moisture can be parameterized with straightforward general relationships. The MAESTRA model balances complex equations against simplifications that are acceptable and facilitate modeling of the carbon dioxide exchange of species at higher scales. To our knowledge, this is the first successful attempt at integrating a general seasonality and water stress approach to predict carbon exchange among species.

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