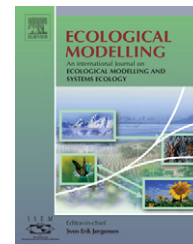




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Predicting the growth of deciduous tree species in response to water stress: FVS-BGC model parameterization, application, and evaluation

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ABSTRACT

An individual-tree, distance-independent forest stand projection model (FVS-BGC) was applied to study deciduous species response to water stress. FVS-BGC couples the process model STAND-BGC to the empirically based forest vegetation simulator (FVS). We sought to determine whether the hybrid model could be expanded to simulate deciduous trees and their response to water stress, where to date the model has not been used beyond coniferous trees. FVS-BGC was parameterized with comprehensive ecophysiological, site, and silvicultural data collected on *Acer rubrum* L. (*A. rubrum*), *Paulownia elongata* (*P. elongata*), *Quercus nuttallii* (*Q. nuttallii*), and *Quercus phellos* (*Q. phellos*). Species-specific carbon gain and growth were simulated under well-watered and water-stressed conditions. Simulations on species-specific bases allowed assessment of drought effects on stand production and the ability to test FVS-BGC's capability to predict the water stress responses of deciduous species. Under well-watered conditions, FVS-BGC height and caliper predictions were not statistically different from measured values for *P. elongata*, *Q. nuttallii* and *Q. phellos*. Under water stress, FVS-BGC accurately predicted height and caliper in *Q. nuttallii* and *Q. phellos*. For carbon sequestration, FVS-BGC predictions agreed with measured values on all study species under well-watered and water-stressed conditions. In general, the simulations showed that modelled height, caliper, and carbon sequestration were consistent with observed data. This study establishes the potential for FVS-BGC applications to include deciduous species-specific simulations and their respective water stress responses.

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1. Introduction

Traditionally, models of forest growth have been classified into two distinct categories: (1) empirical/statistical models, derived from observed relationships in large mensurational data sets that span management practices and site condi-

tions; and (2) process-based models founded on the explicit biochemical and biophysical mechanisms underlying tree growth. Each model type has its own advantages and shortcomings, a full description of which is beyond the scope of this article. Within the last decade, however, forest managers and tree physiologists have attempted to bridge the gap between

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the two tree growth modelling approaches (see, Valentine and Mäkelä, 2005 for a review) to create hybrid models that combine both modelling techniques (e.g., Baldwin et al., 1998; Milner et al., 2003; Valentine and Mäkelä, 2005).

Hundreds of empirical and process-based models have been developed to simulate tree growth (see, e.g., Constable and Friend, 2000; Le Roux et al., 2001; Kramer et al., 2002; Hanson et al., 2004 for model intercomparisons and assessment). However, a “standard model” with an accepted set of assumptions and trade-offs between practicality and detail has yet to be adopted (Valentine and Mäkelä, 2005). In this study, we have chosen to develop a hybrid model that couples the empirical model ‘Forest Vegetation Simulator’ (FVS) (Wyckoff et al., 1982; Dixon, 2002) to a version of the process model ‘FORESTBGC’ (Running and Coughlan, 1988; Running and Gower, 1991; White et al., 2000). ‘STAND-BGC’ (Milner and Coble, 1995) is a derivative of the stand-level physiological model FOREST-BGC, where STAND-BGC is an individual-tree, distance-independent forest stand projection model. Independently, both FVS and FOREST-BGC are described in detail elsewhere (FVS: Dixon, 2002; STAND-BGC: Milner and Coble, 1995) and available for download upon request: www.fs.fed.us/fmrc/fvs/FOREST-BGCdaac.ornl.gov/OTTER/guides/Runnings_Forest_BGC_Model.html.

Many of the models that attempt to study tree responses to climate change have been developed at the forest canopy scale (e.g., Halldin and Lindroth, 1986; Granier and Loustau, 1994; Poyatos et al., 2007). However, the majority of the models do not account for species-specific contributions to net ecosystem carbon fluxes (e.g., Sinoquet et al., 2001; Badeck et al., 2001; Baldocchi et al., 2002), even though it is known that eco-physiological traits influence species response to environment (Ben Haj Salah and Tardieu, 1997; Tardieu, 2003; Raymond et al., 2003). In fact, the effects of impending climate change on species survival will likely vary as species utilize different strategies within their environmental stress tolerance range (Davis and Shaw, 2001). To capture the variation in environmental drivers and subsequent biotic responses, an important attribute of models is their ability to predict the growth of a system as complex as a tree (e.g., Milner and Coble, 1995; Weinstein et al., 1991; Valentine et al., 1998; Baldwin et al., 1998; Landsberg, 2003; Bauerle et al., 2007).

Recently, Milner et al. (2003) linked FVS to STAND-BGC and named the resultant model ‘FVS-BGC’. In the coupled hybrid model, STAND-BGC is initialized from standard forest inventory records. Before tree information is passed from FVS to STAND-BGC, silvicultural treatments may be simulated with FVS. The linkage of the two models thus provides the user with the benefits of both model types, where the process and empirical elements are represented at the same hierarchical level—the linkage details are described in Milner et al. (2003). FVS-BGC operates at the tree level and can be parameterized on a species-specific basis. Theoretically, it is a useful tool for assessing the effects of climate change or alternative management practices on vegetation growth in forest ecosystems. In this study, we parameterize and apply FVS-BGC to deciduous tree species in an attempt to evaluate its ability to estimate tree growth characteristics under well-watered and water-stressed conditions. By so doing, we expand the use of

FVS-BGC to deciduous trees, for which FVS-BGC has not yet been parameterized or validated. The current work investigates the possibility of applying a hybrid model, responsive to water deficits in deciduous trees, with the intent of predicting their species specific response to environmental stress (i.e. drought). Specifically, the objectives of this study were to (1) parameterize and validate the hybrid model FVS-BGC on four common southeastern USA deciduous tree species: *Acer rubrum* L. (*A. rubrum*), *Paulownia elongata* (*P. elongata*), *Quercus phellos* (*Q. phellos*), and *Quercus nuttallii* (*Q. nuttallii*) and, (2) to assess its predictions against independent measurements of growth under well-watered and water-deficit conditions.

2. Materials and methods

2.1. Plant material and site attributes

In May of 2006, South Carolina grown *A. rubrum*, *P. elongata*, *Q. phellos* and *Q. nuttallii* ranging in height from 1.51 to 2.15 m were transferred to an outdoor gravel pad at Clemson University (Clemson, SC). Site attributes involved full sun exposure and a pressure-regulated micro-emitter irrigation system (ML Irrigation Inc., Laurens, SC). A full site description is provided in Bauerle et al. (2002). At the gravel pad, seedlings were transplanted into 57 L plastic containers containing a Fafard 2B substrate (Fafard Inc., Anderson, SC, USA) that incorporated 9 kg m^{-3} of Osmocote Pro[®] 19N-5P-8K (Scotts Company, Marysville, OH, USA). Although containers can induce root restrictions and limit resource availability, this was not a limitation in our study due to the tree size versus 57 L container ratio. Plants were randomly distributed throughout the plot and evenly spaced on a $1.5 \text{ m} \times 1.5 \text{ m}$ grid, initially watered to container capacity, and allowed to drain for 24 h. Pressure compensating 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 160 trees (ML Irrigation Inc., Laurens, SC).

Prior to experimentation, containers were covered with clear plastic sheeting to prevent precipitation recharge and the exterior of each container was wrapped with aluminum foil to reduce the radiation load. The plastic did not impede soil or root system gas exchange due to a loose seal at the stem interface and numerous air exchange openings on the side and bottom of the containers (Bauerle et al., 2002). Bulk soil volumetric water content (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 substrate surface. Readings were taken by inserting the probe into predrilled holes at two depths, and taking the average to estimate bulk VWC for each container (Bauerle et al., 2003). In all, 40 trees of each species were randomly distributed within the plot and VWC was monitored on each individual tree. Meteorological data (air temperature, humidity, wind speed, wind direction, and direct and diffuse solar radiation) were collected at a height of 3 m using a Campbell Scientific Weather Station located on the north side immediately adjacent to the experimental plot and within 0.25 m of canopy level.

2.2. Drought treatment

After monitoring trees under well-watered conditions for 45 d, a randomized drought treatment was applied. Per species, 20 replicate trees were randomly assigned to a drought treatment and 20 trees to a well-watered treatment. The 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 VWC in the drought treatment was $<0.3\text{ m}^3\text{ m}^{-3}$ and the well-watered treatment VWC remained $>0.3\text{ m}^3\text{ m}^{-3}$ (a predetermined value shown to not induce water stress). The VWC well-watered and water stress thresholds in our study were similar to those reported by Sinclair et al. (2005) in the woody perennial species of *Acer rubrum* L., *Hibiscus* sp., *Ilex aquifolium* L., *Thuja plicata* Donn ex D. Don, and *Robinia pseudoacacia* L.

2.3. Seasonal growth and gas-exchange measurements

At day 0 of the experiment (Julian day 138) and 1 day prior to each destructive harvest throughout the season (approximately 3 week intervals), tree height, crown width, stem length, stem caliper (10 cm above the first lateral root), and three dimensional live crown size (x, y, and z directions in m) were measured on all trees in the plot. Tree mensuration data, along with site parameters such as slope and aspect, were used as input to parameterize the model FVS-BGC. In addition, leaf transpiration and photosynthesis measurements were randomly taken on multiple leaves ($n=3-4$) of three replicate trees per species under well-watered conditions. The clonal nature of the plant material minimized variation among replicates. Gas exchange was measured on the first fully expanded and undamaged leaves using a portable steady state gas-exchange system (CIRAS-I, PP Systems, Haverhill, MA) equipped with a light and temperature controlled cuvette (Model PLC5 (B); PP Systems) from 09:00 to 12:30 h. The leaves were tagged and measurements were taken in random order to compensate for any effects caused by time of sampling. Additionally, all leaves measured were fully exposed to incoming radiation to reduce environmental interactions. Leaf temperature was controlled at 25 °C; Photosynthetic Photon Flux Density (PPFD) was maintained at $1000\ \mu\text{mol m}^{-2}\text{ s}^{-1}$ with the cuvette light source; and vapor pressure deficit in the cuvette

was kept at 1.3 ± 0.4 kPa. Measurements were recorded after reaching steady state. PP Systems Inc., CIRAS-I software calculated photosynthesis, respiration, and stomatal conductance values using the models of von Caemmerer and Farquhar (1981) and Ball et al. (1987).

2.4. Destructive harvests

Beginning at day 0 and at 3-week intervals thereafter, three trees of each species per treatment (24 total) were randomly selected and destructively harvested on a 3-week interval during the study (seven total harvests). The trees were separated into leaf, stem, coarse (root diameter: >3 mm) and fine roots (root diameter: 0–3 mm), and immediately measured for respiration on an organ basis with an SRC-1 chamber (PP Systems, Haverhill, MA) under temperature-controlled (25 °C) laboratory conditions. Leaf samples were stored in a walk in cooler and leaf area was measured with an LI-3100 leaf area meter (Li-Cor Inc., Lincoln, NE) within 4 days of harvest. Individual organs (leaves, stem, coarse roots, and fine roots) were then placed in paper bags, dried at 70 °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 canopy gap effects.

2.5. Model parameterization and application

A full description of FVS-BGC is provided in detail by Milner et al. (2003), where STAND-BGC functions as an extension of FVS. The STAND-BGC component of the hybrid model is a climate-driven, carbon and water balance model that operates at a daily resolution for growth processes and at an annual resolution for carbon allocation (Milner and Coble, 1995). FVS, as a single entity, has been empirically tested and used in the United States on coniferous species (Dixon, 2002). Different from the application of FVS as a stand-alone empirical model, we deployed a fully coupled hybrid version, where STAND-BGC is linked and periodically updates FVS with STAND-BGC calculations to mechanistically predict tree and forest stand growth dynamics (Milner et al., 2003). Moreover, the modelled trees in FVS-BGC were initialized by the FVS tree list at the beginning of the simulation, updated by STAND-BGC on a daily cycle, and updated by FVS at the beginning of each subsequent annual cycle. The linkage between these two models has been described in detail elsewhere

Table 1 – The physiological parameter values of the four species under well-watered conditions

Species	<i>A. rubrum</i>	<i>P. elongata</i>	<i>Q. phellos</i>	<i>Q. nuttallii</i>
Max. Leaf conductance	0.0040 ± 0.0002	0.0076 ± 0.0005	0.0031 ± 0.0004	0.0033 ± 0.0004
Stem respiration ($\mu\text{mol m}^{-2}\text{ s}^{-1}$)	0.0005 ± 0.00002	0.0015 ± 0.00004	0.0007 ± 0.00003	0.0017 ± 0.00006
Fine root respiration ($\mu\text{mol m}^{-2}\text{ s}^{-1}$)	0.0008 ± 0.000032	0.0010 ± 0.00004	0.0009 ± 0.00003	0.0042 ± 0.00007
Max. A_{net} rate ($\mu\text{mol m}^{-2}\text{ s}^{-1}$)	37.0 ± 1.9	46.0 ± 2.1	44.9 ± 2.4	40.7 ± 2.2
Optimum A_{net} temperature (°C)	30.0 ± 1.2	30.0 ± 1.9	30.0 ± 2.1	30.0 ± 2.5
Leaf area index (m^2)	4.0 ± 0.3	4.0 ± 0.5	1.4 ± 0.2	2.0 ± 0.3
Max. ratio of leaf C/(leaf + fine root)C	0.73	0.4	0.81	0.86
Specific leaf area (m^{-2}/Kg)	13.0 ± 1.3	36.0 ± 3.5	11.5 ± 2.1	11.3 ± 1.9

Values are means \pm standard deviation developed from field-based measurements of gas exchange, leaf area, and dry weights. Abbreviations: net photosynthesis (A_{net}), maximum (Max.).

Table 2 – The physiological parameter values of the four species under water-stress conditions

Species	<i>A. rubrum</i>	<i>P. elongata</i>	<i>Q. phellos</i>	<i>Q. nuttallii</i>
Max. Leaf conductance	0.0040 ± 0.0002	0.0076 ± 0.0005	0.0031 ± 0.0004	0.0033 ± 0.0004
Stem respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.0002 ± 0.00001	0.0004 ± 0.00002	0.0003 ± 0.00001	0.0002 ± 0.00001
Fine root respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.0003 ± 0.00002	0.0003 ± 0.00003	0.0004 ± 0.00002	0.0009 ± 0.00004
Max. A_{net} rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	37.0 ± 1.9	46.0 ± 2.1	44.9 ± 2.4	40.7 ± 2.2
Optimum A_{net} temperature ($^{\circ}\text{C}$)	30.0 ± 1.2	30.0 ± 1.9	30.0 ± 2.1	30.0 ± 2.5
Leaf area index (m^2)	3.4 ± 0.2	2.2 ± 0.4	1.4 ± 0.3	1.5 ± 0.4
Max. ratio of leaf C/(leaf + fine root)C	0.73	0.4	0.66	0.7
Specific leaf area ($\text{m}^{-2} \text{kg}^{-1}$)	14.82 ± 1.3	15.92 ± 1.9	10.48 ± 2.3	13.63 ± 2.7

Values are means ± standard deviation developed from field-based measurements of gas exchange, leaf area, and dry weights. Abbreviations: Net photosynthesis (A_{net}), Maximum (Max.).

(McMahan et al., 2002; Milner et al., 2003). We invoked FVS-BGC by a set of keywords, where three external files must be present to run the extension: (1) a daily climate file—MTCLIM (Hungerford et al., 1989), (2) a site file supplying information on soil depth and texture (Tables 1 and 2) and, (3) a BETA file supplying the physiological and control parameters (Table 3). The model simulated the growth and mortality of individual trees within a stand, using characteristics such as species, diameter, height, crown length, and relative size. Thus, key outputs were produced at the individual tree and stand level including: volume, density, species, diameter, height, annual increment, and crown length. Because of its internal structure, FVS-BGC has the ability to simulate mixed species, thus our application to several deciduous tree species in a mixed stand.

Using climate data as driving variables, the simulations were performed on a daily time step via input from MTCLIM, a climate simulator which extrapolates base station weather data to other sites. FVS-BGC uses the MTCLIM file format for weather data as described in McMahan et al. (2002). Since we collected our own on-site weather data, we were able to directly input our meteorological data into MTCLIM, where it only functioned as a weather data input file in this study.

The parameter values in the BETA tables are all measured from gas exchange or calculated from organ dry weights. Using the values we report in Tables 1–3, we simulated stands and each tree in the tree list on both a daily and annual basis. It is important to note that the model calculated and predicted daily whole tree height increments and dimension increments on a per tree basis, which allowed us to directly compare against our measured values. However, as documented by

McMahan et al. (2002), the FVS-BGC model will only function on trees with a minimum height of 1.37 m. Therefore, we only compared our estimates to measured values after a tree reached the threshold height, which was temporally variable among species and treatments. In addition, although the model calculates yearly increments of carbon allocation, our comparison only included growth after the minimum height was reached.

In summary, FVS-BGC output pertinent to this study was (1) tabular presentation of the annual and daily predictions of stand and tree-level carbon and water balance, and annual tree-level growth increments and, (2) the daily site water balance for each year of the simulation. The daily growth increments and daily carbon gain were the main focus of measurement versus comparison.

2.6. Statistical analysis

A paired sample t-test for each measured tree height, caliper, and carbon value 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 $\alpha = 0.05$.

3. Results

FVS-BGC predicts tree growth and carbon gain on a daily and annual basis, but we focused on the increase in daily tree height growth, caliper expansion, and carbon sequestration. Fig. 1 illustrates the prediction in height versus measured values among the four study species under both well-watered and water-stressed conditions and Fig. 2 illustrates the caliper comparison. In general, FVS-BGC height and caliper predictions were similar to measured values (Figs. 1 and 2). Under well-watered conditions, we found the most significant difference between the model estimate and measured values to occur within the species *Q. phellos*, where height and caliper measurements were significantly different ($p = 0.0024$; 0.0005 , respectively). In contrast to *Q. phellos*, the other three species in this study had similar measured versus modelled values as compared to within season observations (Figs. 1 and 2). Moreover, under well-watered conditions, mean seasonal differences between the estimates and measured values only ranged from 0.0076 to 0.0838 cm (Fig. 3).

In response to water stress conditions, we found no significant difference in height or caliper for *Q. nuttallii* and *Q.*

Table 3 – Summary of site file parameter values under well-watered and water-stressed conditions

	Well-watered	Water-stressed
Initial soil water content ($\text{m}^3 \text{ha}^{-1}$)	1692	1692
Soil depth (m)	0.36	0.36
Max. volumetric water content ($\text{m}^3 \text{m}^{-3}$)	0.46	0.14
Initial snowpack (m^3 of $\text{H}_2\text{O ha}^{-1}$)	0.0	0.0
Sand (%)	40.0	40.0
Silt (%)	40.0	40.0
Clay (%)	20.0	20.0

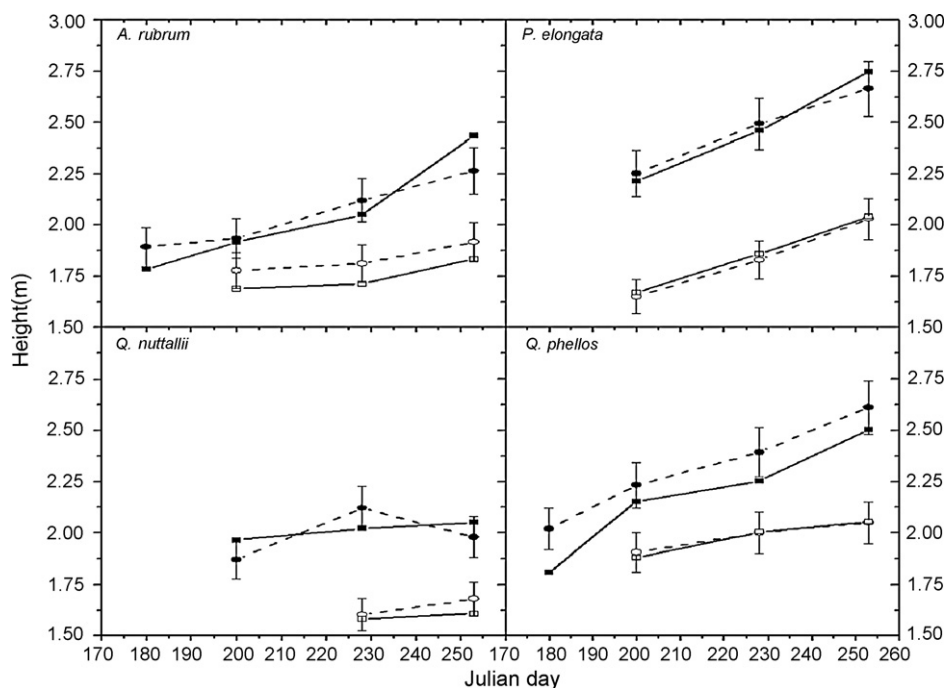


Fig. 1 – Comparison between predicted vs. measured height (m) for *A. rubrum*, *P. elongata*, *Q. nuttallii*, and *Q. phellos* under well-watered and water-stressed conditions. The solid line represents field-measured data and the dashed line depicts model estimates. Under well-watered conditions, solid squares (■) depict measured data, whereas solid circles (●) illustrate model estimates. Under water-stress conditions, open squares (□) depict measured data, whereas open circles (○) illustrate model estimates. Error bars represent standard errors.

phellos, with the mean difference between the modelled and field observations ranging from 0.0082 to 0.0838 for height and 0.0076 to 0.0457 for caliper. On the other hand, there was a significant difference (p -value = 0.0042) between the predicted *A. rubrum* versus measured height. However, Fig. 1 illustrates that the difference, although significant, is due to a consistent ~ 0.1 m over estimate of height. In addition, there was a significant difference in *A. rubrum* ($p = 0.0294$) and *P. elongata* (p -value 0.0189) predicted versus measured seasonal caliper means. *A. rubrum* and *P. elongata* measured versus modelled values within the season, however, were not substantially different (Fig. 2). In addition, regardless of species, the simulated caliper trajectory over the season was similar to observed values.

The carbon comparison resulted in no significant differences between measured and predicted values among any of the four study species over the course of the season. Surprisingly, *Q. phellos* had the smallest divergence from model estimates (0.1818 kg) under well-watered conditions. Under water stress conditions, *Q. phellos* simulation results were similar to those of well-watered conditions in that compared to other study species, *Q. phellos* had the second most similar modelled versus measured value.

Among species, physiological variation was present under both well-watered and water-stressed conditions (Tables 1 and 2). In addition, total leaf and specific leaf area were variable among species under both well-watered and water-stressed conditions (Tables 1 and 2). Interestingly, *Q. nuttallii* had the highest rate of fine root respiration under well-watered and water-stressed conditions. Under well-watered conditions, *P. elongata*'s maximum rate of leaf conductance to

water vapour was almost twice that of *A. rubrum*, the species with the second highest in the study. *P. elongata* also possessed the highest specific leaf area under both well-watered and water-stressed conditions (Tables 1 and 2). Under well-watered conditions, stem respiration was similar in *Q. nuttallii* and *P. elongata*, the two species with the highest respiration rates. However, in response to water stress, *P. elongata*'s stem respiration rate was 50–100% higher than the other study species.

In summary, there were altogether no significant differences under well-watered conditions for three species' height and caliper measured versus FVS-BGC model predictions: *A. rubrum*, *P. elongata*, and *Q. nuttallii*. For water-stress conditions, conversely, FVS-BGC accurately predicted both height and caliper in two of the four study species, namely *Q. nuttallii* and *Q. phellos*. It also accurately predicted the height of *P. elongata*. For carbon sequestration, FVS-BGC predictions were not significantly different from measured values on any of the four deciduous study species under either well-watered or water-stressed conditions. It should be noted that the substantial physiological variation among the four species resulted in very different response parameters, which allowed us to test the models ability to predict across a wide diversity of deciduous species.

4. Discussion

The last two decades have seen a proliferation of process-based forest growth models and there are many reviews available on various aspects of their use and associated prob-

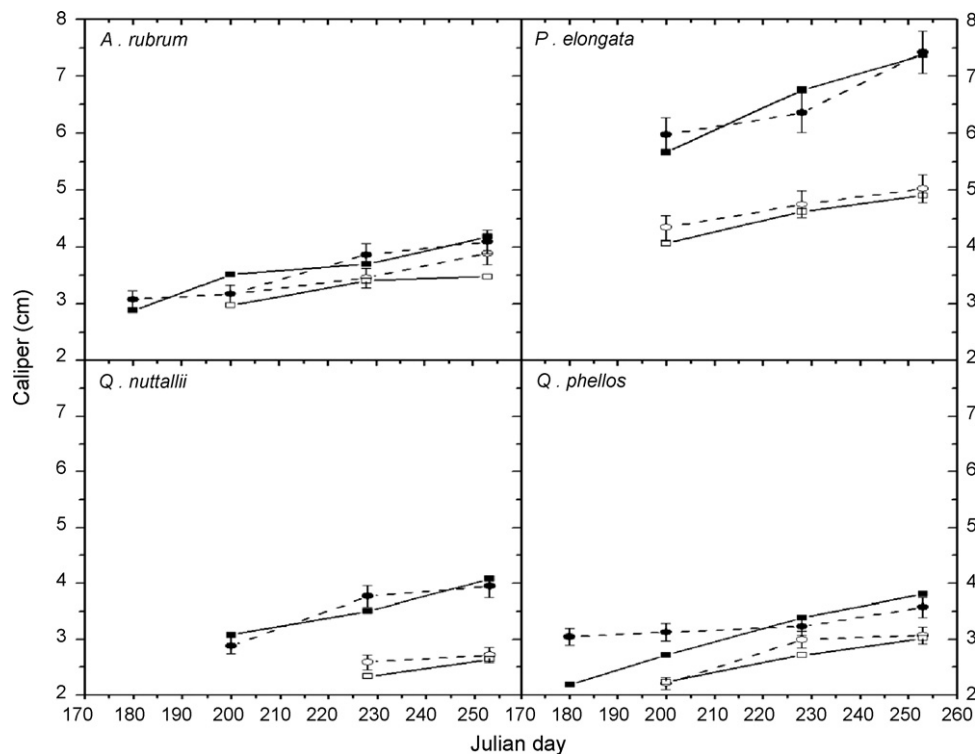


Fig. 2 – Comparison between predicted vs. measured caliper (cm) for *A. rubrum*, *P. elongata*, *Q. nuttallii*, and *Q. phellos* under well-watered and water-stressed conditions. The solid line represents field-measured data and the dashed line depicts model estimates. Under well-watered conditions, solid squares (■) depict measured data, whereas solid circles (●) illustrate model estimates. Under water-stress conditions, open squares (□) depict measured data, whereas open circles (○) illustrate model estimates. Error bars represent error.

lems (Agren, 1981; Dale et al., 1985; Ford and Bassow, 1989; Kimmins et al., 1990; Landsberg et al., 1991; Titak and van Grinsven, 1995). The prevalent perception is that process-based models are suited only to research and that silvicultural management questions are better matched to descriptive empirical models (Battaglia and Sands, 1998). That is, empirical models have been constructed from mensurational data and successfully applied to estimate variables of interest to silviculturalists, namely tree height, diameter at breast height (DBH), and total volume for identical and/or similar conditions (Zhou et al., 2005). Process-based models, on the other hand, are not as straightforward since the database required for model parameterization is usually more extensive and not always available to most forest managers. Moreover, the estimates are not in straightforward bole increment growth. Therefore, they primarily have been used as a research tool to estimate carbon and water flux in response to climate change.

This study parameterized, applied, and evaluated a hybrid model, FVS-BGC, in southeastern USA deciduous tree species under both well-watered and water-stressed conditions. In the last few decades, several factors have led to the coupling of process and empirical models, with tree physiologists and forest managers often working closely together to bridge the gap in an attempt to understand forest climate interactions. The cooperation has been spurred by changing environmental conditions that conflict with the need to maximize yield, while simultaneously minimizing the risk of long-term eco-

logically sustainable forest management practices (Dewar and McMurtrie, 1996). Moreover, predicting the influence of abiotic stress (e.g., Weinstein et al., 1991; Bauerle et al., 2007) and climate change impacts (e.g., Friend et al., 1993; Kirschbaum, 1994) on forest growth and survivorship are two key determinants of forest sustainability that can be addressed by models that possess both empirical and mechanistic attributes.

The model we use in this study, FVS-BGC, is a hybrid of both empirical and process-based approaches. As such, it can provide a dynamic means to analyze the impact of various climate scenarios on forest growth and yield (Milner et al., 2003). Unlike its predecessors FOREST-BGC (Running and Coughlan, 1988) and FVS (Wykoff et al., 1982), FVS-BGC simulates biogeochemical processes on individual trees and couples empirical data with mechanistic processes; hence it operates at a spatial scale that can be parameterized and validated at the individual tree-level. To be evaluated for its applicability to analyze the physiological response of trees and forest stands under different hypothesized climate and/or management scenarios, however, model validation must be done on the species for which one expects to forecast (Bauerle et al., 2007). Even though the structure, size, and longevity of trees presents a formidable challenge that can make model validation an arduous task, we were able to characterize a physiologically diverse set of deciduous tree species and effectively test the FVS-BGC model's predictive abilities within a mixed species stand under uniform environmental conditions. Due to the fact that

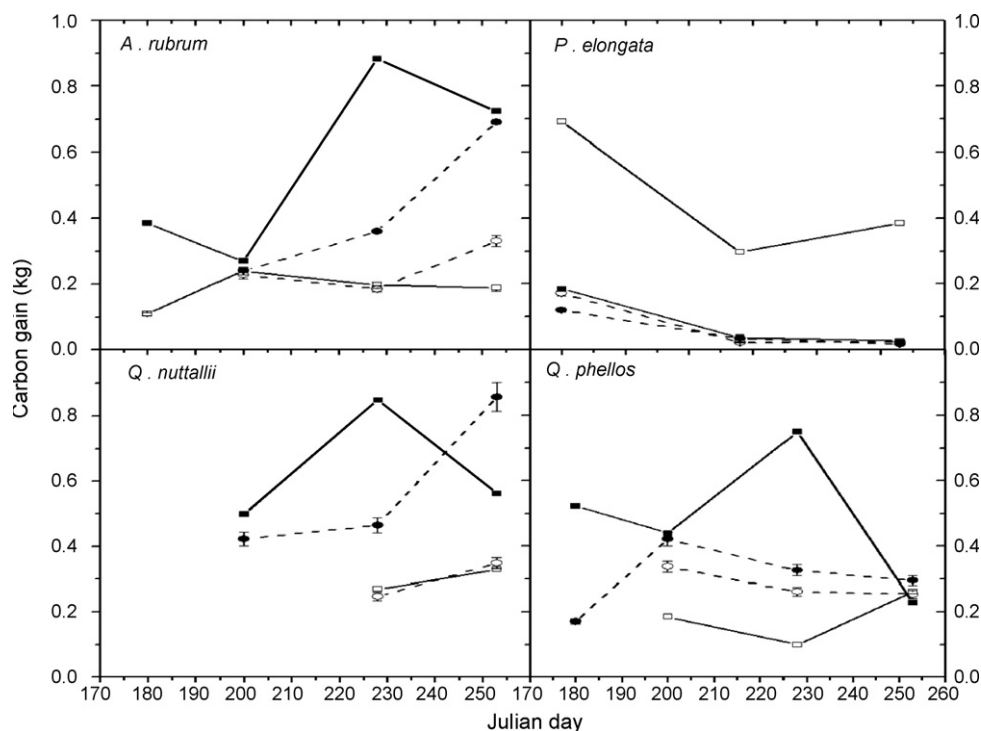


Fig. 3 – Comparison between predicted vs. measured carbon (kg) for *A. rubrum*, *P. elongata*, *Q. nuttallii*, and *Q. phellos* under well-watered and water-stressed conditions. The solid line represents field-measured data and the dashed line depicts model estimates. Under well-watered conditions, solid squares (■) depict measured data, whereas solid circles (●) illustrate model estimates. Under water-stress conditions, open squares (□) depict measured data, whereas open circles (○) illustrate model estimates. Error bars represent error.

FVS-BGC has characteristics that are informative to both forest managers and researchers alike, we sought to decipher its limitations on deciduous species and potentially broaden its applicability both spatially and temporally.

The overall structure of forest process models consists of spatial and temporal resolution, as well as complexity and generality. An increase in model resolution is often accompanied by an increase in model complexity; however, complexity is not always associated with accuracy or the ability to generalize a response (Battaglia and Sands, 1998). So, process modelers often try to advance the highest resolution with the least complexity, while at the same time, retaining the ability to generalize across forest ecosystems. Even though agreement between predicted and observed output does not necessarily verify the conceptual structure of a particular model (Passioura, 1973), we found the FVS-BGC model capable of predicting the dynamic response of deciduous trees, further supporting the model's generality via the transition from coniferous to deciduous tree species. Moreover, the input data for FVS-BGC is grounded in extensive silvicultural and ecophysiological research, so that potential users of the model are not required to establish values for most of the coefficients (although they are user definable). The output (the carbon/water balance, dimensions, and growth increment on a daily and annual time step) is useful to both researchers and forest managers alike. Therefore, the combination of relatively low model complexity, good agreement between measured and estimated values, and broad species functionality make

FVS-BGC an effective forest hybrid model with potentially high applicability for both forest managers and researchers.

Soil water deficits are a key controller of net ecosystem productivity in deciduous trees and it has been reported that water availability controls net ecosystem productivity in 64% of all deciduous broadleaf tree growth area (Churkina and Running, 1998). While FVS-BGC has not been tested previously in response to controlled soil water deficits, we examined FVS-BGC under water stressed conditions to get an idea of the influence of soil water stress on model estimates. With respect to carbon sequestration, height, and growth estimates, we observed that FVS-BGC is responsive to soil water deficits. In fact, the model worked very well in predicting the carbon accumulation in all four study species (*A. rubrum*, *P. elongata*, *Q. nuttallii*, and *Q. phellos*). However, there were a few instances where FVS-BGC estimates of the height and/or caliper were inadequate, namely for *A. rubrum* and *P. elongata*. One possible explanation for the discrepancy could be due to the adopted stress condition classification. When the maximum volumetric water content is changed in the model, a drastic response ensues. The resultant response indicates that this parameter plays a substantial role in appropriate parameterization of FVS-BGC under water-limiting conditions. In addition, the available soil water fraction threshold contributed to the water deficit response. Our threshold values are comparable to those reported by Sadras and Milroy (1996) and Sinclair et al. (2005) and resulted in a similar pattern of response to soil drying. However, threshold values may differ among soil types

(Sinclair et al., 1998). Therefore, we recommend future studies derive a set of species-based maximum volumetric water content parameters that have been tested under conditions that bracket those for which one will forecast.

To our knowledge, FVS-BGC has never been validated on deciduous tree species. In fact, prior to this study FVS-BGC was used primarily on 11 species, all of which are conifers. Moreover, validation has only occurred in eight western USA FVS variants. We parameterized, applied, and evaluated FVS-BGC's ability to operate on four common southeastern USA deciduous tree species. In so doing, our findings show that the hybrid model FVS-BGC can be used to predict the diameter, height and carbon increment for *Q. nuttallii* and *Q. phellos* under water stressed conditions. It can also predict height, diameter, and carbon increment on the species of *Q. nuttallii* both under well-watered and drought-stress conditions. Additionally, FVS-BGC can predict height and diameters for the species *A. rubrum*, *P. elongata*, and *Q. nuttallii*. In general the model worked well, however, accuracy varied on a species-specific and stress condition basis. Although we found that the integration of FVS and STAND-BGC into a linked hybrid model is dynamic and inclusive enough to capture the influence of environment on deciduous species stand productivity, we strongly recommend that validation occur on a species and stress condition basis before forecast estimates can be deemed reliable. In conclusion, our results indicate that the model is useful beyond conifers and further model calibration and opportunities for improving deciduous tree prediction accuracy are warranted.

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