

Predicting yields of short-rotation hybrid poplar (*Populus* spp.) for the United States through model–data synthesis

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Abstract. Hybrid poplar (*Populus* spp.) is an important biomass crop being evaluated for cellulosic ethanol production. Predictions of poplar growth, rotation period, and soil carbon sequestration under various growing conditions, soils, and climates are critical for farmers and managers planning to establish short-rotation forestry (SRF) plantations. In this study, we used an ecoinformatics workflow, the Predictive Ecosystem Analyzer (PEcAn), to integrate literature data and field measurements into the Ecosystem Demography 2 (ED2) model to estimate yield potential of poplar plantations. Within PEcAn 164 records of seven different traits from the literature were assimilated using a Bayesian meta-analysis. Next, variance decomposition identified seven variables for further constraint that contributed >80% to the uncertainty in modeled yields: growth respiration, dark respiration, quantum efficiency, mortality coefficient, water conductance, fine-root allocation, and root turnover rate. Assimilation of observed yields further constrained uncertainty in model parameters (especially dark respiration and root turnover rate) and biomass estimates. Additional measurements of growth respiration, mortality, water conductance, and quantum efficiency would provide the most efficient path toward further constraint of modeled yields.

Modeled validation demonstrated that ED2 successfully captured the interannual and spatial variability of poplar yield observed at nine independent sites. Site-level analyses were conducted to estimate the effect of land use change to SRF poplar on soil C sequestration compared to alternate land uses. These suggest that poplar plantations became a C sink within 18 years of conversion from corn production or existing forest. Finally, poplar yields were estimated for the contiguous United States at a half degree resolution in order to determine potential productivity, estimate the optimal rotation period, and compare poplar to perennial grass yields. This regional projection suggests that poplar yield varies considerably with differences in soil and climate, reaching as much as 18 Mg·ha⁻¹·yr⁻¹ in eastern, southern, and northwest regions. In New England, the upper Midwest, and northern California, yields are predicted to exceed those of the highly productive C₄ perennial grass, *Miscanthus*. In these poplar-productive regions, 4–11 year rotations give the highest potential yields. In conclusion, poplar plantations are predicted to have a high yield potential across a wide range of climates and soils and could be sustainable in soil C sequestration.

Key words: Bayesian meta-analysis; data assimilation; Ecosystem Demography model; poplar plantation; *Populus* spp.; Predictive Ecosystem Analyzer; sensitivity analysis; short-rotation forestry; soil carbon; variance decomposition.

INTRODUCTION

Climate change and energy security have driven renewable energy production to the top of global agendas (Karp and Shield 2008). Renewable energy sources will play a key role in meeting CO₂ emission reduction objectives, given that renewable sources of energy have low net CO₂ emissions when substituted for fossil fuels (Khesghi et al. 2000). In the United States the Advanced Energy Initiative (AEI) mandates that renewable bioethanol displace 30% of 2005 petroleum use in the transportation sector by 2030 (Milliken et al.

2007). Corn ethanol is currently the major source of fuel ethanol in the United States. However, due to the competition with food supply, high resource demand, and greenhouse gas (GHG) emissions, the AEI supports the production of ethanol from cellulose and hemicellulose from perennial grasses, wood chips, and agricultural residues (Heaton et al. 2008, Somerville et al. 2010, Wang et al. 2010, 2012).

The cultivation of fast-growing woody plants within short-rotation forestry (SRF) can provide a potentially important source of alternative and renewable energy. Compared to annual crops, woody species grown in a SRF have higher energy densities, lower transportation costs, and reduced needs for annual inputs; these factors minimize the utilization of fossil fuels during production and thus improve the overall energy balance of the fuel

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(Hill et al. 2006). Compared to conventional agriculture, SRF can have a positive impact on biodiversity, nutrient retention, and soil protection from wind and water erosion (Isebrands and Karnosky 2001).

Hybrid poplars are among the most widely cultivated hardwood species, and many factors make them top candidates for sustainable biofuel production. Traits that make these species strong candidates include their fast growth, high light-use efficiency, photosynthetic capacity, ease of vegetative propagation, and adaptation to a wide variety of soils (Mead 2005). Furthermore, interspecific hybridization within this genus has facilitated the development of highly productive hybrid genotypes (Ceulemans and Isebrands 1996, Bradshaw et al. 2000, Dickman et al. 2001).

Poplar yields vary considerably and are affected by the influence of genetics, climate, and management on survival, competition, and vigor of the stand (Mead 2005). Harvestable yields of poplar in temperate regions of Europe and North America range between 10 and 15 Mg·ha⁻¹·yr⁻¹ (Kauter et al. 2003, Lewandowski et al. 2006, Van de Walle et al. 2007). Rotations shorter than three years lead to reduced yields after several rotations due to physiological problems including stump aging and depletion of carbohydrate reserves (Auclair and Bouvarel 1992), and maximum biomass productivity is expected with harvest cycles of three to 11 years (Sartori and Lal 2006). In the present study, we predict yield potentials and the rotation times that maximize these yields of poplar for regions within the coterminous United States and suggest rotation times under different soil properties and climate conditions.

Although aboveground woody biomass is the economically important component of SRF ecosystems, enhanced carbon sequestration in roots and soil has a large impact on the net carbon balance. This carbon sequestration is important for CO₂ mitigation, and the ecological benefits of SRF are likely to acquire economic value in the future (Calfapietra et al. 2010). Growing public awareness and the discussion of sustainability criteria of biofuel production require the assessment of the environmental consequences of intensively grown biomass from SRF on soil carbon sequestration and other ecosystem services. Soils are the largest terrestrial pool of carbon (C), accounting for ~80% of all C stored on land (Lal 2004, Sartori and Lal 2006). SRF can rapidly accumulate C in stable components such as stems, branches, and coarse roots, while at the same time cycling C and nutrients to the soil through more labile litter pools consisting of leaves, twigs, and fine roots (Meiresonne et al. 2006, Sartori and Lal 2006). Observed patterns of soil organic carbon (SOC) dynamics under SRF include short-term losses (Hansen 1993), long-term gains (Hansen 1993, Makeshin 1994), and no changes (Ulzen-Appiah et al. 2000). Historical land use changes and conversion of forest to large-scale agriculture has led to increased atmospheric CO₂ (Fargione et al. 2008). Converting some of this land to

SRF could restore or improve on the soil C storage of historically forested ecosystems (Trumbore 1997).

As growth and yield data for poplar become increasingly available for varying soil and climatic conditions across the United States, farmers and foresters planning to establish SRF systems will be able to make better management decisions. However, data on the growth, yield, and ecosystem impacts of hybrid poplar are still sparse. In this study we predict hybrid poplar yield and rotation period at a national scale under varying growing conditions using the Ecosystem Demography model (version 2.1, hereafter ED2). The specific objectives of the present study are to (1) parameterize ED2 for predicting the potential yield of hybrid poplar for the United States; (2) compare model performance to observations from field trials; (3) suggest guidelines for coppice frequency to optimize poplar yield in SRF; (4) compare the bioenergy potential of poplar to the high-yielding perennial grass *Miscanthus*; and (5) estimate the effect of land use change to SRF poplar on soil C sequestration compared to alternate land uses.

METHODS

Model description

The Ecosystem Demography model (ED2) is a mechanistic terrestrial biosphere model that includes an efficient and sophisticated scaling of forest dynamics from individual trees to landscapes (Moorcroft et al. 2001, Medvigy et al. 2009). Plant growth in ED2 uses established models of leaf-level physiology (Farquhar et al. 1980, Leuning 1995), allocation (Saldarriaga et al. 1988), biogeochemistry (Parton et al. 1988, 1993), land surface biophysics (Walko et al. 2000), and hydrology (Sellers 1992). ED has previously been used to simulate regional carbon fluxes (Desai et al. 2007, Medvigy and Moorcroft 2012), the magnitude of the eastern U.S. carbon sink (Hurt et al. 2004, Albani et al. 2006), and the net ecosystem productivity of the Amazon basin (Moorcroft et al. 2001). These simulations indicate that ED can accurately predict the different C pools in mixed forests under both current and future climate conditions and under different land use scenarios. Unlike other mechanistic models that simulate individual growth of poplar and the resulting responses to environmental stress, such as ECOPHYS (Rauscher et al. 1990), SOILN-FOREST (Eckersten and Slapokas 1990), and SECRETS (Host and Isebrands 1997), ED predicts transient carbon, water, and energy fluxes resulting from both exogenous and endogenous drivers. Exogenous drivers include abiotic variations in the physical landscape and climate, while endogenous drivers include biotic processes such as tree mortality and disturbance processes. Thus, ED provides information about biogeochemical as well as demographic processes. This feature enables ED to not only predict poplar yield, but also the effects of land use transitions to poplar SRF and the subsequent impacts on the water carbon cycling,

TABLE 1. Location and management information at nine sites in the United States used for model calibration and evaluation.

Sites	Latitude, longitude (°)	Species	Clones
Rhineland, Wisconsin	45.5 N, 89.5 W	hybrid poplar	NE-41, NE-386
New Franklin, Missouri	39.0 N, 92.5 W	<i>P. deltoides</i> × <i>P. nigra</i> <i>P. deltoides</i> × <i>P. nigra</i> <i>P. deltoides</i> <i>P. deltoides</i> <i>P. deltoides</i>	145/51, Eugeneii, 26C6R51, 2059, 1112
Olympia, Washington	47.0 N, 122.9 W	<i>P. trichocarpa</i> Torr. & Gray × <i>P. deltoides</i> Bartr. ex Marsh, <i>P. trichocarpa</i>	11–11, 47–174, 49–177, CL
Sioux Falls, South Dakota	43.5 N, 96.5 W	hybrid poplar	DN17, DN34, DN182
Mondovi, Wisconsin	44.5 N, 91.5 W	hybrid poplar	DN17, DN34, DN182
Granite Falls, Minnesota	44.4 N, 95.7 W	hybrid poplar	DN17, DN34, DN182
Fargo, North Dakota	46.5 N, 96.5 W	hybrid poplar	DN17, DN34, DN182
Escanaba, Michigan	45.5 N, 87 W	<i>P. deltoides</i> × <i>P. nigra</i> <i>P. euramericana</i> <i>P. nigra</i> × <i>P. maximowiczii</i> <i>P. tremula</i> × <i>P. tremuloides</i>	Ne–222, DN-5, DN-34, NM6
Aiken, South Carolina	33.5 N, 93.5 W	<i>P. deltoides</i> , hybrid poplar	18 clones

and mass and energy exchanges between the atmosphere and biosphere.

Because the sub-models in ED have been extensively described elsewhere (Moorcroft et al. 2001, Medvigy et al. 2009), the following description focuses on parameters relevant to the present analysis. The ecophysiological sub-model employs the coupled photosynthesis and stomatal conductance schemes developed by Farquhar and Sharkey (1982) and Leuning (1995) respectively, in which leaf-level fluxes of carbon and water are constrained by the maximum carboxylation rate ($V_{c,max}$, at 15°C), quantum efficiency, leaf dark respiration (R_d), and the slope parameter (stomatal slope) in the relationship between stomatal conductance and photosynthesis, vapor pressure deficit, and CO₂ concentration from the Leuning model. Specific leaf area (SLA) has units of leaf area per unit leaf carbon and is used to convert plant investment in foliar biomass to gains in leaf area. While stomatal conductance and leaf area are the dominant controls on water loss via evapotranspiration, the water conductance parameter moderates root water uptake as a function of soil moisture, root morphology, root system topology, and fine-root biomass (Nardini et al. 1998, Jackson et al. 2010). Growth respiration is assumed to be a constant proportion to net photosynthesis and this relationship is controlled by the growth respiration factor. Maintenance respiration is proportional to biomass growth in the leaf, stem, and root pools, respectively. Empirical allometric curves (Ter-Mikaelian and Korzukhin 1997), in conjunction with the prescribed rates of leaf and fine-root turnover, determine the size-specific pattern of carbon and nitrogen allocation between different biomass compartments (Moorcroft et al. 2001). Fine-root biomass is controlled by a constant biomass ratio between fine roots and leaves. Tree mortality is calculated as the sum of a density-independent mortality

rate, frost mortality, losses to disturbance, and a density-dependent mortality rate. The density-dependent term is calculated as a negative exponential function of a plant's current carbon balance and is controlled by the mortality coefficient rate parameter (Desai et al. 2007). Forest harvesting in ED2 is treated as a removal of the aboveground stem biomass, with roots and leaves entering the litter pool.

Model parameterization and calibration

To explicitly integrate data obtained from experimental and/or observational studies into ED2, we employed the Predictive Ecosystem Analyzer (PEcAn 1.1) scientific workflow (LeBauer et al. 2013). A virtual machine version of PEcAn with all of the data, model inputs, and code required to reproduce the present analysis is *available online*.⁴ The first step in the workflow synthesizes trait data from the literature using a Bayesian meta-analytical model. Meta-analysis priors were specified by fitting distributions to raw data collected from literature searches, unpublished data sets, or from expert knowledge on temperate hardwood trees using the techniques described by LeBauer et al. (2013). Trait data were collected from a systematic survey of the literature on *Populus* species. Peer-reviewed journal articles published before the end of 2011 were obtained by searching the Science Citation Index (SCI) of the Institute of Scientific Information using “poplar” or “Populus” and the targeted trait as key words; relevant citations within these publications were also considered. Trait data are presented in the Appendix and are made available in the PEcAn virtual machine. Trait data were also entered into the Biofuel Ecophysiological Traits and Yield Database (BETY-

⁴ <http://hdl.handle.net/2142/34619>

TABLE 1. Extended.

Spacing (m)	Growing period	References
$0.5 \times 1, 1 \times 1,$ 1×1.5	1981–1988	Strong and Hansen (1993)
1×1	2000–2005	Dowell et al. (2009)
$0.5 \times 0.5, 1 \times 1,$ 1.5×1.5	1990–1992	DeBell and Harrington (1997)
2.4×2.4	1987–1996	Netzer et al. (2002)
2.4×2.4	1987–1997	Netzer et al. (2002)
2.4×2.4	1987–1997	Netzer et al. (2002)
2.4×2.4	1988–1996	Netzer et al. (2002)
2.5×2.5	1999–2007	Miller and Bender (2008)
2.5×2.5	2001–2004	Coyle et al. (2006)

db). A description of BETY-db can be found in LeBauer et al. (2013).

The meta-analysis model was fit in JAGS (version 2.2.0; Plummer [2010]) using standard Markov chain Monte Carlo (MCMC) methods with four parallel chains of length 10^5 . The beginning half of each chain was discarded as “burn-in” of the chains. Trace plots and Gelman-Rubin’s statistic were used to assess model convergence (Gelman and Rubin 1992). The resulting posterior distributions of plant trait values were then sampled to generate an ensemble of 1000 model runs for our calibration site (Rhineland, Wisconsin; Table 1). This ensemble is then used to estimate the predicted mean yield and CI.

At the second step, a sensitivity analysis was conducted in PEcAn by running ED2 across a range of parameters of interests for the Rhineland site in order to determine how much a change in a model parameter affects model output. In the sensitivity analysis, the model was evaluated for each parameter at the median and at six posterior quantiles equivalent to $\pm[1,2,3]\sigma$ in the standard normal while the other parameters are held at their median. The relationship between model output (f , aboveground biomass, AGB) and each model parameter (ϕ_i) was approximated by a natural spline $g_i(\phi_i)$ through these seven model runs. The derivative of the spline at the posterior median is taken as the model sensitivity to each parameter and the elasticity is the sensitivity normalized by the ratio of median model output to mean parameter value:

$$\text{elasticity} = \frac{dg_i}{d\phi_i} \bigg/ \frac{\bar{f}}{\bar{\phi}} \quad (1)$$

where \bar{f} is the median of the model output, and $\bar{\phi}$ is the median of a parameter.

Our third step in the PEcAn workflow was a variance decomposition analysis, which uses results from the

meta-analysis and sensitivity analysis to estimate the contribution of each parameter to uncertainty in poplar yield from the model ensemble. Using a first-order approximation the decomposition of the total variance in modeled AGB is:

$$\text{Var}(f(\Phi)) \approx \sum_{i=1}^n \text{Var}(g_i(\phi_i)) + \bar{\omega} \quad (2)$$

where $\text{Var}(f(\Phi))$ is the total variance of the ensemble runs, and $g_i(\phi_i)$ is the spline approximation of model response f to each parameter ϕ_i from the sensitivity analysis. $\text{Var}(g_i(\phi_i))$ is the partial variance contribution of each parameter i , generated by evaluating g_i for samples from the meta-analysis posterior of ϕ_i . The closure term, $\bar{\omega}$, represents parameter interactions that are not accounted for in the first-order variance decomposition. The proportional contribution of each parameter (ϕ_i) to the total variance was calculated by dividing its partial variance by the total variance. A full description of this variance decomposition analysis is given by LeBauer et al. (2013).

In our final calibration step, we used data assimilation to further constrain model parameters and yield estimates. PEcAn’s data assimilation module is a Bayesian approach to model calibration (M. C. Dietze, P. Moorcroft, and A. Richardson, *unpublished manuscript*). The yield data being assimilated come from a field trial of two poplar clones at three densities established in 1981 in Rhineland, Wisconsin and grown without irrigation. Based on the variance decomposition we restricted this analysis to six variables including growth respiration, dark respiration rate, quantum efficiency, water conductance, fine-root allocation, and root turnover rate, which accounted for >80% of the model ensemble variance and had relatively high elasticity. The combined set of runs from the ensemble analysis and the sensitivity analysis were used as the design space for this analysis. Model-data mismatch was calculated for each of these runs assuming a Normal likelihood and meta-analysis posteriors as priors. A Gaussian process (GP) model, an anisotropic multivariate generalization of the Kriging model, was employed as an emulator to interpolate the log of the Normal likelihood in parameter space. The final data assimilation posteriors were estimated by applying MCMC methods to the normalized posteriors probability surface. Variance decomposition analysis was also performed on the data assimilation posteriors.

Model validation

To validate ED2, modeled yield was compared to yields reported in eight independent field trials conducted in diverse ecoregions of the United States (Table 1). Each trial included between three and 18 clones and between one and three planting densities; thus, the model was compared to a total of 57 growth time series. Hourly temperature, humidity, radiation, precipitation,

wind, and atmospheric pressure drivers for each site were derived from the North American Regional Reanalysis database (NARR; Mesinger et al. 2006). Soil depth and textural class for each site were obtained from the published literature.

In order to propagate parameter uncertainty into model projections and to estimate a forecast confidence interval, an ensemble of 1000 runs was conducted at each site using parameter sets sampled from data assimilation posterior distributions. The initial planting density and stem diameter at breast height (dbh) at each site were set using values reported in the literature when available and set to 1 stem/m² and 1 cm, respectively, if not reported. The field trials used in the validation step include diverse climates, soils, and growing conditions across the forested regions of the United States. The species tested in these field trials included over 10 hybrid poplars and three native species (Coyle et al. 2008, Dowell et al. 2009). Modeled poplar yield was compared to the observed yield of the highest yielding clone and the averaged yield of multiple clones to evaluate model performance with respect to regional yield estimation.

Regional projections

Regional simulations were run for 13 years (1996–2008) on a half-degree grid over the contiguous United States. Because full ensemble analysis was computationally prohibitive at this scale, ED2 was run using the parameter set with the maximum posterior probability. Soil textural classes were assigned from the STATSGO database and meteorological drivers were obtained from NARR reanalysis data (Mesinger et al. 2006). Initial planting density was 1 tree/m². We estimated the optimal harvest interval by selecting the rotation time that maximizes the mean annual harvestable biomass based on the modeled change in AGB over time. The maximum annual increment (MAI) was calculated for each grid cell as the average annual AGB increment at the optimal harvest interval assuming a December harvest (excluding leaf and storage biomass). In order to compare the potential performance of hybrid poplar to the potential yield of perennial grass biofuel crops, we compared our yield map to equivalent estimates of *Miscanthus × giganteus* yield (Miguez et al. 2012). *Miscanthus* is a perennial C₄ rhizomatous grass with strong potential as a biofuel crop that achieves yields as high as 40 Mg/ha in field trials in Europe (Miguez et al. 2008) and regularly outperforms switchgrass in head-to-head trials in the United States (Heaton et al. 2004). Because ecological regions depict ecosystem patterns and effects, they have been proposed as an appropriate geographic framework for ecosystem management (Bryce et al. 1999). Therefore, MAI of poplar was also summarized using the level II ecological regions defined by Omernik (1987) and later refined at the U.S. Environmental Protection Agency (Bryce et al. 1999).

Land use transition

To estimate the effect of land use change on SOC sequestration, we evaluated four land use scenarios at the Rhinelander, Wisconsin site as a case study. For scenarios 1 and 3, the model was run for 61 years for growing corn or native forest, respectively. For scenario 2, the model was run for 11 years growing corn and then growing poplar for 50 years in a seven-year SRF rotation. For scenario 4, the model was run for 11 years with natural forest and then switched to poplar for 50 years. The initial plant community composition for the native forest in this region was based on the U.S. Forest Service Forest Inventory and Analysis (FIA). Species in the FIA database were grouped into four plant functional types (PFT): early, mid- and late-successional temperate hardwoods and northern pines; corn plants were assigned to the C₄ crop PFT (Medvigy et al. 2009). ED2 default parameters were used for all PFTs except for early successional hardwoods, which were assigned the optimized poplar parameters. The initial growing density for corn was set as 10 plants/m². The initial fast, structural, and slow soil carbon pools in the corn field and native forest were set as 1.0, 2.8, and 0.05 kg/m² (King et al. 2001, Loya et al. 2003, Talhelm et al. 2009). Meteorological drivers were obtained from NARR reanalysis data (Mesinger et al. 2006) and were sequentially cycled over years from 1981 to 2008.

RESULTS

Model parameterization and calibration

Fifteen parameters were initially considered for parameterization based on previous experience with the ED2 model (Table 2). Species-level data were available for seven parameters: leaf width, SLA, quantum efficiency, stomatal slope, root respiration rate, leaf dark respiration rate, and $V_{c,max}$ (Appendix). The priors, trait data, meta-analysis posteriors, and data assimilation posteriors are presented in Fig. 1. Bayesian meta-analysis generally reduced the parameter uncertainty relative to the prior distributions (Fig. 1) but there was little data constraint on quantum efficiency ($n = 24$, from one study) and dark respiration rate ($n = 6$, from one study). Six parameters were selected, based on the variance decomposition, for further constraint in the data assimilation step (dashed line, Fig. 1), and the reduction in parameter uncertainty that resulted from the data assimilation step is seen as a more narrow probability distribution of data assimilation posteriors relative to priors and meta-analysis posteriors (Fig. 1).

The variance decomposition indicated that some traits contributed substantially more than others to uncertainty in modeled yield (Fig. 2). At the Rhinelander, Wisconsin site, parameters controlling photosynthetic processes (such as quantum efficiency and dark respiration), allocation (growth respiration and fine-root allocation), and belowground processes (root turnover rate) contributed most to model uncertainty (Fig. 2).

TABLE 2. Prior distributions used in meta-analysis and model parameterization (units are given in Fig. 1).

Parameters	Distribution	<i>a</i>	<i>b</i>	<i>n</i>	Mean	LCL	UCL	References
Mort2†	gamma	1.47	0.0578	0	25.43	1.75	79.90	‡
F_labile§	beta	1.5	1.5	0	0.50	0.06	0.94	‡
Vm_low_temp¶	norm	−3	2	0	−3.00	−6.92	0.92	‡
Water_conductance	lnorm	−5.4	0.4	0	0.00	0.00	0.01	‡
Root_turnover_rate	Weibull	1.55	0.862	47	0.78	0.08	2.00	Gill and Jackson (2000)
Leaf_width	gamma	12.8	0.18	50	71.11	37.65	115.04	McGlone et al. (2010)
Quantum_efficiency	Weibull	8.32	0.0552	74	0.05	0.04	0.06	Skillman (2008)
Root_respiration_rate	gamma	4.95	0.762	36	6.50	2.09	13.35	George et al. (2003)
Growth_resp_factor	beta	4.06	7.2	0	0.36	0.12	0.65	Litton et al. (2007)
								Waring et al. (1998)
Nonlocal_dispersal#	beta	1.1	1.5	0	0.42	0.02	0.92	‡
Stomatal_slope	Weibull	7.11	6.29	16	5.89	3.75	7.56	LeBauer et al. (2012)
Fineroot2leaf	lnorm	0.21	0.6	0	1.48	0.38	4.00	Heinsoo et al. (2009)
Dark_respiration_factor	lnorm	−3.9	0.4	0	0.02	0.01	0.04	‡
SLA	Weibull	2.1	12.1	967	10.72	2.10	22.53	Wright et al. (2004)
V _{c,max}	Weibull	7.42	60.6	94	56.86	36.92	72.26	Wullschleger (1993)

Note: Parameters *a*, *b*, and sample size (*n*), mean, lower 95% confidence limit (LCL), upper 95% confidence limit (UCL) for describing each distribution are provided.

† Mortality coefficient.

‡ Information about prior comes from expert opinion or default ED2 parameterization.

§ Fraction of litter that goes into the labile (fast) carbon pool.

¶ Temperature below which photosynthesis begins to rapidly decline.

Proportion of dispersal that is global.

These parameters tended to have both high uncertainties in the parameter values and high sensitivities. The contribution of the mortality coefficient parameter to model uncertainty was mainly caused by high posterior uncertainty, despite the low sensitivity of AGB to this parameter. SLA, on the other hand, had a high sensitivity but contributed little to the model uncertainty because this parameter is well constrained by data (Fig. 2). The remaining parameters tended to have very low sensitivities, and thus contributed little to model variability even when they had high parameter uncertainties. The variance of the ensemble (9.23 in standard deviation scale) was less than the variance calculated in the variance decomposition (10.2). The difference between the two (the closure term, ω) indicates that nonlinear parameter interactions only accounted for ~10% of the predictive uncertainty.

Data assimilation not only constrained the uncertainty for the six parameters (Figs. 1 and 2), but also changed the relative contribution of each parameter to model uncertainty (Fig. 2). For example, after assimilation, the percentage of dark respiration and root turnover rate contributed to model uncertainty decreased. The uncertainty in the mortality coefficient and SLA declined by less during data assimilation, and thus on a proportional basis contributed relatively more to the remaining uncertainty.

The mean of the ensemble runs was comparable to the mean poplar yield of two clones (Fig. 3) and the confidence intervals of the ensemble output captured the range of the observed yields. The model–data mismatch was smallest at intermediate planting density of 1 tree/m² (Fig. 3B) and at high growing density of 1.5 tree/m² (Fig. 3C). ED2 tended to slightly underestimate AGB at the lower growing density of 0.5 tree/m² (Fig. 3A). The

mean modeled AGB fell between the yields of clones NE-41 and NE-386 at 1.5 trees/m² density, and was slightly lower than the observed yield of the two clones at 0.5 tree/m² and 1 tree/m².

Model validation

Modeled poplar yields fell within the uncertainty range of yields at eight different sites across the continental United States (Fig. 4, Table 1). The 95% confidence interval (CI) of modeled yields covered the observed yields for all the sites (except the clone 20 at the New Franklin site). Among the validated sites the highest unfertilized and unirrigated poplar yield was 18 Mg/ha (70 Mg/ha over 5 years) for the most productive clone at New Franklin, Missouri (Dowell et al. 2009). From field trials conducted across the Great Lakes Region (Netzer 2002), the averaged observed MAI of three nine-year-old poplar clones was 7.2 Mg/ha at Fargo (North Dakota), 8.5 Mg/ha at Granite Falls (Minnesota), 8.1 Mg/ha at Mondovi (Wisconsin), and 5.1 Mg/ha at Sioux Falls (South Dakota), respectively. In Escanaba, Michigan (Miller and Bender 2008) the observed yield of different clones varied considerably and the modeled AGB was lower than the yield of best clone but was higher than the mean AGB of the remaining five clones. In the northwestern United States, the modeled AGB was close to a reported 58 Mg/ha for four-year-old monoclonal plots at Olympia, Washington (DeBell and Harrington 1997). In the South Carolina site (Coyle et al. 2006), where biomass was not reported, the modeled stem volume, which was calculated using the same equation ($\text{dbh}^2 \times \text{height}$) as used in the paper, was comparable to the mean stem volume of 14 different clones.

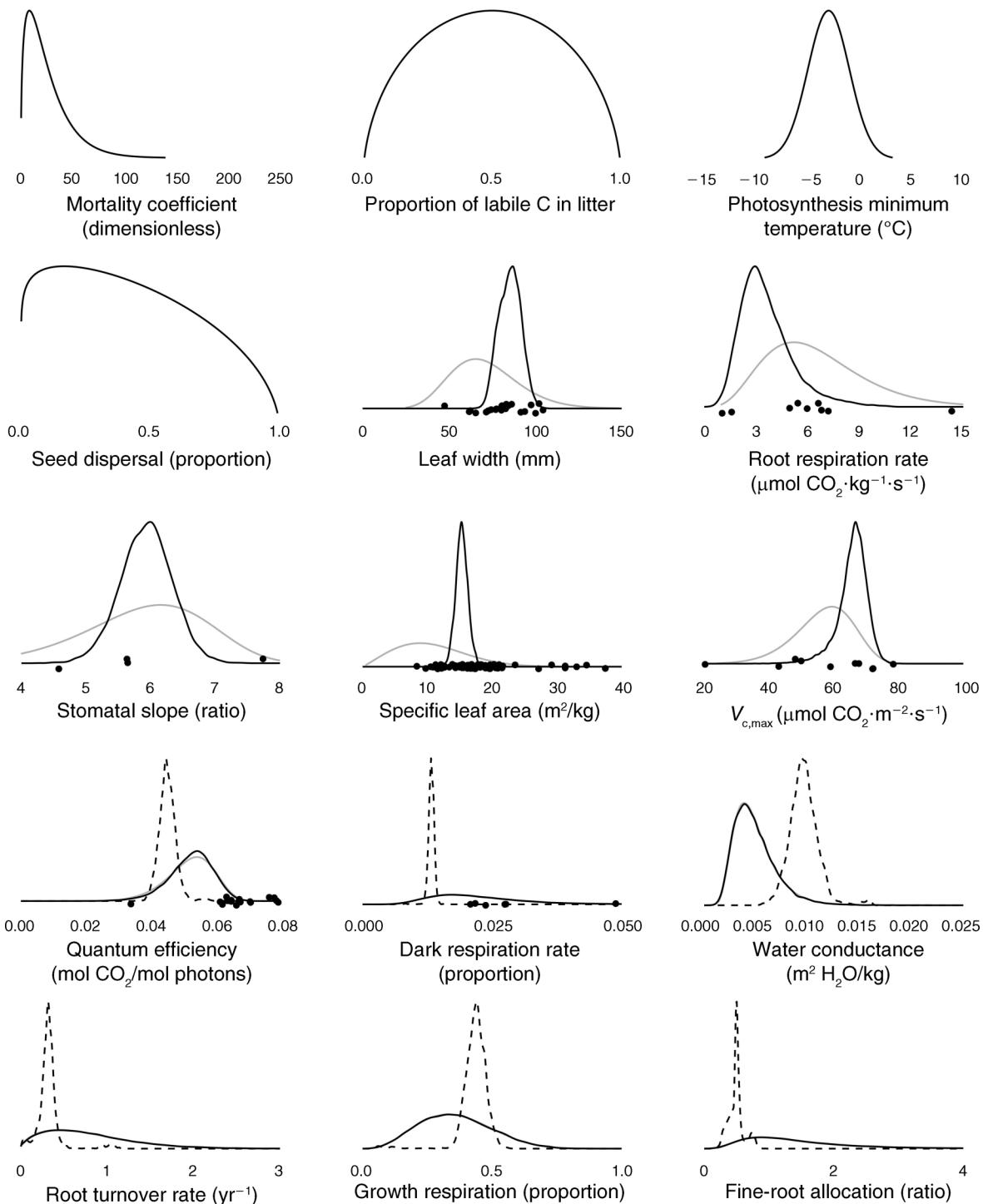


FIG. 1. Probability distribution functions (PDFs) of priors (gray), meta-analysis posteriors (black), and data assimilation posteriors (dashed). The parameter value is on the x-axis, and probability is on the y-axis. Species-level data used to constrain priors are shown as solid dots on the bottom of the plot for leaf width, root respiration rate, stomatal slope, specific leaf area, $V_{c,\text{max}}$, quantum efficiency, and dark respiration rate. For the parameters without species-level data, PDFs of priors and posteriors are identical. For fine-root allocation, the ratio is the ratio of fine root to leaf.

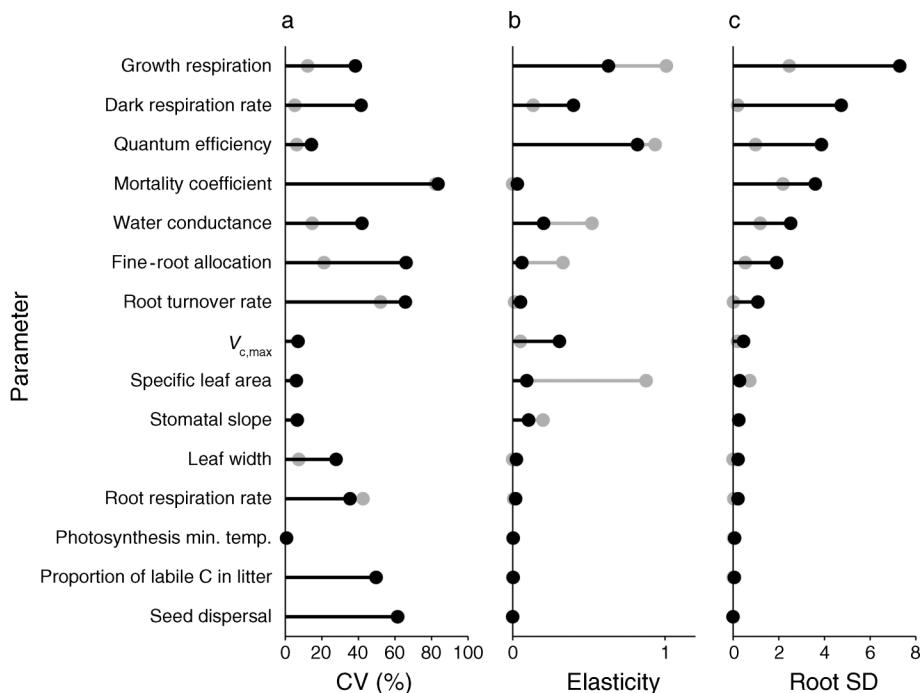


FIG. 2. Partitioning of variance by parameters. Results from variance decomposition conducted before (black) and after (gray) updating parameter estimates with observed field data using our data assimilation technique. (a) The uncertainty associated with each parameter (coefficient of variation, CV). (b) Elasticity (normalized sensitivity of modeled aboveground biomass to each parameter). Large values of elasticity indicate that aboveground biomass (AGB) is strongly affected by changes in the parameter value; positive elasticities indicate that biomass increases with increasing parameter values, and vice-versa. (c) Percentage of total variance explained by each parameter relative to the total variance (%). This is a function of both parameter uncertainty (CV) and sensitivity (elasticity).

Regional projections

The modeled output showed spatial variability of MAI across different climates and soils (Fig. 5A). The highest MAI was achieved in the Atlantic highlands (14.7), mixed wood plains (14.5), and central U.S. plains (14.1). High yields were also observed in the southeastern U.S. plains (13.6), mixed wood shield (13.1), temperate prairies (12.7), Mississippi alluvial and southeast U.S. coastal plains (11.9), and Ozark, Ouachita-Appalachian forests (11.0) (Fig. 5D). Across most of the West and southcentral semiarid prairies and warm and cold deserts, poplar could not achieve high yield. Detailed ecoregional MAI projections are presented in the Appendix.

The optimal harvest interval also varied across different regions (Fig. 5B). In the eastern and southern United States, poplar reached MAI after ~ 9 years; however, for the portion of the Pacific coast where poplar can achieve high annual yield, it takes ~ 4 years to reach MAI.

Comparing the potential yields of poplar and *Miscanthus* (Miguez et al. 2012), we found that poplar yield was comparable to or higher than *Miscanthus* over a significant portion of the northern Great Lakes region, New England, and northern California (Fig. 5C), while

MAI of poplar was lower for many of the regions where *Miscanthus* and poplar can both achieve high yields. Specifically, *Miscanthus* was more productive across the southeast and the agricultural regions of the Midwest. In most of the intermountain west, Rocky Mountains, and southwestern United States, neither poplar nor *Miscanthus* achieved agronomically useful yields.

Land-use-change effect

The calibrated model was used to predict potential SOC sequestration for Rhinelander, Wisconsin under different land use scenarios for 61 years (Fig. 6). Corn production consistently depleted SOC. Land use conversion of corn or native forest to poplar plantations resulted in a large initial loss of SOC during the first 10 years; this initial SOC loss was recovered after eight more years, after which poplar plantations accumulated carbon.

DISCUSSION

Our study is the first to predict the yield and SOC change of SRF ecosystems at a continental scale using a terrestrial biosphere model. We show that the ED2 model calibrated within the PEcAn framework successfully captures the spatial and interannual variability of poplar yield across a wide range of climate and soils.

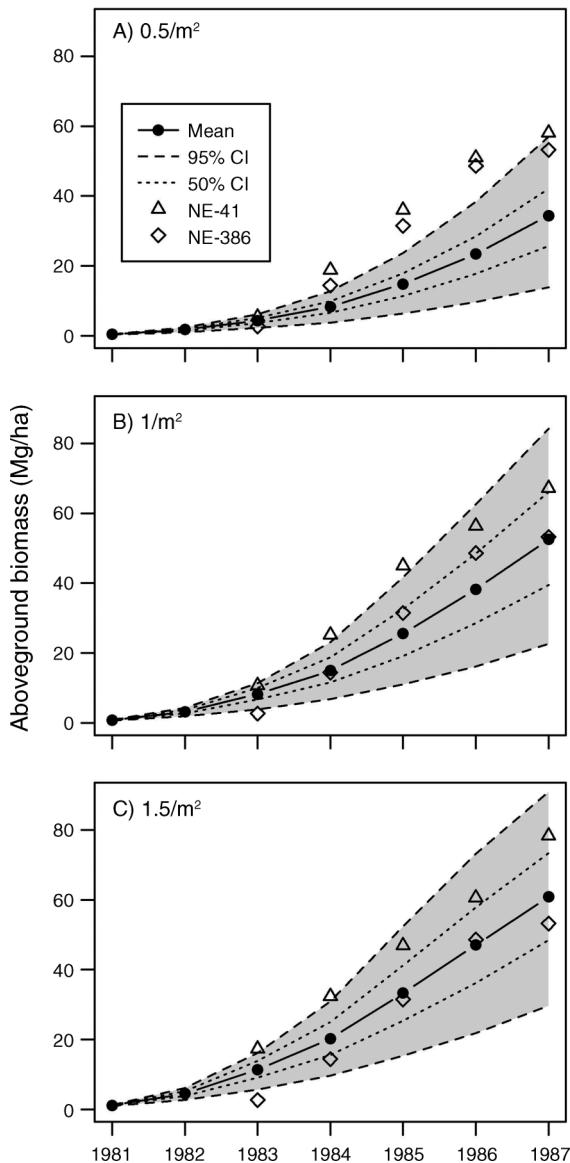


FIG. 3. Model-data mismatch between simulated (lines, parameters sampled from data assimilation posteriors) and observed (symbols) aboveground biomass (AGB) of poplar clones NE-41 and NE-386 at three planting densities: (A) 0.5 plants/m²; (B) 1 plants/m²; (C) 1.5 plants/m² over seven years at Rhinelander, Wisconsin, USA, a northern continental climate site (observed data are from Strong and Hansen [1993]).

Our approach provides a robust estimate of model uncertainty, and identifies key data requirements to reduce this uncertainty. Bayesian model calibration synthesized available data and knowledge on the parameters and provided parameter estimates with measures of uncertainty. The data assimilation step further constrained model parameters using observed yields. Results from the variance decomposition can inform future targeted data collection required to efficiently constrain forecast uncertainty. These results

can guide further research, policy, and management decisions.

Parameter sensitivity to AGB

Manually tuning parameters is not sufficient to reduce uncertainties in parameters and model predictions and thus provides little information on what data are essential to constrain the models (Tang and Zhuang 2009). In this regard, sensitivity analysis, variance decomposition, and data assimilation provide valuable methods to identify critical input parameters and rank them in order of importance. This ranking can guide the design and data collection of experimental programs. The contribution of each parameter to model uncertainty in this study is a function of both parameter sensitivity and uncertainty. Even though some parameters have a relatively high sensitivity, such as SLA, the relatively low uncertainty associated with these parameters resulted in only a minor contribution to the overall model uncertainty. It is important to note that the ranking of the sensitive parameters based on variance decomposition depends on the response variable of choice (AGB in this study) as well as the conditions of the run. In the current study, we ran the sensitivity analysis and variance decomposition at three growing conditions (planting density at 1 plant/m² in Fig. 2 and at 0.5 and 1.5 plants/m² in the Appendix). At the lowest planting density, water conductance and fine-root allocation contributed more to the overall uncertainty than at higher densities.

Incorporating species-level data and field-observed yield data reduced parameter uncertainty and the contribution of data-constrained parameters to model uncertainty estimated by the ensemble variance. For example, compared with prior runs (S3), the contribution of SLA and $V_{c,max}$ to the overall model variance decreased significantly (Fig. 2). After incorporating trait data, seven key parameters including growth respiration, dark respiration rate, quantum efficiency, mortality coefficient, water conductance, fine-root allocation, and root turnover rate, became the most important contributors to model uncertainty. After assimilation with yield data, five of the seven key parameters were still among the most important parameters, and dark respiration rate and root turnover rate were dropped out of the initial list. This demonstrates the use of variance decomposition to guide future data collection by identifying target parameters based on their contribution to model variance. To further reduce uncertainty in SRF poplar yield, data collection on growth respiration, mortality, water uptake, and quantum efficiency would be of high priority for field measurements. While growth respiration is very difficult to measure in situ, studies on the biochemical composition of different poplar plant tissues could be used to estimate construction costs (Amthor 2000), and would provide a valuable data constraint. Importantly, the parameters targeted for future constraint through direct observation and data

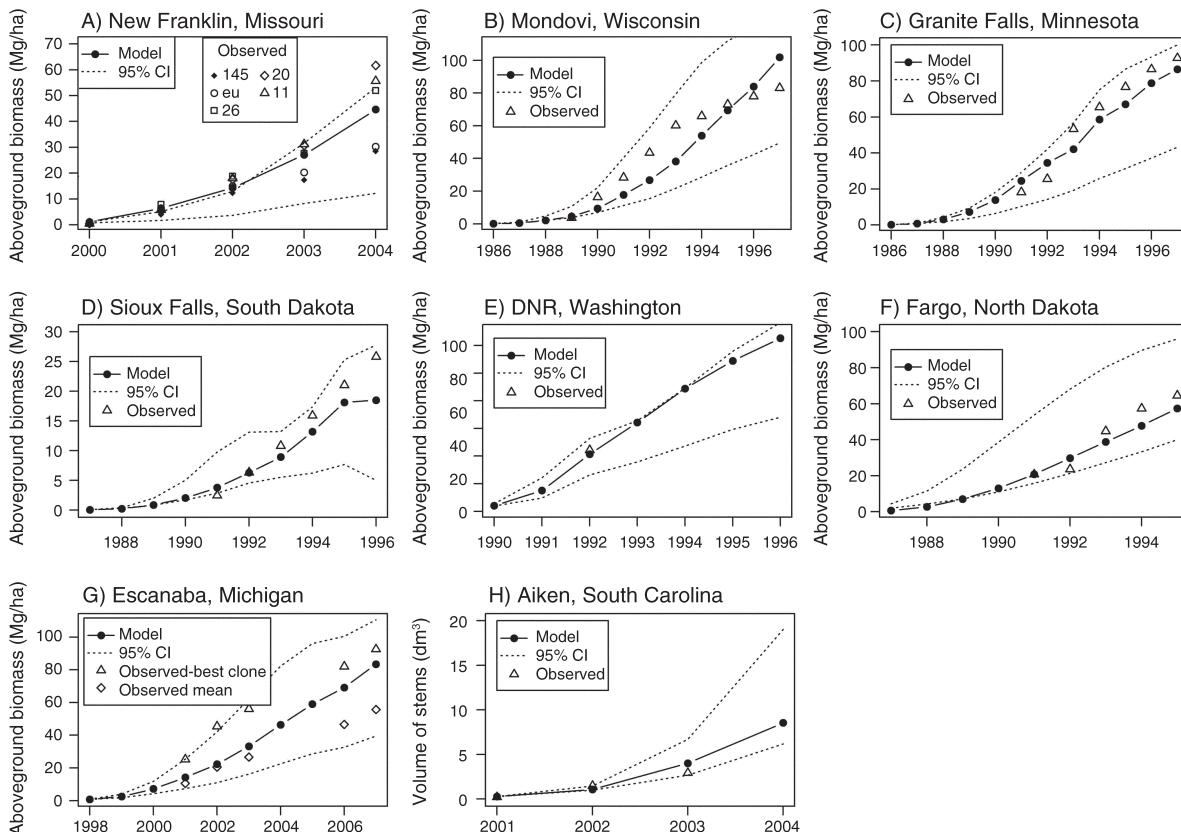


FIG. 4. Independent validation of modeled yield. Simulated (parameters sampled from data assimilation posterior) and observed AGB and stem volume of multiple poplar clones at eight validation sites (A–H). For New Franklin, Missouri (A), different labels for the observed data indicate different poplar clones (eu represents Eugeneii). Panel (E) shows the mean of three clones at three planting densities for Olympia, Washington. For Aiken, South Carolina (H), the yield is given as the volume of stems. See Table 1 for site descriptions and references.

assimilation will depend upon the species chosen, the availability of data on that species in the literature, and the responsive variable of choice.

Model performance

The modeled AGB closely followed the observed yields across a wide range of locations in the United States representing much of the continental climate space (Figs. 4 and 5). From this we conclude that the model was able to account for the variability in environmental and soil conditions. Projected yields are comparable to the reported average MAI of 12 Mg/ha across the reproductive ecoregions of the United States (Hofmann-Schielle et al. 1999, Sartori and Lal 2006). Rotation times that maximize the modeled MAI can be used to inform the time period of rotation cycles. SRF includes single stem production followed either by replanting or by coppicing. The simulations in this study assumed replanting; therefore results would vary under a coppice system, and in general will enable a shorter rotation cycle and produce higher yields. A coppice system should consider the growth vigor and coppicing ability when deciding the clone to select and

rotation cycles to utilize (Sims et al. 2001). The MAI-achieving year reported in this study should be integrated with the knowledge on morphological, physiological, and cultural factors influencing the regeneration and sustainability of the coppicing system, as well as the economic costs of harvesting and postharvest processes to evaluate the relative benefits of different rotation cycles.

Compared with *Miscanthus*, poplar had a lower yield at most areas in the eastern and southern United States (Fig. 5C), but had higher yield in the upper Midwest and New England and most of areas in the Pacific Southwest and Northwest region. It is also critical to note that this study only estimated the direct yield of poplar and does not account for the full life cycle analysis. Accounting for the reduced management, greater flexibility in harvest timing, and reduced transportation costs of trees relative to grasses is likely to tip a substantially larger area in favor of poplar due to its lower management intensity, greater flexibility in harvest timing, and denser fuel, which reduces transportation costs compared to perennial grasses.

Water availability has a large impact on the yield of poplar (Davis et al. 2012). A hybrid poplar clone OP367 was reported to achieve 72.2 Mg/ha after six-year growth only with regular irrigation in western Colorado (Pearson et al. 2010). Our results show that at the desert and semiarid prairie ecoregions, unirrigated poplar does not achieve high yields (Fig. 5d). These model results provide a framework for predicting yield outside the current range of experience in the United States and guidance in choosing growing poplar or *Miscanthus* based on the yield potential in targeted locations.

Impact of land use change on SOC sequestration

SOC sequestration is a key component in the life cycle of biofuel production and is crucial in determining the greenhouse gas reduction potential of biofuels relative to fossil fuels (Anderson-Teixeira et al. 2009). Although SOC sequestration is impacted by multiple factors (including temperature, precipitation, soil and vegetation type, initial soil C stock, and management practices; Sartori and Lal [2006], Trumbore [2006]), conversion of unmanaged land to agriculture usually leads to rapid and large C losses (Guo and Gifford 2002). In the present analysis we find that corn production reduces soil C while poplar plantations result in net SOC sequestration after 21 years. Specifically, corn production reduced SOC by 31.3 Mg/ha within 61 tested years (Fig. 6). This rate is comparable to the estimate that harvest of corn residues reduces SOC by 3–8 Mg/ha within the first few years (Anderson-Teixeira et al. 2009). By contrast, conversion of corn fields or native forests to poplar plantations resulted in accumulations of 34.1 and 30.3 Mg/ha SOC, respectively. The rate of SOC accumulation under poplar plantations was very close to what has been reported in a direct investigation on the impact of land use on soil SOC sequestration wherein SOC increased from 10.4 to 16.07 g/kg after 10-year growth of poplar plantation with three-year harvesting cycle. However, SOC decreased from 10.4 to 10.0 g/kg for a maize–wheat cropping system in the same time frame (Pellegrino et al. 2011). The modeled result is similar to the result reported by Hansen (1993), wherein 12- to 18-year-old poplar plantations sequestered SOC at a rate of 1.6 Mg·ha⁻¹·yr⁻¹ on 11 sites across North Dakota, Minnesota, Iowa, and Wisconsin. Likewise, our results are consistent with the SOC increase of 17 Mg/ha over four seven-year rotations observed by Garten et al. (2011).

Deforestation usually results in significant losses of soil organic carbon (SOC), because inputs from new plants are too low to counteract losses by soil respiration. The recovery time for SOC was 18 years after conversion in the forest–poplar and corn–poplar simulations. This recovery time is consistent with other studies. For example, Bashkin and Binkley (1998) found that site preparation caused an initial SOC loss, and net recovery occurred about 10 years after plantation establishment. This may explain why short-term exper-

iments usually fail to detect changes in SOC pools under poplar plantations (Coleman et al. 2004, Sartori et al. 2007). Our results are therefore consistent with several studies that report long-term positive SOC changes following poplar afforestation of formerly cultivated lands (Hansen 1993, Makeschin 1994, Coleman et al. 2004).

Sources of bias and potential suggestions for model improvement

Though the model was well calibrated and performed well at independent sites covering nine states, we identify seven key areas for future development. (1) We assumed independence between the model parameters in the Bayesian meta-analysis and sensitivity analysis. While this allows a tidy decomposition of the total variance into component variances, it could be improved by the inclusion of parameter covariance, which would result in stronger parameter constraints. For example, there are strong correlations among many of the leaf-level traits (Reich and Oleksyn 2004, Wright et al. 2004) that were not incorporated. Posterior distributions taking parameter correlations into account could potentially reduce the selection of unrealistic parameter sets from the joint posterior. (2) Although we constrained six parameters in data assimilation by using observed field data for the purpose of poplar yield projection, including additional data sources would provide more robust constraint in this step. For example, eddy flux data would improve inferences about mass and energy exchange between the ecosystem and atmosphere, and biometric data could more effectively constrain carbon allocation parameters (Williams et al. 2005, Luo et al. 2009). (3) In an agricultural context, incorporating a coppice routine into the current model would allow us to predict coppicing effects on plant survival and regrowth. This routine is under development but will require additional calibration and verification beyond the scope of this paper. (4) Similar to other models (Garten et al. 2011), the predictions of soil C sequestration have not yet been explicitly validated because the required data are not available. The model would benefit from a long-running survey of belowground processes in poplar plantations, including changes in SOM pools that could be assimilated to provide an important constraint on C cycling. (5) The *Populus* genus contains more than 30 species and many more hybrid genotypes. Genetic variation exists in almost all traits that impact biomass production, allocation, and the rate of soil C sequestration. This variation could be incorporated into our analysis to make more specific management recommendations. Clone-level data are currently too sparse to support robust parameterization. (6) The sensitivity of yield to climate and environmental factors was not explicitly quantified in this study, but would provide additional insight into best management practices and could improve yield forecasts. (7) Field trials used for model validation were mostly located in the eastern

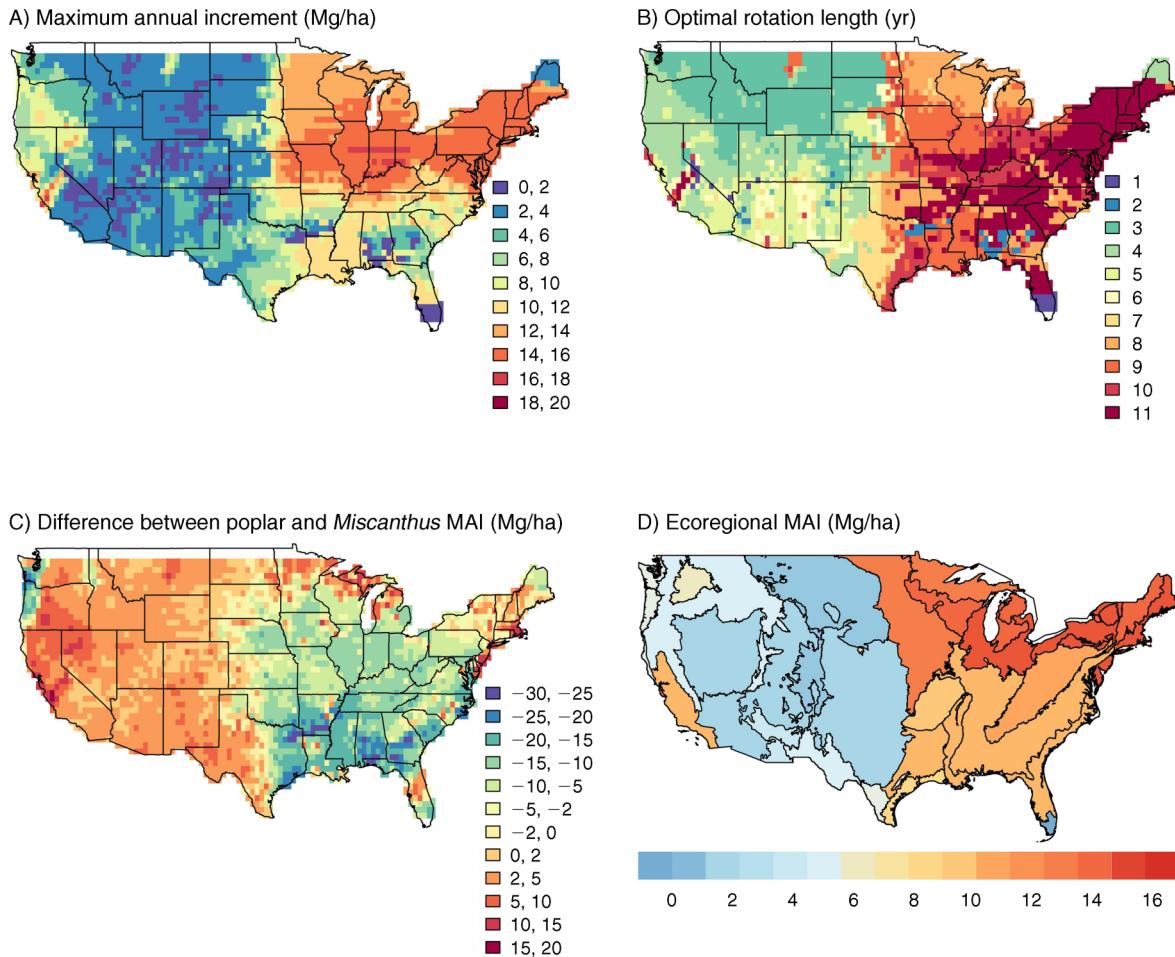


FIG. 5. Map of potential growth of poplar plantations in the United States. (A) maximum annual increment (MAI); (B) length (in years) of the rotation (i.e., planting to harvest) for optimal MAI; (C) the difference between MAI of poplar and *Miscanthus* (Mg/ha). Negative values favor *Miscanthus* and positive values favor poplar. Note that for most of the West, neither poplar nor *Miscanthus* achieves high yield. (D) Poplar MAI across different ecoregions (Mg/ha).

United States. More field trials of poplar SRF should be conducted in the South, Pacific Northwest, and West in order to improve confidence in our continental-scale projections.

CONCLUSION

This study provides forest managers and policy makers with a process-based modeling approach to estimate the yield and carbon sequestration potential of hybrid poplar for a given climate and soil. Three key results from this study are as follows. First, variance decomposition showed that the uncertainty of the model output was initially explained by growth respiration, dark respiration rate, mortality coefficient, quantum efficiency, water conductance, and belowground parameters such as root turnover rate and fine-root allocation. After data assimilation, uncertainty is dominated by growth respiration, mortality, water conductance, and quantum efficiency. These results can be used to guide

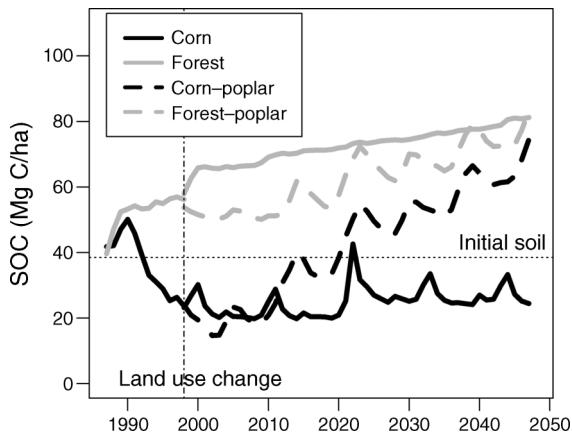


FIG. 6. Projected relative soil organic carbon (SOC) changes under different land-use-change scenarios at Rhineland, Wisconsin.

more efficient experimental design and model calibration. Second, ED2 coupled with Bayesian meta-analysis and data assimilation successfully predicts the yield of poplar at nine different sites in the United States and captured the interannual and spatial variability across a wide range of climates and soils. The MAI of poplar plantations varied considerably across different regions, with high yields in the East and along the Pacific coast. The predicted time required to achieve MAI varied across the United States, with longer rotation years in the East and shorter rotation years in the Pacific region. Based on the difference yield between *Miscanthus* and poplars, poplar growth is favored in New England, the upper Midwest, and northern California regions, but life cycle considerations may influence local management decisions. Finally, our estimates of the land-use-change effect on soil C sequestration showed that planting poplars in a short-rotation system could increase SOC sequestration relative to conventional crops such as corn, even though an initial SOC loss could occur during land conversion and site preparation.

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SUPPLEMENTAL MATERIAL

Appendix

Data used in the meta-analysis, maximal annual yield of poplar for different ecoregions, and variance decomposition plot for model runs using only priors and at different densities ([Ecological Archives A023-048-A1](#)).