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Review and model-based analysis of factors influencing soil carbon sequestration under hybrid poplar☆

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ABSTRACT

The potential for soil carbon (C) sequestration under short-rotation woody crops, like hybrid poplar (*Populus* spp.), is a significant uncertainty in our understanding of how managed tree plantations might be used to partially offset increasing atmospheric CO_2 concentrations. Through development of a multi-compartment model, we reviewed information from studies on hybrid poplar and analyzed the potential impact of changes in plant traits and nitrogen (N) fertilization on soil C storage. For a hypothetical setting in the southeastern U.S.A., and starting from soils that are relatively depleted in organic matter (2.5 kg C m^{-2}), the model predicted an increase in mineral soil C stocks (1.7 kg C m^{-2}) over four 7-year rotations of hybrid poplar. However, at the end of the fourth rotation, both cumulative soil C gains and annual rates of soil C accrual (23–93 g C m^{-2} yr^{-1}) varied widely depending on fertilization rate, biomass yield, and rates of dead root decomposition (three factors that were examined in a factorial model-based experiment). Our analysis indicated that processes linked to genetically modifiable poplar traits (aboveground biomass production, belowground C allocation, root decomposition) are potential controls on soil C sequestration. Key measures of model performance were sensitive to how aboveground biomass production responded to N fertilization. Site specific properties that were independent of plant traits were also important to predicted soil C accumulation and point to possible genotype x site interactions that may explain contradictory data from both empirical and theoretical studies of C sequestration under hybrid poplar plantations.

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1. Introduction

Recent research indicates an interest in the establishment and growth of hybrid poplar (*Populus* spp.) plantations in the southeastern United States for rapid production of fiber and as a potential bioenergy feedstock [1,2]. The availability of high-yielding clones, coupled with promising gains through genetic improvement, make hybrid poplar an attractive model perennial for the production of ethanol from renewable biomass. High annual rates of aboveground biomass production, up to 20 Mg biomass ha^{-1}, have also stimulated considerable interest in the possibility of soil carbon (C) sequestration beneath tree plantations as an ancillary ecosystem service that would help partially offset anthropogenic CO_2 emissions to the atmosphere [3]. Intensive management of *Populus* plantations has the potential to sequester soil C, through repeated fine-root turnover and longer-term accumulation and decomposition of larger roots and stumps [4,5], but the fundamental mechanisms

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that could be tapped to realize this potential are not well understood. Significant genetic variation exists for poplar traits related to C sequestration [6], but studies of how targeted genetic changes in hybrid poplar might directly influence soil C sequestration are limited [7].

Field studies indicate that poplar-based agro-forestry has the potential to increase C stocks in intensively cultivated soils [8]. However, other research (over time frames of approximately a decade) indicates that growing hybrid poplar may not increase soil C stocks [9], at least in the short-term. For example, in the Pacific Northwest, Sartori et al. [10] found no statistically significant increase in mineral soil C stocks over a 10-year chronosequence of poplar stands. Similarly, Coleman et al. [11] reported no significant difference in soil C storage beneath poplar (up to 12-years old) and adjacent agricultural crops in the north central United States. Conclusions from these studies on soil C sequestration could be misleading if there are site-specific delays in soil C accrual that extend beyond twelve years of plantation growth [12]. The chief limitations associated with empirical studies are (1) potential rates of soil C sequestration are highly site dependent (which contributes to conflicting results) and (2) measurements may not extend over a sufficiently long period of time to detect statistically significant changes in soil C stocks.

Multi-compartment modeling is a useful tool for summarizing information, gaining a greater understanding of ecosystem controls and feedbacks, and conducting analyses to forecast changes over time. Modeling may not necessarily resolve site-specific differences that contribute to discrepant results from studies on soil C sequestration, but does permit forecasting of soil C sequestration under hybrid poplar plantations on a much longer time frame than field studies. Modeling also allows analyses of hypothetical situations that would take decades and millions of dollars to examine under field conditions, and enables identification of environmental factors and ecosystem processes that are important to maximize soil C sequestration. In this respect, initial soil C stocks, soil C inputs via root and litter production, rates of root turnover, the turnover times of major soil C pools, and management practices are indicated to be important controls on soil C sequestration under short-rotation woody crops [4,13]. However, modeling has its own unique set of limitations. Foremost, parameter values for model equations are often unknown, or poorly known, and no single mathematical model can capture all of the possible interacting factors and feedbacks that determine soil C dynamics in the real world. These limitations contribute to uncertainty in quantitative predictions (especially over the long-term).

The *Populus* genome has been sequenced [14], and there is interest in the analysis of poplar gene expression as well as the prospect of selecting tree characteristics in ways that would further enhance biomass production and soil C sequestration. For example, Hancock et al. [7] reported differences in soil C formation between wild-type and transgenic poplar that exhibited differences in lignin biosynthesis. Genetically based differences in leaf chemistry (e.g., condensed tannin concentrations) that may affect litter decomposition [15] and belowground C inputs through increased fine root production [16] are also potentially important. The suite of poplar traits that could be selected to influence soil C sequestration includes: (1) rates of aboveground biomass production, (2) the ratio of above-to-belowground C allocation, (3) proportional C allocation to fine and coarse roots, and (4) differences in root chemistry that determine root decomposition rates. However, genetic modifications to the foregoing traits are expressed against a background of variation in the environment and could give rise to genotype x environment interactions. These interactions are another limitation to empirical studies of soil-plant relationships in hybrid poplar. Modeling, on the other hand, can forecast how genetically modified poplar might promote soil C sequestration in different environmental settings.

Soil C sequestration is one objective in a suite of technologies aimed at mitigating CO_2 emissions to the atmosphere from fossil fuel use [17,18]. The purpose of our research was to use a model-based analysis to summarize information on soil C dynamics under hybrid poplar, and to explore how nitrogen (N) fertilization in combination with changes in particular genetically-controlled poplar traits might impact soil C sequestration. Following model development, a sensitivity analysis was used to identify parameters important to predicted soil C accumulation rates. We then conducted a model-based analysis, with stochastically varying model parameter values, to assess the effect of changes in poplar traits and fertilization on soil C sequestration.

2. Methods

2.1. Model description

2.1.1. Overall structure

The overall model (Fig. 1) was built from four sub-models: (1) aboveground tree biomass, (2) root biomass, (3) soil C, and (4) soil N. There were a total of ten state variables (Table 1). The first-order, multi-compartment model (RSPM 3.9) was formulated using Stella® software (isee Systems, Inc., Lebanon, NH). Differential equations (Table 1) were solved on an annual time step with Euler's method. Although less precise than Runge-Kutta integration, particular "if-then" formulations in the model mandated Euler's method. Equations for the fluxes between state variables are presented in Table 2.

2.1.2. Parameter uncertainty

Uncertainty was assigned to all parameters (Table 3) that were not explicitly defined as constants (e.g., annual N fertilization or rotation time) because there is a finite but unknown degree of variation in each parameter caused by year-to-year variation in environmental conditions (like temperature and precipitation). Parameter values in Table 3, not identified as constants, were chosen randomly at each annual time step from a normal distribution defined by the default value (mean) and a standard deviation set to 20% of the default. This approach produced stochastic model predictions, and statistics (means and standard errors) reported in the results were calculated based on 30 model runs.

2.1.3. Performance measures and simulation time

Four predictions were chosen as key performance measures in the model-based analysis: (1) the cumulative harvested aboveground biomass (CUH, kg m^{-2}), (2) the cumulative change in mineral soil C stock (ΔMSC, kg C m^{-2}), (3) the annual rate of change in mineral soil C stock (ΔSCA, g C m^{-2} yr^{-1}), and

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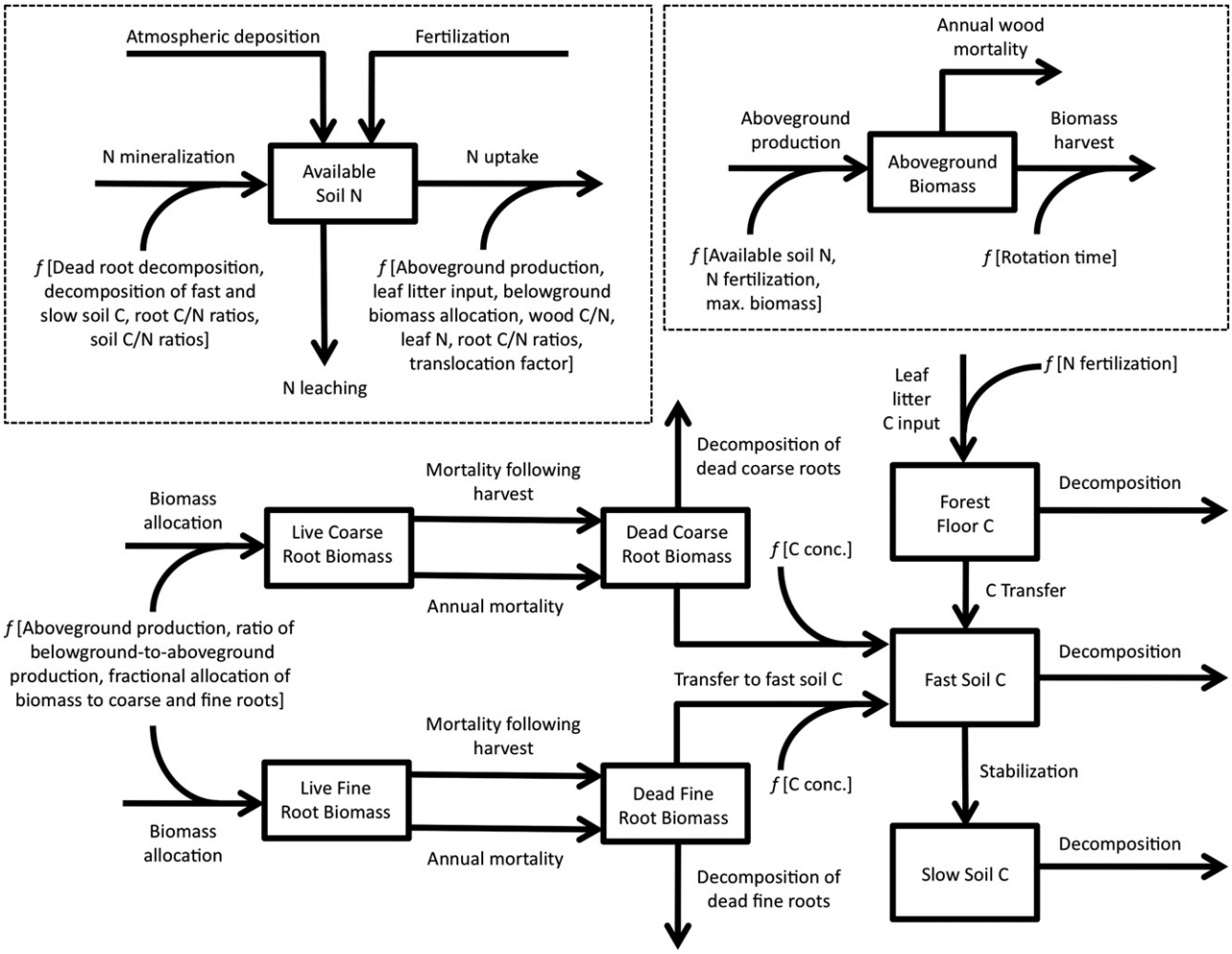

Fig. 1 – Conceptual diagram of the hybrid poplar model (RSPM 3.9) showing state variables (boxes), processes controlling material fluxes (arrows), and functional relationships of fluxes to various model processes and parameter values.

(4) cumulative N losses (CNL, g N m^{-2}). Simulations with the model were limited to four 7-year rotations (i.e., the time between planting and tree harvest) and a fallow year immediately following each harvest. The fallow year represented a time during which herbicides were used to suppress weeds and kill remaining stumps from the previous crop.

2.1.4. *Environmental setting and initial conditions*

The model was used to simulate C storage to a 40-cm soil depth beneath hybrid poplar growing on a highly weathered Ultisol derived from sandy coastal plain or alluvial deposits. Throughout the southeastern United States, Ultisols have been depleted of organic matter through agriculture and have

Table 1 – State variables along with their abbreviations and differential equations in the hybrid poplar model (RSPM 3.9). Abbreviations that refer to various fluxes to, from, and between state variables in the model equations are defined in Tables 2 and 3.

Sub-model	State variable	Abbreviation	Equation
Aboveground biomass	Aboveground biomass	AGB	d(AGB)/dt = AGB + (AGP − AGM − AGH)
	Cumulative harvest	CUH	d(CUH)/dt = CUH + AGH
Root biomass	Live coarse root biomass	LCR	d(LCR)/dt = LCR + (ACR − CRM − CRH)
	Live fine root biomass	LFR	d(LFR)/dt = LFR + (AFR − FRM − FRH)
	Dead coarse root biomass	DCR	d(DCR)/dt = DCR + (CRM + CRH − CRS − DCD)
	Dead fine root biomass	DFR	d(DFR)/dt = DFR + (FRM + FRH − FRS − DFD)
Soil carbon	Forest floor C stock	FFC	d(FFC)/dt = FFC + (LFI − LFS − DLF)
	Fast soil C stock	FSC	d(FSC)/dt = FSC + (FRS + LFS + CRS − STB − DFS)
	Slow soil C stock	SSC	d(SSC)/dt = SSC + (STB − DSS)
Soil nitrogen	Available soil N	NAV	d(NAV)/dt = NAV + (FRT + NAD + NMN − NLH − NDM)

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Table 2 – Annual fluxes to, from, and between state variables along with their abbreviations and equations used to calculate fluxes in the hybrid poplar model (RSPM 3.9).

Sub-model	Flux	Abbreviation	Equation
Aboveground biomass	Realized aboveground biomass production	AGP	If NAV > 0.01 then ((ANP × NFF) × ((AMB-AGB)/AMB) × DELAY) else AGM
	Wood mortality	AGM	AGM = AGB × ATM
	Harvested biomass	AGH	If (HAR = 1) then AGB else 0
Root biomass	Biomass allocation to live coarse roots	ACR	ACR = BGP × (1 − BAF)
	Mortality of live coarse roots	CRM	CRM = LCR × (1/BCL)
	Live coarse root mortality following harvest	CRH	If (HAR = 1) then LCR else 0
	Biomass allocation to live fine roots	AFR	AFR = BGP × BAF
	Mortality of live fine roots	FRM	FRM = LFR × (1/BFL)
	Live fine root mortality following harvest	FRH	If (HAR = 1) then LFR else 0
	Transfer dead coarse roots to soil	CRS	CRS = (DCR − DCD) × CRC
	Dead coarse root decomposition	DCD	DCD = DCR × BCD
	Transfer dead fine roots to soil	FRS	FRS = (DFR − DFD) × CRC
	Dead fine root decomposition	DFD	DFD = DFR × BFD
	Belowground biomass production	BGP	BGP = AGP × RBA
Soil carbon	Litterfall C input	LFI	LFI = CLF × 0.48 × NFF
	Leaf litterfall mass	CLF	If (HAR = 1) then 50 else (500 × DELAY)
	Transfer of litter C to fast soil pool	LFS	LFS = FFC × CTS
	Transfer of fast soil C to slow soil pool	STB	STB = FSC × STR
	Decomposition of forest floor C	DLF	DLF = FFC × (1/COT)
	Decomposition of fast soil C	DFS	DFS = FSC × (1/CFT)
	Decomposition of slow soil C	DSS	DSS = SSC × (1/CST)
Soil nitrogen	Net N mineralization	NMN	NMN = (DFS/CNF) + (DSS/CNS) + ((DCD × 0.45)/NCR) + ((DFD × 0.45)/NFR)
	Plant N demand	NDM	NDM = NDA + NDB
	Aboveground plant N demand	NDA	NDA = ((1 − NTR) × (CLF × NFL)) + (AGP/NWR)
	Belowground plant N demand	NDB	NDB = (ACR/NCR) + (AFR/NFR)
	Annual N loss via leaching	NLH	NLH = NAV − NDM

the potential to gain soil C following tree plantation establishment [19]. It was assumed that plantation management would not include coppicing and that hybrid poplar would be re-established from seedlings at the start of each rotation, without plowing, following a fallow year prior to planting.

2.1.5. *Aboveground biomass sub-model*

Aboveground biomass (AGB) was modeled as the difference between annual aboveground biomass production (AGP) and the sum of two principal means of biomass removal: (1) annual tree mortality (AGM) and (2) periodic tree harvesting (AGH) (see Fig. 1 and Table 1). Realized aboveground production (AGP) was calculated as a function of annual aboveground production (ANP), available soil N (NAV), N fertilization (FRT), and a fertilization factor (NFF) (Table 2). Aboveground production was constrained by both available soil N and a value for maximum aboveground biomass (AMB) such that aboveground production equaled annual tree wood mortality (AGM) when available soil N stocks were depleted ($\leq$0.01 g N m^{-2}) and/or aboveground production declined as aboveground biomass approached its maximum. Thus, aboveground biomass increased only when not limited by available soil N and aboveground production was maximized soon after plantation establishment. Removal of aboveground biomass via tree mortality (AGM) was calculated as a function of standing biomass and a mortality rate constant (ATM), while removal of aboveground biomass via tree harvesting (AGH) depended on the rotation period of the plantation (Table 2). Tree harvesting was controlled by a pulse function (HAR) that signaled the standing stock of aboveground biomass was to be removed at the end of each rotation, otherwise annual losses of aboveground biomass through harvesting were zero. Following tree harvest, there was a delay (designated "DELAY" in Table 2) in the resumption of aboveground production for one-year while the site remained fallow prior to seedling establishment at the start of the next rotation.

Initial conditions for aboveground biomass (200 g m^{-2}) represented seedling biomass at establishment of the plantation. Maximum aboveground biomass (AMB) was set to 20 kg m^{-2} (Table 3) based on studies of 10- to 14-year old poplar plantations [10,20,21]. Annual dry matter production in hybrid poplar is highly variable depending on the ecotype, site conditions, and plantation management [22–24]. The value of annual aboveground biomass production (ANP) was randomly drawn each year from a normal distribution with a mean and standard deviation of 1400 and 280 g m^{-2} yr^{-1}, respectively, which was representative of poplar yields in temperate climates [25,26].

Tree mortality in poplar plantations can occur as a result of disease and weather damage. For example, hybrid poplars vary in their resistance to disease from Septoria canker [22], a fungus that weakens both branches and main stems and can lead to tree death. For healthy, well-managed plantations, we assumed that 2% of the trees die each year from various causes (i.e., ATM = 0.02 yr^{-1}). Short-rotation woody crops managed for bioenergy feedstocks are generally harvested at

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Table 3 – Model parameters, units, default values, and sensitivity indices of different parameters in the hybrid poplar model (RSPM 3.9). The sensitivity index is the predicted change in mineral soil C (g C m^{-2}) relative to a 1% change in the parameter value. Parameter values marked with an asterisk were treated as constants in the calculations.

Sub-model	Parameter (abbreviation)	Units	Default value	Sensitivity index (SI)
Aboveground biomass	Annual aboveground production (ANP)	kg m^{-2}	1.4	2.55
	Tree wood mortality rate (ATM)	yr^{-1}	0.02	0.03
	Upper limit on aboveground biomass (AMB)	kg m^{-2}	20*	0.82
	Rotation time (ART)	years	7*	–
Root biomass	Fraction of belowground biomass production allocated to fine roots (BAF)	Fraction	0.3	−0.85
	Belowground biomass production-to-aboveground biomass production (RBA)	Ratio	0.4	3.33
	Turnover time of live coarse roots (BCL)	years	5	−0.17
	Turnover time of live fine roots (BFL)	years	1.3	−0.03
	Decomposition rate of dead coarse roots (BCD)	yr^{-1}	0.2	−1.30
	Decomposition rate of dead fine roots (BFD)	yr^{-1}	0.67	−0.97
Soil carbon	Transfer rate from litter to fast soil C (CTS)	yr^{-1}	0.17	0.53
	Transfer rate from fast to slow soil C (STR)	yr^{-1}	0.15	0.90
	Turnover time of forest floor C (COT)	years	1	0.45
	Turnover time of fast soil C (CFT)	years	5	1.50
	Turnover time of slow soil C (CST)	years	60	1.15
	Initial mineral soil C stock (CIS)	kg C m^{-2}	2.5*	1.48
	Fraction of initial soil C in fast pool (CFP)	Fraction	0.20	−0.10
Soil nitrogen	Leaf N concentration (NFL)	g N g^{-1}	0.03	0.95
	Translocation factor (NTR)	Fraction	0.5	1.52
	Annual N fertilization (FRT)	g N m^{-2}	12*	1.52
	Annual atmospheric N deposition (NAD)	g N m^{-2}	0.5	0.00
	C:N ratio fast soil C pool (CNF)	Ratio	30	−0.28
	C:N ratio slow soil C pool (CNS)	Ratio	15	−0.60
	C:N ratio fine roots (NFR)	Ratio	65	0.03
	C:N ratio coarse roots (NCR)	Ratio	130	0.03
	C:N ratio woody biomass (NWR)	Ratio	300	0.60

1–5 year intervals while plantations managed for greater product flexibility are subject to longer rotations of 8–12 years [27]. Consistent with published practices [25], a rotation time of seven years was used in the model.

Some studies indicate that annual applications of N fertilizer can increase aboveground growth and/or biomass production in poplar plantations [28,29]. Therefore, a fertilization factor (NFF) was used in the model (Table 2) that increased aboveground biomass production with increasing levels of fertilization (see default curve in Fig. 2). The default nonlinear fertilization factor was consistent with studies indicating no significant increase in aboveground production of some poplar clones receiving fertilization exceeding 5 g N m^{-2} yr^{-1} [28,30–32]. The effect of a modified fertilizer response curve (Fig. 2) on model performance was also evaluated as part of a sensitivity analysis (see Results).

2.1.6. *Belowground biomass sub-model*

The sub-model for roots predicted belowground biomass in live fine roots (LFR), dead fine roots (DFR), live coarse roots (LCR), and dead coarse roots (DCR) (Fig. 1 and Table 1). Total annual production of belowground biomass (BGP) was calculated on the basis of a ratio of belowground-to-aboveground production (RBA) (Tables 2 and 3). Belowground production was divided between live fine roots and live coarse roots based on biomass allocation factors (AFR and ACR, respectively). Live fine and coarse root biomass were modeled as the difference between production inputs and biomass losses that were comprised of losses from annual mortality as well as mortality associated with tree harvesting (Table 1). The annual mortality of live fine roots (FRM) and live coarse roots (CRM) was predicted on the basis of live root biomass and turnover times for the different root size classes (BFL and BCL, respectively) (Tables 2 and 3). In addition, following tree harvest, the model transferred all biomass in live roots to dead roots based on the boundary condition of post-harvest tree planting instead of coppicing. The mass of dead fine roots was calculated from the difference between inputs from root mortality and two loss processes (Table 1): (1) the decomposition of dead fine roots (DFD), and (2) the transfer of dead fine roots to the soil C sub-model (FRS). The loss of fine dead roots (DFD) was calculated on the basis of the pool size (DFR) and a fractional annual loss through decomposition (BFD) (Table 2). The annual transfer of dead fine roots to the soil sub-model was calculated on the basis of dead roots remaining after decomposition and their respective C concentration (CRC). The mass of dead coarse roots was calculated in a manner identical to the mass of fine dead roots but with different equations and parameter settings (Tables 1–3).

Based on studies indicating total root biomass on the order of 30–50 g m^{-2} in newly established poplar plantations [5,28] the initial values for live fine root biomass and live coarse root biomass were both set to 20 g m^{-2}. The fraction of belowground biomass production allocated to live fine roots (BAF) was set to 0.3 (Table 3) based on a review of data that indicated small and fine roots are approximately 30% of total

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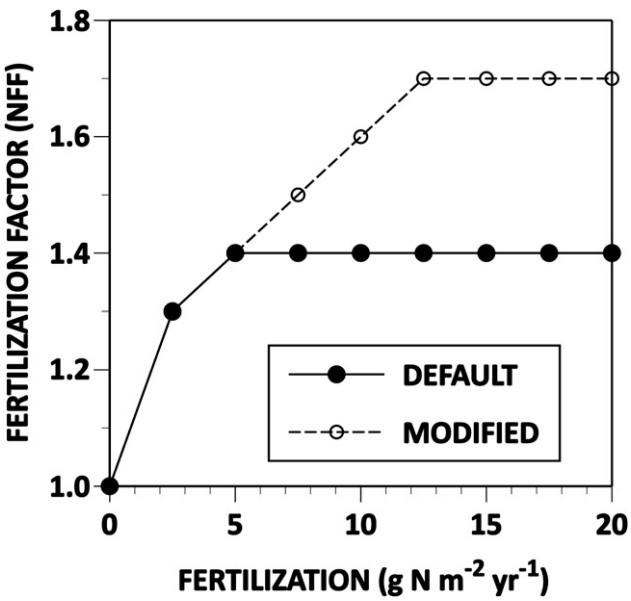

Fig. 2 – Fertilizer response curves used to model annual aboveground biomass production (AGP) in RSPM 3.9. The "default" curve was parameterized based on available literature while the "modified" curve was based on anticipated future genetic improvements to hybrid poplar.

root biomass in 4-year old trees [33]. The parameterization resulted in predicted fine root production in the model on the order of 150–300 g m^{-2} yr^{-1}. Lee and Jose [34] reported fine root production rates in the range of 200–250 g m^{-2} yr^{-1} for 7-year old *Populus* plantations on well-drained soils in southern Florida. Based on a review of root-to-shoot ratios in 4-year old *Populus* [33], the default value for RBA was set to 0.40 (Table 3).

Reported turnover times for live fine roots (0–5 mm diameter) in temperate forest ecosystems are approximately 2 years [35]. Studies of *Populus* root dynamics, in particular, indicate fine root turnover times can range from approximately 0.5–2 years [5]. The turnover time of live fine root biomass (BFL) was assigned an intermediate value of 1.3 years (Table 3) which is in agreement with fine root turnover times in *Populus* grown under varying regimes of N fertilization [28]. Data for the parameterization of the turnover time of coarse poplar roots were unavailable, but tree root turnover times decline with increasing root diameter to a maximum value of approximately 5 years [35]. Using these assumptions, the turnover time of live coarse root biomass (BCL) was assigned a value nearly four times that of fine live roots (Table 3). Dead poplar roots of different sizes decay at different rates, in part because larger *Populus* roots (5–10 mm diameter) have higher lignin:N ratios [36]. Chemistry has a strong influence on the decay of dead roots, but it is confounded with root diameter. The global average turnover time of dead roots <5 mm diameter (lignin:N ratio = 37) is nearly 1.2–1.9 years while that for roots >5 mm diameter (lignin:N ratio = 73) is approximately 5 years [37]. On this basis, rate constants for the decomposition of dead fine (BFD) and dead coarse (BCD) roots, respectively, were set to 0.67 and 0.2 yr^{-1} (Table 3). The concentration of C in dead root biomass was assumed to be 0.45 g C g^{-1}.

2.1.7. *Soil carbon sub-model*

The soil C sub-model (Fig. 1) predicted forest floor C (FFC) and two soil C pools that were distinguished on the basis of their relative turnover rates: (1) fast soil organic C (FSC), and (2) slow soil organic C (SSC) (Table 1). Forest floor C was calculated as the difference between an aboveground C flux from litterfall (LFI) and two outputs: (1) litter decomposition (DLF), and (2) incorporation of forest floor C into the mineral soil (LFS). Nitrogen fertilization of poplar plantations increases aboveground litterfall inputs [29]. To reflect this effect, the dry mass of annual aboveground litterfall was multiplied by the fertilization factor (NFF) and converted to g C m^{-2} yr^{-1} (Table 2). The annual loss of forest floor C via decomposition was calculated based on a predicted forest floor C stock and its mean residence time (COT). A fraction of forest floor C was also transferred annually to the fast soil C pool (LFS) via leaching or bioturbation. In addition, fast soil C received inputs from residual dead roots. The fast soil C stock was calculated as the difference between these former inputs and annual C losses through decomposition and transfers to slow soil C (Table 1). Decomposition of fast soil C (DFS) was calculated based on the pool size and a turnover time (CFT). The annual flux from fast to slow soil C (STB) was calculated based on the pool size of fast soil C and a "stabilization" rate constant (Tables 2 and 3). Slow soil C stocks were predicted as the difference between inputs via soil C stabilization and decomposition (determined by the mean residence time of slow soil C, CST) (Tables 1 and 2). Mineral soil C stocks (MCS) were calculated as the sum of fast and slow soil C pools and, based on the initial soil C, both cumulative and annual changes over time were calculated for mineral soil C stocks.

Initial stocks of forest floor C in the model were assigned a value of zero. In non-harvest years, the dry mass of aboveground litterfall (CLF) was assigned a value of 500 g m^{-2} yr^{-1} (Table 2) based on data from poplar plantations [33]. In harvest years, litterfall (CLF) was reduced to 10% of its assigned value to reflect reduced litterfall inputs as a consequence of tree removal. In the fallow year, following harvest, litterfall was set to zero. Each year, a fraction of forest floor C moved into the mineral soil via leaching of dissolved organic C and/or via soil fauna that break down or otherwise process surface litter. For example, earthworms may transfer a significant portion of the forest floor litter belowground. Based on reviews of C leaching from forest litter layers [38], the transfer from litter to soil (CTS) was assigned a default value of 0.17 yr^{-1}. The default value for the mean residence time of forest floor C (COT) was set to 1 year (Table 3) which reflected a rapid decomposition of forest litter and was in agreement with measured turnover times in poplar agro-forestry systems in warm climates [24].

Initial conditions for mineral soil C (CIS) and the fraction of soil C in the fast pool (CFP) (Table 3) were set on the basis of measured soil C stocks in abandoned agricultural fields in Tennessee and South Carolina [19]. The turnover time of fast soil C can vary widely depending on climate, location, and land management. The mean residence time of rapidly cycling soil C in temperate and tropical forests is ≤5 years but considerably longer (10–30 years) at higher and cooler latitudes [39]. Based on studies of C turnover in sand size soil fractions at agricultural sites [40] and in forest ecosystems along a temperature gradient [41], the mean residence time of fast soil C (CFT) was assigned a value of 5 years (Table 3). Slow

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soil C has a longer turnover time because of greater physical and/or chemical protection of soil C from decomposition. The mean residence time of slow soil C (CST) was set to 60 years (Table 3) based on a literature review [42]. The latter value was also consistent with measured turnover times of C in the silt and clay (0–50 μm) fraction of temperate agricultural soils [40]. Last, a portion of fast soil C was stabilized each year through physical and/or chemical mechanisms that increasingly protect soil C from decomposition by soil microorganisms. This transformation results in a net transfer from fast to slow soil C (STB). Based on prior modeling studies [43,44], the stabilization rate of fast soil C (STR) was assigned a default value of 0.15 yr^{-1} (Table 3).

2.1.8. Soil nitrogen sub-model

A sub-model that predicted available soil N (NAV) was used to constrain production of aboveground biomass. Inputs to available soil N (Fig. 1) included atmospheric deposition (NAD), fertilization (FRT), and net soil N mineralization (NMN). Outputs included the N demand associated with tree growth (NDM) and N leached below the rooting zone (NLH). Available soil N was modeled as the difference between these inputs and outputs (Table 1). Annual net soil N mineralization was calculated based on C fluxes associated with the decomposition of dead coarse roots (DCD), dead fine roots (DFD), fast soil C (DFS), slow soil C (DSS), and the respective C/N ratios of the foregoing transfers (Table 2). Annual N demand included N needed to grow both aboveground (NDA) and belowground biomass (NDB). Aboveground N demand (Table 2) was calculated from (1) annual aboveground production and the C/N ratio of wood (NWR), (2) annual litterfall production and the foliar N concentration (NFL) and (3) a translocation factor (NTR) that determined what fraction of foliar N demand was met by N cycling within the tree. Belowground N demand (NDB) was calculated from the annual flux of C to coarse and fine roots and their respective C/N ratios (Table 2). Inorganic soil N has no propensity to accumulate in either agricultural or forest soils, hence the commonly encountered practice of annual N fertilization. Therefore, annual N leaching was calculated as the difference between available soil N and tree N uptake (NDM) (Table 2). Mineral soil nitrogen, which is primarily organically bound nitrogen, was calculated on the basis fast soil C, slow soil C, and C/N ratios.

Available soil N represented inorganic N stocks (i.e., extractable NH_4–N and NO_3–N) that are small in relation to soil organic nitrogen. For example, pools of extractable inorganic N in hybrid poplar plantations in Minnesota (0.07 g N m^{-2}) were only about 0.01% of the measured pool of organic soil N [45]. The initial condition for available soil N was 0 g N m^{-2}. Annual additions of fertilizer to poplar plantations range from 5 to 17 g N m^{-2} [46]. Fertilization in the model was set at 12 g N m^{-2} yr^{-1} (Table 3) which is comparable to fertilizer N rates used in experimental poplar plantations in the southeastern United States [1]. No N fertilizer was applied in the fallow year following tree harvest. Atmospheric N deposition varies regionally and in proximity to emission sources. Based on rates in southern Georgia (http://nadp.sws.uiuc.edu), inorganic N deposition in precipitation is approximately 0.25 g N m^{-2} yr^{-1}. Total atmospheric N deposition was calculated as twice wet deposition [47], or 0.5 g N m^{-2} yr^{-1} (Table 3).

Carbon-to-nitrogen ratios for roots and soil C pools were derived from various sources [19,37]. Carbon-to-nitrogen ratios vary with root diameter and, based on summary data presented by Silver and Miya [37], the default C/N ratios in coarse and fine roots were 130 and 65, respectively. Concentrations of N in tree wood are low (approximately 0.16%) relative to C (48%). Therefore, a value of 300 was adopted for the wood C/N ratio (Table 3). Several studies [28,29,48] indicate that poplar leaf N concentrations range from 0.02 to 0.038 g N g^{-1}. A default value of 0.03 g N g^{-1} dry leaf was used in the model. Moreover, it is well established that plants utilize internally stored N to meet some of their N demand during the growing season. In the model, all of the foliar N demand was met by internal cycling when the translocation factor (NTR) equaled unity (or 100% translocation). Nitrogen translocation in the model was assigned a default value of 0.5 (Table 3).

2.2. Sensitivity analysis

Following development of model equations (Tables 1 and 2), but prior to model-based experiments, a sensitivity analysis was performed by individually varying each parameter by ±20% of its default setting and predicting the change in mineral soil C stocks at the end of four 7-year rotations. A sensitivity index (SI) was calculated for each parameter as follows:

$$SI = [(SCS_b - SCS_a)/X_r] \times 100$$

where SCS_b was the predicted soil C stock with a 20% increase in the parameter value, SCS_a was the predicted soil C stock with a 20% decrease in the parameter value, and X_r was the range over which the sensitivity analysis was conducted (i.e., 40%). The sensitivity analysis was different from the model-based experiments in which all parameter values, not defined as constants, varied simultaneously. Sensitivity analysis revealed the influence of each individual parameter on predicted cumulative soil C storage. In addition to the sensitivity analysis, we evaluated the effect of a modified fertilizer response curve (Fig. 2) on measures of model performance. The default fertilizer response curve was modified to yield greater fertilization factors (NFF), and consequently greater annual aboveground production of poplar biomass, at increasing levels of N fertilization up to an asymptote at 12.5 g N m^{-2} yr^{-1}.

2.3. Experimental

Following the sensitivity analysis, the model was used to forecast soil C sequestration using a factorial design that included three levels of N fertilization (3, 6, and 12 g N m^{-2} yr^{-1}), two levels of net annual aboveground production, and two annual rates of dead root decomposition (Table 4). The latter two processes (production and decomposition) are potentially determined, in part, by poplar genotype. Annual aboveground production was set to 1400 and 1800 g m^{-2} yr^{-1} for "low" and "high" yielding clones, respectively, based on data in Kauter et al. [25] and Heilman and Norby [33]. Reduced dead root decomposition (Table 4) refers to changes in both BCD and BFD (Table 3) that could arise from changes in root chemistry (e.g., concentrations of lignins, tannins, and C/N ratios) and thereby increase the overall refractory nature of dead root debris. Less

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Table 4 – Design of the factorial experiment to test the effects of fertilization, different rates of aboveground production, and different rates of dead root decomposition on predicted soil C sequestration beneath hybrid poplar plantations.

Fertilization	Annual aboveground production	Dead root decomposition
No N additions	Low yielding clone (1400 ± 280 g m^{-2} yr^{-1})	Default (values for BCD and BFD in Table 3)
		Reduced (BCD and BFD reduced by 30%)
	High yielding clone (1800 ± 360 g m^{-2} yr^{-1})	Default (values for BCD and BFD in Table 3)
		Reduced (BCD and BFD reduced by 30%)
N fertilization	Low yielding clone (1400 ± 280 g m^{-2} yr^{-1})	Default (values for BCD and BFD in Table 3)
		Reduced (BCD and BFD reduced by 30%)
	High yielding clone (1800 ± 360 g m^{-2} yr^{-1})	Default (values for BCD and BFD in Table 3)
		Reduced (BCD and BFD reduced by 30%)

dead root decay potentially increases annual soil C inputs and may therefore benefit belowground soil C sequestration. In the factorial experiment, effects of fertilization, aboveground production, and rates of dead root decomposition on soil C sequestration and other key measures of model performance were evaluated at the end of four 7-year rotations.

3. Results

3.1. *Sensitivity analysis*

The sensitivity analysis indicated changes in soil C storage were affected by variables that could be linked to particular hybrid poplar traits like rates of aboveground production (ANP), fractional belowground C allocation (BAF), and rates of root decomposition (Table 3). A higher ratio of belowground to aboveground production (RBA) was especially important and directly related to increased soil C storage. Faster decomposition rates for coarse and fine dead roots (BCD and BFD, respectively) resulted in a greater loss of C to the atmosphere as CO_2 and less residual organic C for transfer to the fast soil C pool. Hence, changes in root chemistry that prolonged dead root decomposition rates were predicted to increase soil C storage via higher soil C inputs. The latter hypothesis was further tested using the factorial, model-based experiment (see following section).

Under conditions of the sensitivity analysis, predictions of soil C sequestration were relatively insensitive to the turnover time of coarse and fine live roots (BCL and BFL, respectively) or changing C/N ratios in biomass and soil pools (Table 3). Predicted changes in soil C were directly related to the amount of internal N cycling within the tree (i.e., plant N demands met through translocation). Thus, genotypes with higher N use efficiency could be more beneficial to soil C sequestration at sites where there is a strong N limitation on poplar production. Site-specific properties that were independent of plant traits, like initial soil C stocks (CIS) or the transfer of surface litter C into the fast soil C pool (CTS), were also important to predicted rates of soil C accrual (Table 3). The predicted cumulative change in mineral soil C stocks (ΔMSC) over four 7-year rotations was inversely related to initial soil C stocks and indicated soil C loss under hybrid poplar when initial soil C stocks exceeded 6 kg C m^{-2} (Fig. 3).

Key measures of model performance, including soil C sequestration, were also sensitive to the shape of the model's fertilizer response curve (Table 5). Because of the equivalency of the default and the modified fertilizer response curves at fertilizer levels ≤5 g N m^{-2} yr^{-1} (Fig. 2), there was no effect of the modified response curve on predicted biomass yield and soil C accrual at lower rates (3–6 g N m^{-2} yr^{-1}) of N fertilization. At highest fertilization rate, the modified response curve increased cumulative harvested biomass by 11% and increased soil C sequestration by 21% (both relative to the default fertilizer response curve) (Table 5).

3.2. *Baseline simulations*

Fig. 4 illustrates the time history of predicted changes in aboveground biomass and soil C stocks over four 7-year rotations when the default parameter values in Table 3 were randomly varied (with a coefficient of variation equal to 20%) in 30 independent model runs. Aboveground biomass increased with time over each rotation (Fig. 4A) and predicted mean aboveground poplar biomass (with the 95% confidence interval in parenthesis) varied between 7.3 (7.0–7.6) kg m^{-2} at the end of the first rotation and 8.2 (8.0–8.5) kg m^{-2} at the end of the fourth

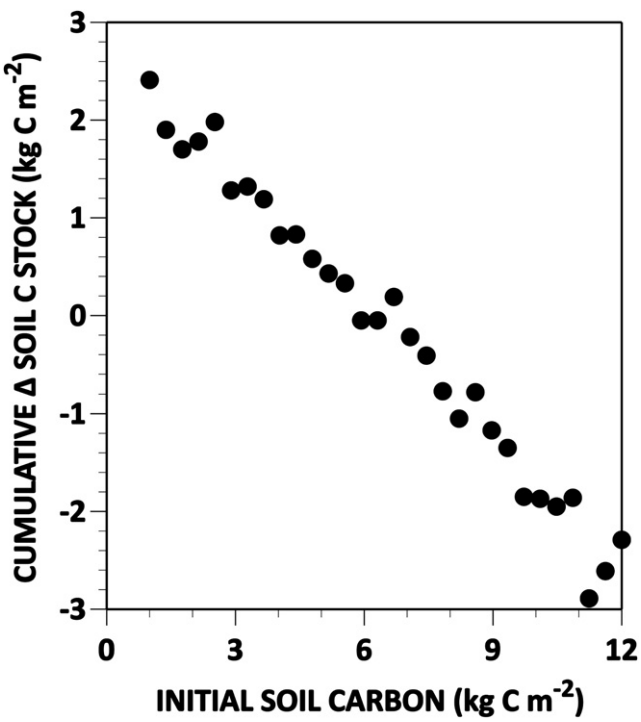

Fig. 3 – Predicted cumulative change in soil C stocks (ΔMSC) under hybrid poplar over four 7-year rotations as a function of initial (time zero) soil C stocks.

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Table 5 – Effect of fertilizer response curves (see Fig. 2) on predicted (mean ± SE) cumulative harvested biomass (CUH), cumulative change in mineral soil C (ΔMSC), annual rate of change in mineral soil C (ΔSCA), and cumulative N leaching (CNL) at the end of four 7-year rotations of low yielding hybrid poplar (see Table 4) under three different rates of annual soil N fertilization.

Fertilizer ($g\ N\ m^{-2}\ yr^{-1}$)	Fertilizer response curve	CUH ($kg\ m^{-2}$)	ΔMSC ($kg\ C\ m^{-2}$)	ΔSCA ($g\ C\ m^{-2}\ yr^{-1}$)	CNL ($g\ N\ m^{-2}$)
3	Default	18.6 ± 0.42	0.64 ± 0.04	22.1 ± 1.3	17 ± 1.3
	Modified	18.9 ± 0.37	0.73 ± 0.03	25.2 ± 1.2	16 ± 1.2
6	Default	26.0 ± 0.38	1.27 ± 0.04	43.6 ± 1.5	28 ± 1.2
	Modified	26.6 ± 0.33	1.29 ± 0.04	44.3 ± 1.2	29 ± 1.3
12	Default	31.4 ± 0.19	1.65 ± 0.03	57.0 ± 1.0	124 ± 2.8
	Modified	35.0 ± 0.23	2.00 ± 0.04	68.6 ± 1.3	118 ± 2.9

rotation. The predicted, cumulative, harvested biomass at the end of four rotations was 31.7 $kg\ m^{-2}$, or 317 $Mt\ ha^{-1}$. The mean root:shoot biomass ratio at the end of each rotation ranged from 0.26 to 0.29. Fast soil C stocks were highly dynamic and increased sharply at the beginning of each rotation as a result of belowground C inputs from root mortality following tree harvest (Fig. 4B). Following an initial lag of about 6–7 years, increasing stocks were predicted for both slow soil C (Fig. 4C) and total soil C (Fig. 4D).

The predicted increase in mineral soil C stocks over the four 7-year rotations was 1.7 $kg\ C\ m^{-2}$ (95% confidence interval = 1.61–1.75 $kg\ C\ m^{-2}$) and the predicted annual rate of soil C accrual at the end of the fourth rotation was 57 $g\ C\ m^{-2}\ yr^{-1}$. Predicted soil C partitioning among forest floor, fast soil C, and

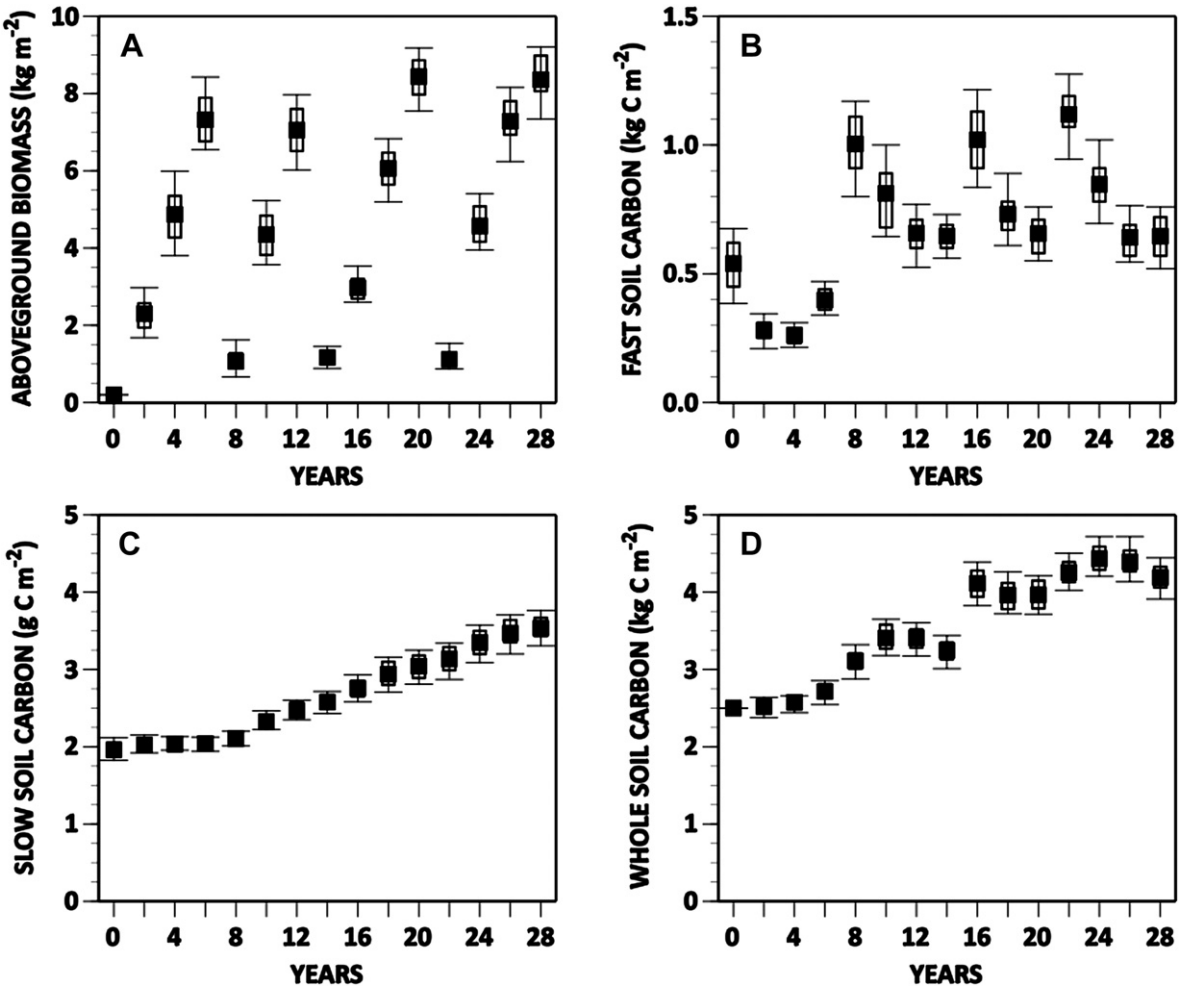

Fig. 4 – Predicted aboveground biomass (A), fast soil C (B), slow soil C (C), and total soil C stocks (D), including the forest floor, beneath a hybrid poplar plantation over four 7-year tree rotations. Solid symbols are the median predicted value and whiskers show the 10th and 90th percentiles for predicted values in each year from 30 model runs with stochastically varying parameter values (see Table 3 and text).

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slow soil C at the end of the last rotation was 6.3, 14.5, and 79.2%, respectively, indicating relatively more predicted C storage in the soil pool with the longest turnover time. The predicted mean soil CO_2 efflux from heterotrophic decomposition at the end of four rotations was 555 g C m^{-2} yr^{-1} (95% confidence interval = 519–591 g C m^{-2} yr^{-1}). Predicted rates of net soil N mineralization at the end of each rotation varied from 0.039 to 0.046 yr^{-1}, and predicted cumulative N leaching increased from the first (19 g N m^{-2}) to the last rotation (124 g N m^{-2}).

3.3. *Predictions from the factorial experiment*

Nitrogen fertilization increased predicted cumulative harvested biomass in both low and high yielding clones, as well as the cumulative change in mineral soil C stocks, the annual rate of change in soil C, and predictions of cumulative N leached over four 7-year rotations of hybrid poplar (Table 6). Nitrogen leaching was more affected by fertilization than other measures of model performance. Relative to the lowest fertilizer treatment, predicted N leaching increased by a factor of 6- to 8-fold under the highest fertilizer addition. When N fertilization was held constant, more soil C sequestration was predicted under the high yielding poplar clone, particularly at the lowest rate of N addition. Reduced decomposition of coarse and fine dead roots increased predicted soil C sequestration under both the low and high yielding clones by 53–59% at the lowest fertilization rate and by 30–35% at the highest fertilization rate (Table 6).

4. Discussion

The potential for soil C sequestration under short-rotation, perennial, bioenergy crops, like hybrid poplar, is an important uncertainty in our understanding of how managed plantations might be used to partially offset increasing atmospheric CO_2 concentrations as part of a larger climate change mitigation strategy. Mathematical modeling is a valuable tool for developing hypotheses about how to maximize C sequestration beneath short-rotation, woody biomass plantations. Two other studies have used modeling as an approach to forecasting soil C sequestration under managed forests. Grogan and Matthews [13] predicted soil C sequestration (nearly 41 g C m^{-2} yr^{-1}) under short rotation willow plantations in southern England. Our results are similar to their findings in two respects. First, predictions of soil C accrual are highly sensitive to rates of aboveground net primary production and the mean residence time of C in different soil pools (Table 3). Second, the potential for soil C sequestration is best realized on degraded soils that have low initial soil C stocks (Fig. 3). However, our prediction of C sequestration under poplar plantations grown on soils with depleted C stocks are contrary to those of Luxmoore et al. [49] who predicted that poplar biomass is inversely related to growing degree days and that poplar growth in response to N additions will be minimal in the warmest parts of the southeastern United States. Moreover, results from modeling by Luxmoore et al. [49] indicated an overall trend of decreasing soil C under *Populus* and increasing soil C under loblolly pine (*Pinus taeda*) plantations.

Our results indicated that both biomass production and soil C sequestration can increase under hybrid poplar in response to N fertilization (Table 6). However, the response of biomass and soil C sequestration was highly dependent on the shape of the fertilizer response curve that was used to determine the multiplier (NFF) for annual aboveground production (Fig. 2). Greater soil C sequestration was predicted when poplar biomass exhibited a pronounced response to N fertilization (i.e., modified curve in Fig. 2) as opposed to a more muted response (default curve in Fig. 2) that was indicated by several field studies [28,30,32]. The shape of fertilizer response curve may be amenable to genetic selection, but is also potentially site-specific. Due to random variations in model parameters that occasionally depressed available soil N and annual aboveground production, some decline in poplar production was predicted at the intermediate rate of N fertilization even though the default fertilizer response curve was flat at fertilizer rates exceeding 5 g N m^{-2} yr^{-1} (Fig. 2). Hence, both the fertilizer response curve in combination with processes influencing available soil N (like net soil N mineralization) had the potential to impact predictions of hybrid poplar production and soil C sequestration.

Table 6 – Effect of N fertilization, biomass yield, and the rate of dead root decomposition on mean (±SE) predicted cumulative harvested biomass (CUH), cumulative change in mineral soil C (ΔMSC), annual rate of change in mineral soil C (ΔSCA), and cumulative N leaching (CNL) at the end of four 7-year rotations of hybrid poplar. Default parameter values for root decomposition are presented in Table 3.

Fertilizer (g N m^{-2} yr^{-1})	Yield	Dead root decomposition	CUH (kg m^{-2})	ΔMSC (kg C m^{-2})	ΔSCA (g C m^{-2} yr^{-1})	CNL (g N m^{-2})
3	Low	Default	18.7 ± 0.38	0.66 ± 0.03	23 ± 1.1	18 ± 1.1
		Reduced 30%	19.3 ± 0.45	1.05 ± 0.05	36 ± 1.8	19 ± 0.9
	High	Default	24.1 ± 0.42	1.07 ± 0.04	37 ± 1.4	16 ± 1.7
		Reduced 30%	25.5 ± 0.43	1.64 ± 0.05	56 ± 1.8	19 ± 1.2
6	Low	Default	25.6 ± 0.35	1.23 ± 0.04	42 ± 1.3	27 ± 1.4
		Reduced 30%	26.6 ± 0.34	1.75 ± 0.04	60 ± 1.2	34 ± 1.7
	High	Default	30.3 ± 0.35	1.59 ± 0.04	55 ± 1.5	27 ± 2.0
		Reduced 30%	31.5 ± 0.41	2.17 ± 0.06	75 ± 2.0	35 ± 2.2
12	Low	Default	31.4 ± 0.19	1.65 ± 0.03	57 ± 1.0	124 ± 2.8
		Reduced 30%	31.3 ± 0.23	2.15 ± 0.05	74 ± 1.8	144 ± 2.9
	High	Default	36.6 ± 0.24	2.00 ± 0.04	69 ± 1.4	105 ± 3.7
		Reduced 30%	37.0 ± 0.28	2.70 ± 0.06	93 ± 2.1	129 ± 3.4

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Similar to other models, predictions of soil C sequestration using RSPM 3.9 are complicated hypotheses that have not yet been validated with data from long-term field experiments. The predicted rates of soil C accumulation ranged from 23 to 93 g C m^{-2} yr^{-1} depending on fertilization rate, poplar clone, and rates of dead root decomposition (Table 6). Our predicted annual rates of soil C sequestration were generally greater than the measured average rate of 34 g C m^{-2} yr^{-1} (up to a maximum of 62 g C m^{-2} yr^{-1}) following forest establishment on abandoned agricultural land in temperate climates [50]. The range of predicted annual rates of soil C sequestration (Table 6) were well within measured rates of mineral soil C accumulation (40–170 g m^{-2} yr^{-1}) beneath recently established tree plantations in the southeastern United States [19], but well below rates reported in other studies [8,51]. Predictions from the model indicated no net change in soil C stocks during the first decade of plantation growth (Fig. 2) and increased N leaching with increasing rates of N fertilization. The former prediction is consistent with reports from some field studies showing no net increase in soil C stocks during the first decade of poplar plantation establishment [9,10,52] while the latter prediction is consistent with field measurements showing increased nitrate leaching from *Populus* plantations along a N fertilization gradient [30]. Our predicted rates of N leaching (4–5 g N m^{-2} yr^{-1}) at the highest fertilizer treatment were somewhat less than rates measured under poplar stands receiving comparable levels of N fertilizer [30]. Nevertheless, the foregoing broad agreements between model predictions and field data tend to support the face validity of calculations using RSPM 3.9.

Currently, our understanding of how variation in genetic traits of hybrid poplar might impact soil C accumulation is somewhat clearer than our understanding of how soil C sequestration is affected by site-specific, edaphic factors. Genotypic variation in poplar traits affecting aboveground production, belowground C allocation, and plant N cycling were indicated by the sensitivity analysis to be important controls on soil C sequestration. Our hypothesis that changes in root chemistry that prolong dead root decomposition can increase soil C storage was also supported by the model-based experiments (Table 6). Roots that are more resistant to attack by soil microorganisms could also prolong the turnover times of fast and slow soil C pools, although the possibility of cascading effects from changing root chemistry to downstream model components was not evaluated here. The turnover time of soil C is critically important to predicted long-term soil C sequestration potential. The default parameter set (Table 3) could not sustain high soil C stocks (Fig. 3) due to the turnover times used in the model for fast and slow soil C. Most of the soil C in our model was partitioned to a slow pool that had a mean residence time of 60 ± 12 years. In the real world, there will be large site-to-site differences in the mean residence time of forest floor, fast, and slow soil C that could accentuate the importance of study site, relative to poplar genotype, as a factor controlling variation in predicted soil C sequestration. This kind of genotype x environment interaction could produce contradictory findings from both empirical and theoretical studies on the potential for long-term soil C sequestration under hybrid poplar.

The management of hybrid poplar plantations for maximizing soil C sequestration is also undertaken against a backdrop of potential genetic and environmental conditions. Modeling can help in the design of fertilization regimes to optimize both cumulative biomass production and rates of soil C sequestration over the life of a plantation. Unlike the consideration of coppiced short-rotation woody crops [13,53,54], the model-based analysis discussed here was limited to no-till replanting of poplar plantations following whole-tree harvest. One consequence of the replanting strategy was a reservoir of dead root C residing in the soil immediately after each harvest. The transfer of dead root C to the fast soil C pool in the year following tree harvest accounted for step-like increases in predicted soil C stocks over the life of the plantation (Fig. 4). Whether these step-like increases in soil C storage exist in actual managed plantations needs to be determined through field measurements.

Worldwide, the *Populus* genus contains more than thirty species, resulting in a wide range of genetic variation that segregates for nearly all traits, and many traits potentially of interest to enhancing soil C sequestration in managed plantations. Progeny from crosses within and between species, for example, have shown considerable variation for the above- and belowground distribution of biomass, tissue chemistry, and rates of litter decomposition [6,15,16,55]. In at least one of these studies, traits associated with soil C sequestration such as productivity, biomass distribution to roots, and fine root/coarse root ratios in progeny from two advance-generation hybrid poplar pedigrees were subjected to quantitative trait loci analysis and regions of the genome linked to these traits were identified [6]. It seems reasonable based on the analysis in this paper, and prior studies [56], that advanced breeding and targeted genetic manipulation could be used to select or develop hybrid poplars that display traits favoring the enhanced capacity to store C in long-lived soil pools. The greatest benefits could occur if multiple traits of hybrid poplar are modified in ways that promote soil C accumulation, even though genotype x environment interactions are expected to be significant. However, if only two or three hybrid poplar traits are amenable to manipulation, the greatest predicted gains in soil C sequestration may be realized by increasing annual aboveground biomass production, the ratio of belowground biomass allocation-to-aboveground production, and the growth response to N fertilizer. Studies designed to explore these findings in more detail, taking advantage of natural populations, segregating populations, and accelerated domestication approaches to identify genes that underlie important processes of plant productivity, biomass distribution to roots, litter quality, and the contribution of these traits to C cycle processes under realistic field environments could deepen our understanding of biological mechanisms to enhance soil C sequestration.

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