

CHAPTER 5

PROCESS-BASED MODELING OF SOIL RESPIRATION FLUXES USING A MODEL-DATA FUSION ANALYSIS

5.1 Abstract

We integrated soil carbon models with an established ecosystem process model (SIP-NET, simplified photosynthesis and evapotranspiration model) to investigate the influence of soil carbon processes on modeled values of soil CO₂ fluxes (R_{SOIL}). Model parameters were determined from literature values and a data assimilation routine that utilized a seven year record of the net ecosystem exchange of CO₂, H₂O, and environmental variables collected at a high-elevation subalpine forest (the Niwot Ridge AmeriFlux site). These soil carbon models were subsequently evaluated in how they estimated (a) the seasonal contribution of R_{SOIL} to total ecosystem respiration (TER), (b) the seasonal contribution of root respiration (R_{ROOT}) to R_{SOIL} , and (c) microbial biomass.

Explicit modeling of root dynamics led to better agreement with literature values of the contribution of R_{SOIL} to TER . Estimates of R_{SOIL}/TER when root dynamics were considered ranged from 0.3-0.6; without modeling root biomass dynamics these values were 0.1-0.2. Hence we conclude that modeling of root biomass dynamics is critically important to compare modeled and measured values of R_{SOIL}/TER .

We were not successful in modeling R_{ROOT}/R_{SOIL} or reproducing expected patterns in soil microbial biomass. We conclude that net ecosystem exchange of CO₂ and H₂O measurements alone can not constrain specific rhizospheric and microbial components of soil respiration. Reasons for this include inability of the data assimilation routine to constrain soil parameters using ecosystem CO₂ and H₂O flux measurements and not considering the effect of multiple resource limitations on the microbe biomass. Future data assimilation studies with these models should include multiple resource limitations

on soil microbial dynamics and ecosystem-scale measurements of R_{SOIL} in the parameter estimation routine, as well as experimentally determine soil model parameters not constrained by the parameter estimation routine.

5.2 Introduction

Soils are important in the terrestrial carbon cycle for their roles in the cycling and storage of carbon (*Raich and Schlesinger, 1992; Jobbagy and Jackson, 2000; Trumbore, 2000; Raich et al., 2002*). Global twentieth-century mean CO_2 emissions from soils are estimated to be 79-82 Pg C per year (*Raich and Schlesinger, 1992; Raich et al., 2002*), with a significant proportion (40-50%) of this flux derived from recently-fixed carbon that has resided for less than one year in the soil (*Trumbore, 2000*).

The soil itself plays a large role in shaping soil processes and is host to a large diversity of microbial communities whose ecological interactions influence soil CO_2 fluxes (*Fierer et al., 2003; Lipson and Schmidt, 2004; Crawford et al., 2005; Monson et al., 2006b; Göttlicher et al., 2006*). The assemblage of microbial species can vary seasonally (*Lipson and Schmidt, 2004*) as well as spatially (*Fierer et al., 2003*). Temperature and other environmental factors such as moisture strongly influence these microbial communities and their associated CO_2 fluxes from soil (*Davidson and Janssens, 2006*). Current projections of increased surface temperature and changes in moisture (*Alley et al., 2007*) will likely affect soil microbial interactions, ultimately changing the efflux of CO_2 from soils (*Schimel and Gullledge, 1998*).

From an ecosystem perspective, the CO_2 produced from respiration by soil organisms and its subsequent diffusion from the soil is a large component in the overall net ecosystem CO_2 exchange (NEE , a complete list of symbols used to refer to fluxes is given in Table 5.1) (*Goulden et al., 1996b; Lavigne et al., 1997; Janssens et al., 2001; Griffis et al., 2004b; Davidson et al., 2006b; Monson et al., 2006a,b*). Measurements of NEE can complement manipulative experiments and elucidate how biological processes contribute to terrestrial ecosystem CO_2 exchange. For example, recent studies at a high-elevation subalpine forest (the Niwot Ridge AmeriFlux site) demonstrated that winter soil respiration (R_{SOIL}) contributes 35-48% of total ecosystem respiration (TER), with a large proportion of this respiration due to microbial community composition (*Monson et al., 2006a,b*). Additionally, seasonal variation in observed soil respiration fluxes is coincident with seasonal variation in microbial community biomass (*Lipson et al., 2000; Lipson and*

Table 5.1. List of abbreviations for flux variables used in text. Flux values are integrated over the length of the timestep.

Symbol	Units	Description
GEE	g C m^{-2}	Gross primary production flux
TER	g C m^{-2}	Total ecosystem respiration flux
R_H	g C m^{-2}	Soil heterotrophic respiration flux
R_W	g C m^{-2}	Wood respiration flux
R_L	g C m^{-2}	Leaf respiration flux
R_{ROOT}	g C m^{-2}	Root respiration flux
R_{SOIL}	g C m^{-2}	Soil respiration flux (includes root and heterotrophic components)
R_A	g C m^{-2}	Autotrophic respiration flux (includes wood, leaf, and root components)
NEE	g C m^{-2}	Net ecosystem exchange of $[\text{CO}_2]$ ($GEE - TER$)
NPP	g C m^{-2}	Net primary production ($GEE - R_A$)
ET	cm water equivalent	Evapotranspiration
E_I	cm water equivalent	Immediate evaporation flux of incoming precipitation
E_S	cm water equivalent	Soil evaporation flux
E_P	cm water equivalent	Snowpack sublimation flux
T	cm water equivalent	Transpiration flux
\overline{GEE}	g C m^{-2}	Mean GEE over the last five days
\overline{NPP}	g C m^{-2}	Mean NPP over the last five days

Schmidt, 2004; *Monson et al.*, 2006b). These observations suggest that measurements of NEE , in addition to plot-level measurements of soil CO_2 fluxes, potentially provide a tool to investigate how environmental variation affects soil carbon processes and soil microbial communities.

Modeling is an approach well-suited to exploring how soil carbon processes affect NEE , as direct soil measurements can induce a disturbance to the soil matrix and potentially bias results (*Ryan and Law*, 2005). Recent reviews of soil measurements and soil modeling have emphasized the need for greater focus on understanding the short-term controls of soil respiration and coupling of belowground processes with aboveground processes (e.g. photosynthesis) (*Smith et al.*, 1998; *Fitter et al.*, 2005; *Ryan and Law*, 2005; *Trumbore*, 2006; *Davidson et al.*, 2006a).

Model-data fusion, or the utilization of parameter-estimation or data-assimilation techniques to extract information from models and observations (*Raupach et al.*, 2005) is one strategy that is amenable to advancing understanding of soil processes by direct

utilization of long-term records of NEE . One application of model-data fusion in the environmental science community is to extract meaningful information about ecosystem processes (such as process-level parameters) from the inherent stochasticity in environmental observations (*Braswell et al.*, 2005; *Clark*, 2005; *Knorr and Kattge*, 2005; *Raupach et al.*, 2005; *Xu et al.*, 2006; *Sacks et al.*, 2007). Model-data fusion can determine what parameters can be well-constrained from the existing data, ultimately reducing the number of model parameters that need to be determined via literature or by direct determination.

Measurements of R_{SOIL} are part of the standard measurements at many FLUXNET sites (<http://www.fluxnet.ornl.gov/fluxnet>). At the Niwot Ridge AmeriFlux site, *Scott-Denton et al.* (2003) showed that the rhizospheric component (roots plus nearby microbes) of R_{SOIL} is a significant contributor to R_{SOIL} . A subsequent study showed that autotrophic (roots) and heterotrophic respiration (microbes) responded differently to environmental variation (*Scott-Denton et al.*, 2006), as summertime decreases in R_{SOIL} resulted from lower heterotrophic, rather than autotrophic, contributions to R_{SOIL} .

SIPNET is an ecosystem model that has been demonstrated to be a useful tool at FLUXNET sites to decompose NEE into its component fluxes of photosynthesis (GEE) and TER (*Braswell et al.*, 2005; *Sacks et al.*, 2006, 2007). SIPNET does not explicitly model the contribution of roots or microbes to R_{SOIL} . Hence, in order to investigate autotrophic and heterotrophic contributions to R_{SOIL} using SIPNET, it is necessary to explicitly model the contributions of roots and microbes to R_{SOIL} .

The objective of this study was to model soil carbon processes with measurements of NEE . We utilized a multi-year dataset that consists of net CO_2 and H_2O fluxes made at the Niwot Ridge AmeriFlux site in conjunction with a model-data fusion approach to estimate model parameters. Hence models were evaluated by (a) model predictions of measured ecosystem fluxes, (b) the number of parameters needed for the model, and (c) comparisons of the modeled contributions of R_{SOIL} to TER , root respiration (R_{ROOT}) to R_{SOIL} , and in addition literature comparisons of these quantities and estimated parameters.

5.3 Site description

Measurements for this study were made at the Niwot Ridge AmeriFlux site, a sub-alpine forest at 3050 m elevation west of Boulder, Colorado (40°1' 58"N; 105°32' 46"W).

The three dominant conifer species at Niwot Ridge include subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*). Mean annual precipitation averages 800 mm and the mean annual temperature is 1.5 °C (Monson *et al.*, 2002). The site has been extensively studied; for further details see Bowling *et al.* (2001); Monson *et al.* (2002); Scott-Denton *et al.* (2003); Turnipseed *et al.* (2003, 2004); Bowling *et al.* (2005); Yi *et al.* (2005); Monson *et al.* (2006a,b); Scott-Denton *et al.* (2006); Sacks *et al.* (2007).

Net ecosystem exchange (*NEE*) was measured via eddy covariance. Details about the eddy covariance and meteorological measurements at Niwot Ridge can be found in Monson *et al.* (2002). From November 1998 through the present, half-hourly fluxes of CO₂ and H₂O, along with corresponding climate data, have been measured at this site. For this study we utilized flux and meteorological data from 1 November 1998 to 31 December 2005. A net CO₂ flux measurement determines *NEE*, which is equal to the sum of photosynthesis (*GEE*) and total ecosystem respiration (*TER*). Sign conventions in the micrometeorological literature (and here) typically define all nonradiative CO₂ fluxes as positive when directed to the atmosphere, so the *GEE* flux is negative and the *TER* flux is positive. Measurements of the H₂O flux determined *ET*, evapotranspiration, the sum of evaporation and transpiration. For this study we present fluxes integrated over the length of the timestep, hence CO₂ fluxes are reported as g C m⁻² and H₂O fluxes as cm water equivalent. Gaps in the half-hourly flux data arose from (a) instrument malfunction or (b) periods of atmospheric stability which can underestimate the flux measurement. These gaps were then filled with nonlinear regression or functional fits with environmental variables such as incoming radiation, air temperature, or soil temperature (Monson *et al.*, 2002).

Cumulative annual *NEE* for Niwot Ridge ranges from -60 to -80 g C m⁻², suggesting that the ecosystem is a sink for carbon (Monson *et al.*, 2002). These values for cumulative *NEE* are lower than other forest ecosystems and is attributable to the fact that this is a high-elevation site with extreme climate conditions (Monson *et al.*, 2002).

In addition to *NEE* and *ET*, six additional climate variables measured at the site were used in the model: air temperature, soil temperature, precipitation, flux density of photosynthetically active radiation, relative humidity, and wind speed. Sacks *et al.* (2006) further described the gap-filling and data processing methods utilized. Briefly, the model was run on a twice-daily time step. The exact length of each day or night time

step was based on the day of year. Twice-daily time steps that consisted of more than 50% gap-filled eddy covariance data were excluded from the optimization.

5.4 SIPNET ecosystem model

The basic model formulation of SIPNET has been described in previous papers (*Braswell et al.*, 2005; *Sacks et al.*, 2006, 2007). SIPNET is a simplified version of the PnET family of models (*Aber and Federer*, 1992; *Aber et al.*, 1996). The base model for SIPNET has three vegetation carbon pools (wood, leaves, and soil) and includes a model for soil moisture. The soil moisture model was developed by *Sacks et al.* (2007) and is described in detail in that study. SIPNET is run at a twice-daily time step. The initial conditions and fluxes are characterized by parameters listed in Table 5.2. Because Niwot Ridge is a coniferous forest, the model assumes an evergreen phenology where biomass is added at a rate proportional to the net primary productivity (photosynthesis less leaf and wood respiration, *NPP*). Photosynthesis is the only way that carbon can be added to the ecosystem. Photosynthesis adds biomass to the wood carbon pool. Allocation to other carbon pools (such as leaves) decrease the wood carbon pool.

For this study we modified how soil respiration was calculated to improve our the ability to model winter time fluxes. Previous studies (*Braswell et al.*, 2005; *Sacks et al.*, 2006, 2007) reduced soil respiration at all times of the year by a factor proportional to soil wetness. For this study, we applied this modification only when the soil temperature was greater than zero.

The most significant changes to SIPNET are (a) explicit modeling of root carbon dynamics and (b) modeling the influence of soil microbes on the soil carbon pool. Overall, four different model modifications were examined. Model parameters are determined from literature values or estimated with the model-data fusion routine described in Section 5.4.5. The various model structures are described in detail below and are conceptually shown in Figure 5.1. Table 5.2 lists the constant and optimized parameters for each model modification.

5.4.1 Base model

This model is the same one used in *Sacks et al.* (2006, 2007) and is shown in Figure 5.1a. No explicit modeling of root or soil microbial dynamics occurs. The only allocation to new biomass is to the leaf carbon pool. Respiration losses from pool *X* are modeled with the following equation:

Table 5.2. SIPNET parameters and initial conditions

Parameter	Description	Model				Range/value	Source
		Base	Roots	Quality	Microbes		
Initial pool values							
$C_{W,0}$	Initial wood carbon content (g C m^{-2})	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	9600	RM
$C_{L,0}$	Initial leaf area index ($\text{m}^2 \text{ m}^{-2}$)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	4.2	M02
$C_{S,0}$	Initial soil carbon content (g C m^{-2})	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	16000	S03
$C_{B,0}$	Initial microbe carbon content (mg C g^{-1} soil C)			<input type="checkbox"/>	<input type="checkbox"/>	0.5	L04
$C_{FR,0}$	Initial amount of fine roots as a fraction of $C_{W,0}$ (no units)		<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	0.2	NA
$C_{CR,0}$	Initial amount of coarse roots as a fraction of $C_{W,0}$ (no units)		<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	0.2	NA
$W_{S,0}$	Initial soil moisture content (fraction of $W_{S,C}$)	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	0-1	NA
$W_{P,0}$	Initial snow pack (cm water equivalent)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	0	
Photosynthetic parameters							
A_{MAX}	Maximum net CO_2 assimilation rate ($\text{nmol CO}_2 \text{ g}^{-1}$ leaf biomass s^{-1})	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	0-34	A96
F_{AMAX}	Average daily max photosynthesis as fraction of A_{MAX} (no units)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	0.76	
T_{MIN}	Minimum temperature for photosynthesis ($^{\circ}\text{C}$)	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	-8-8	A96
T_{OPT}	Optimum temperature for photosynthesis ($^{\circ}\text{C}$)	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	5-30	
K_{VPD}	Slope of VPD-photosynthesis relationship (kPa^{-1})	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	0.01-0.25	
K	Canopy PPFD extinction coefficient (no units)	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	0.38-0.62	
K_{WUE}	VPD-water use efficiency relationship ($\text{mg CO}_2 \text{ kPa g}^{-1} \text{ H}_2\text{O}$)	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	0.01-0.25	

Table 5.2 continued

Parameter	Description	Model				Range/value	Source
		Base	Roots	Quality	Microbes		
Respiration parameters							
K_F	Foliar maintenance respiration as a fraction of A_{MAX} (no units)	■	■	■	■	0.05-0.3	
K_W	Wood respiration rate at 0°C (yr ⁻¹)	■	■	■	■	0.0006-0.06	
K_H	Soil respiration rate at 0°C and moisture saturated soil (yr ⁻¹)	■	■	■		0.003-0.6	
K_B	Microbial respiration rate at 0°C (hr ⁻¹)				■	0.003-0.03	
K_{FR}	Fine root respiration rate at 0°C (yr ⁻¹)		■	■	■	0.003-0.6	
K_{CR}	Coarse root respiration rate at 0°C (yr ⁻¹)		■	■	■	0.003-0.6	
Q_{10V}	Vegetation respiration Q_{10} (no units)	■	■	■	■	1.4-8	
Q_{10S}	Soil respiration Q_{10} (no units)	■	■	■		1.4-8	
Q_{10FR}	Fine root respiration Q_{10} (no units)		■	■	■	1.4-8	
Q_{10CR}	Coarse root respiration Q_{10} (no units)		■	■	■	1.4-8	
Q_{10B}	Microbe respiration Q_{10} (no units)				■	1.4-8	
Allocation parameters							
α_L	Fraction of mean NPP allocated to leaves (no units)	□	□	□	□	0.4	S07
α_W	Fraction of mean NPP allocated to wood (no units)		□	□	□	0.2	NA
α_{FR}	Fraction of mean NPP allocated to fine roots (no units)		□	□	□	0.2	NA
α_{CR}	Fraction of mean NPP allocated to coarse roots (no units)		(†)	(†)	(†)	(†)	NA
β_{FR}	Fine root exudation as a fraction of mean GEE (no units)		□	□	□	0.05	NA

Table 5.2 continued

Parameter	Description	Model				Range/value	Source
		Base	Roots	Quality	Microbes		
β_{CR}	Coarse root exudation as a fraction of mean GEE (no units)		<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	0.05	NA
ϵ_R	Microbe assimilation efficiency of root exudates(no units)				<input type="checkbox"/>	0.01	NA
Tree physiological parameters							
$SLWC$	C content of leaves on a per-area basis (g C m ⁻² leaf area)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	270	JS
F_C	Fractional C content of leaves (g C g ⁻¹ leaf biomass)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	0.45	A95
Water-related parameters							
$W_{S,C}$	Soil water holding capacity (cm water equivalent)	■	■	■	■	0.1-36	
f_E	Water fraction immediately evaporated (no units)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	0.1	A92
f_D	Fraction of water entering soil that is immediately drained (no units)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	0.1	A92
δ_S	Snow melt rate (cm water equivalent °C ⁻¹ day ⁻¹)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	0.15	A92
R_D	Scalar relating aerodynamic resistance to wind speed (no units)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	36.5	S07
$\Re_{SOIL,1}$	Scalar relating soil resistance to soil wetness (no units)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	8.2	S96
$\Re_{SOIL,2}$	Scalar relating soil resistance to soil wetness (no units)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	4.3	S96
T_S	Soil temperature at which photosynthesis and foliar respiration are shut down (°C)	■	■	■	■	-5-5	
f	Fraction of water removable in a timestep (no units)	■	■	■	■	0.001-0.16	
f_S	Fraction of water available to vegetation in frozen soils (no units)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	0	

Table 5.2 continued

Parameter	Description	Model				Range/value	Source
		Base	Roots	Quality	Microbes		
Turnover parameters							
δ_L	Turnover rate of leaf C (year ⁻¹)	■	■	■	■	0.001-1	
δ_W	Turnover rate of wood C (year ⁻¹)	■	■	■	■	0.001-1	
δ_{CR}	Turnover rate of coarse root C (yr ⁻¹)		■	■	■	0.001-1	
δ_{FR}	Turnover rate of fine root C (yr ⁻¹)		■	■	■	0.001-1	
Soil quality parameters							
q_L	Leaf quality (unitless)			□		0.7	NA
q_W	Wood quality (unitless)			□		0.3	NA
Microbe parameters							
ϵ	Microbe efficiency to convert carbon to biomass (no units)			□	□	0.45	L07
μ_{MAX}	Microbial maximum ingestion rate (hr ⁻¹)			□	□	0.04	L07
θ_B	Microbial saturation ingestion constant (g C m ⁻²)				■	0-10000	T00
Number of optimized parameters:		17	23	23	24		
Number of parameters:		32	44	48	49		

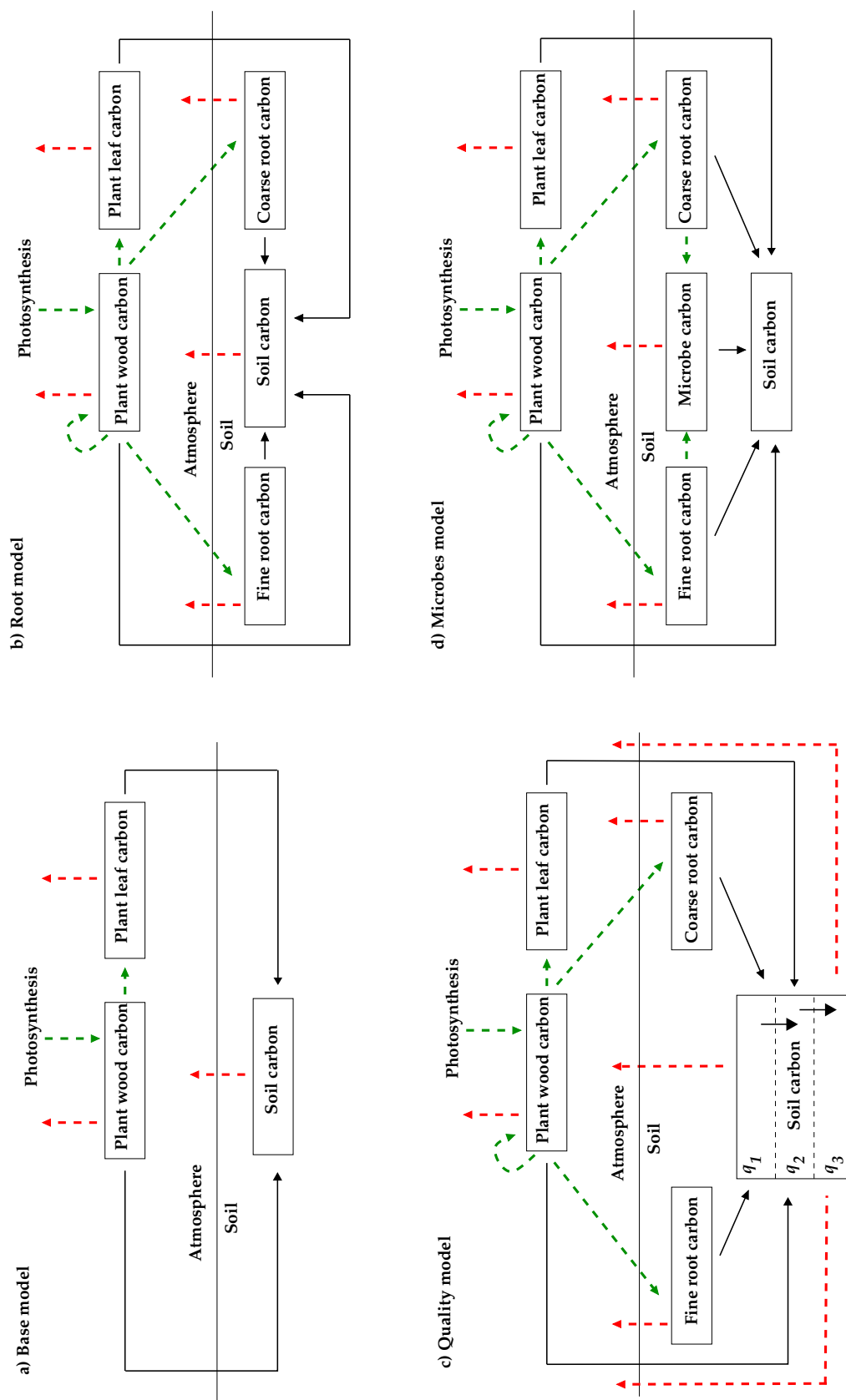
The ranges assume a uniform prior distribution.

□: Constant parameter

■: Optimized parameter

†: α_{CR} is equal to $1 - \alpha_L + \alpha_W + \alpha_{FR}$

Sources are: A92, *Aber and Federer* (1992); A96, *Aber et al.* (1996); L04, (*Lipson and Schmidt*, 2004); L07, *Lipson et al.* (In review); M02, *Monson et al.* (2002); S03, *Scott-Denton et al.* (2003); S07, *Sacks et al.* (2007); S96, *Sellers et al.* (1996); T00, *Toal et al.* (2000)



$$R_X = K_X C_X f(T_{air}; Q_{10_X}), \quad (5.1)$$

where R_X is the actual respiration rate ($\text{g C m}^{-2} \text{ day}^{-1}$), K_X a base respiration rate (day^{-1}), C_X the amount of carbon in a given pool (g C m^{-2}), and f an exponential function dependent on air temperature (T_{air}) parameterized by Q_{10_X} . Needle and wood respiration utilize the same Q_{10} value. Soil respiration is treated as in Equation 5.1, except that soil temperature is used instead of air temperature and is reduced by a factor proportional to the fractional soil wetness when soil temperatures are above zero:

$$R_{SOIL} = \begin{cases} K_S C_S f(T_{SOIL}; Q_{10_S}) (W_S / W_{S,C}) & T_{SOIL} > 0 \\ K_S C_S f(T_{SOIL}; Q_{10_S}), & T_{SOIL} \leq 0 \end{cases} \quad (5.2)$$

where R_{SOIL} is the actual respiration rate ($\text{g C m}^{-2} \text{ day}^{-1}$), K_S a base respiration rate (day^{-1}), C_S the amount of soil carbon (g C m^{-2}), f an exponential function dependent on soil temperature (T_{SOIL}) parameterized by Q_{10_S} , W_S the soil water amount (cm water equivalent), and $W_{S,C}$ the soil water holding capacity (cm water equivalent).

5.4.2 Roots model

This model expands on the Base model and is shown in Figure 5.1b. The wood carbon pool is split into (a) aboveground biomass, (b) fine roots, and (c) coarse roots. The Roots model has a more developed allocation scheme than the Base model. Allocation among the four carbon pools (wood, leaves, fine roots, coarse roots) occurs at a rate proportional to the mean NPP over the past five days in Equation 5.3:

$$\text{Growth allocation to pool X} = \alpha_X \overline{NPP}. \quad (5.3)$$

For the wood pool, this growth allocation is in addition to any carbon added for photosynthesis. To determine appropriate values for the percentage of NPP allocated to coarse and fine roots (α_{CR} and α_{FR} respectively), we assume that total belowground carbon allocation (TBCA) is approximately twice litterfall input I_L (Raich and Nadelhoffer, 1989). Assuming that TBCA is equal to $(\alpha_{CR} + \alpha_{FR})NPP$, the sum of α_{CR} and α_{FR} can be found if litterfall inputs are known:

$$\begin{aligned} TBCA &= 2I_L = (\alpha_{CR} + \alpha_{FR})NPP \\ \alpha_{CR} + \alpha_{FR} &= \frac{NPP}{2I_L}. \end{aligned} \quad (5.4)$$

Litterfall rates (I_L) and NPP derived from the Base model provide an estimate for $\alpha_{CR} + \alpha_{FR}$ in Equation 5.4. Examining the frequency distribution of $\alpha_{CR} + \alpha_{FR}$ showed

that the most frequent value of $\alpha_{CR} + \alpha_{FR}$ is approximately 0.4 (results not shown). Assuming that this belowground allocation is split equally between fine and coarse roots, this yields values of α_{CR} and α_{FR} to be 0.2.

Fine and coarse root respiratory losses (R_{ROOT}) are modeled with Equation 5.1 using soil temperature for the Q10 functional response. In addition to respiration, root carbon losses also occur through exudation into the soil. Root exudation occurs at a rate proportional (β_X) to the mean photosynthesis over the past five days:

$$\text{Root exudation from pool X:} = \beta_X \overline{GEE}. \quad (5.5)$$

5.4.3 Quality model

This model is shown in Figure 5.1c and expands the Roots model by structuring the soil carbon pool into a discrete number of soil pools that theoretically represent a continuum between more labile (high substrate quality, easily decomposed) to more recalcitrant (low substrate quality, less easily decomposed) pools of carbon. For this study, the number of soil carbon pools was fixed at three. These pools are parameterized by a variable q representing the “quality” of a particular pool (*Ågren and Bosatta, 1987; Bosatta and Ågren, 1991; Ågren and Bosatta, 1996*). For this application, the variable q takes on values between zero and one (*Bosatta and Ågren, 1985*). Higher values of q represent more labile soil carbon and lower values more recalcitrant soil carbon.

Variation in the dynamics of each soil pool occurs by associating inputs such as litter with different quality pools. For this study, leaf litter and root exudates enters the highest quality pool, and wood litter enters the second highest quality pool. Associating litter or exudates with a particular soil quality pool potentially leads to different sizes of each of the respective soil pools. As respiration is dependent on pool size, we expect variation in the amount of carbon respired across these soil pools.

In addition to litter inputs and respiration losses, decomposition influences soil pool carbon content in the Quality model. This model assumes that in the process of decomposition, microbes transform soil quality by making it more recalcitrant, thus the quality (q) of carbon that had been decomposed decreases and enters another soil quality pool. Microbial community biomass is not distinguished from soil carbon, however microbes are assumed to consist of an assemblage of carbon of difference soil quality. Soil carbon of quality q_i is incorporated into microbial biomass at the following rate:

$$\text{Ingestion rate: } \epsilon \mu_{MAX} \frac{C_{B,0}}{\sum_j C_{S,j}} C_{S,i}, \quad (5.6)$$

where ϵ is the efficiency in converting carbon into biomass (no units), $C_{S,i}$ the soil carbon in quality pool i (g C m^{-2}), μ_{MAX} the specific microbial ingestion rate (hr^{-1}) and $C_{B,0}$ the microbial biomass density (g C m^{-2}). The parameter $C_{B,0}$ represents the biomass amount of microbes in the soil; hence the term $C_{B,0}/\sum C_{S,j}$ represents the microbial concentration in the soil. For the Quality model $C_{B,0}$ was fixed. Growth respiration was given by Equation 5.7:

$$\text{Growth respiration: } (1 - \epsilon) \mu_{MAX} \frac{C_{B,0}}{\sum_j C_{S,j}} C_{S,i}. \quad (5.7)$$

Maintenance respiration from soil carbon of quality q_i is characterized with Equation 5.8, where K_H is a base respiration rate (day^{-1}):

$$R_{H,i} = \begin{cases} K_H C_{S,i} f(T_{SOIL}; Q_{10S}) (W_S/W_{S,C}) & T_{SOIL} > 0 \\ K_H C_{S,i} f(T_{SOIL}; Q_{10S}). & T_{SOIL} \leq 0 \end{cases} \quad (5.8)$$

Overall soil respiration consists of root respiration and the sum of Equation 5.8 and the soil respiration across all different soil carbon quality pools (Equations 5.7 and 5.8).

5.4.4 Microbes model

This model expands the root model and contrasts with the Quality model by explicitly tracking the microbial biomass. The model is based on past modeling studies of soil microbes (*Parnas, 1975; Smith, 1979; Toal et al., 2000*). The conceptual diagram outlining this model is shown in Figure 5.1d. Instead of using Equation 5.6 for the ingestion rate, a saturating function of C_S is used in the ingestion rate:

$$\text{Ingestion rate: } \epsilon \mu_{MAX} C_B \frac{C_S}{\theta_B + C_S} = \epsilon \mu_{MAX} C_B g(C_S). \quad (5.9)$$

where θ_B is the half-saturation constant. The function $g(C_S)$ represents the reduction in the ingestion rate due to substrate availability (namely C_S). Growth respiration is given by Equation 5.10:

$$\text{Growth respiration: } (1 - \epsilon) \mu_{MAX} C_B g(C_S). \quad (5.10)$$

In addition to this growth, we additionally hypothesized that microbes can directly incorporate root exudates into their biomass proportional to ϵ_R :

$$\begin{aligned}
\text{Root exudates to microbes: } & \epsilon_R \overline{GEE}(\beta_{FR} + \beta_{CR}) \\
\text{Root exudates to soil: } & (1 - \epsilon_R) \overline{GEE}(\beta_{FR} + \beta_{CR}).
\end{aligned} \tag{5.11}$$

Maintenance respiration is given by Equation 5.12:

$$R_H = \begin{cases} K_B C_B f(T_{SOIL}; Q_{10B}) (W_S / W_{S,C}) & T_{SOIL} > 0 \\ K_B C_B f(T_{SOIL}; Q_{10B}), & T_{SOIL} \leq 0 \end{cases} \tag{5.12}$$

where K_B is a specific microbial base respiration rate (day^{-1}), C_B the amount of microbial biomass (g C m^{-2}), and Q_{10B} the base for the Q10 exponential response. Overall soil respiration then is root respiration as well as the sum of growth and maintenance respiration (Equations 5.10 and 5.12 respectively).

5.4.5 Parameter estimation routine

The parameter optimization method used in this study was a variation of the Metropolis algorithm developed by *Hurst and Armstrong* (1996). A similar parameter estimation routine was used in *Braswell et al.* (2005); *Sacks et al.* (2006, 2007); here we only describe the relevant details.

Each given model (Base, Roots, Quality, Microbes) has a set of parameters used to characterize the model (Table 5.2). Each model has two types of parameters: fixed and estimated. Fixed parameter values are derived from literature or from unpublished data collected at the Niwot Ridge site. Estimated parameters are found from the Metropolis algorithm. Each parameter is given a range of allowable values; usually this range is selected from literature or from conventional knowledge. Initially it is assumed that the probability distribution over the range of every parameter was uniform. Data used to estimate parameters include NEE and ET .

The parameter estimation routine proceeds by exploring the parameter space to find the best parameter set that maximizes the likelihood L :

$$L = \prod_{i=1}^n \frac{1}{\sqrt{2\pi}\sigma} \exp \left[-\frac{(x_i - \eta_i)^2}{2\sigma^2} \right], \tag{5.13}$$

where n was the number of data points, x_i and η_i are the measured and modeled data and σ is the standard deviation of data. Values of x_i are either measured twice-daily NEE or ET . This likelihood function assumes that all errors are Gaussian distributed and that the standard deviation σ followed a uniform distribution. As in *Braswell et al.* (2005);

Sacks et al. (2006), for this study σ is estimated by finding the value σ_e that maximizes the likelihood:

$$\sigma_e = \sqrt{\frac{1}{n} \sum_{i=1}^n (x_i - \eta_i)^2}. \quad (5.14)$$

Braswell et al. (2005) used synthetic data sets with different values of σ and found that σ_e did, in fact, seem to reproduce the σ used to generate a synthetic data set.

At each time step, the current parameter set generates estimates of GEE , aboveground leaf respiration (R_L) and wood respiration (R_W), R_{SOIL} , immediate evaporation (E_I), soil evaporation (E_S), transpiration (T), and snowpack sublimation (E_P) using the current parameter set. These fluxes then determine modeled values of NEE and ET via Equations 5.15 and 5.16 respectively.

$$NEE = GEE - R_L - R_W - R_{SOIL} \quad (5.15)$$

$$ET = E_I + E_P + E_S + T. \quad (5.16)$$

Equations 5.15 and 5.16 determine values of η_i in Equation 5.13.

Both measured and modeled values of NEE and ET characterize the likelihood (Equation 5.13). We assumed that NEE and ET are independent measurements. Hence the overall likelihood for this study is the product of the partial likelihoods for CO_2 and H_2O using Equation 5.13. The Metropolis algorithm then proceeds to find the best parameter set that maximizes the likelihood. In the implementation of the Metropolis algorithm we utilize the log-likelihood because it is mathematically and computationally easier to determine.

The parameter optimization proceeds by randomly changing a selected parameter value and evaluating the log-likelihood with the proposed (new) parameter set. If this proposed parameter set increases the log-likelihood, then this parameter set is kept. If the proposed parameter set did not increase the log-likelihood, it is still kept with a probability equal to the ratio of the log-likelihoods. After a suitable spin-up period, the set of accepted parameter points characterizes the posterior probability distribution of the parameters (*Hurst and Armstrong*, 1996; *Braswell et al.*, 2005). Usually 500,000 iterations are used to characterize the posterior distribution.

Past studies with SIPNET (*Braswell et al.*, 2005; *Sacks et al.*, 2006, 2007) estimated parameters by utilizing the entire available record of flux measurements in the

optimization. This approach makes it difficult to evaluate model performance because parameters have already been optimized to match measured data. As a result, for this study we partition the data into two periods: the first three years of flux measurements from Niwot Ridge (November 1, 1998 to December 31, 2001) are used in the parameter estimation routine. This set of flux data will be referred to as the “optimization data.” The remainder of the unused data (January 1, 2002 to December 31, 2005) is subsequently used to evaluate the different models. This set of data will be referred to as the “validation data.”

5.5 Results

The parameter set that yielded the highest log-likelihood in the parameter estimation for each model variation (Base, Roots, Quality, or Microbes) is shown in Table 5.3. In addition, the mean and standard deviation generated from the distribution of each accepted parameter are reported. Three types of behavior characterize the posterior distributions. Well-constrained parameters are ones where the best value and mean value are similar, and the standard deviation is typically small (e.g. A_{MAX} , T_{MIN} , K , δ_L). An edge-hitting parameter is one where the best value or mean value is near the edge of its allowed range (e.g., K_H). Finally, a noninformative parameter is one where the best value and mean value differed significantly and the standard deviation is quite large (e.g. $Q10_{CR}$ and δ_{CR}). This suggests the data used in the parameter optimization (i.e. NEE and ET) could not constrain that particular parameter. Some parameters have remarkable consistency among each model variant (e.g. A_{MAX} , T_{MIN} , K_F , $Q10_V$), whereas others have considerable variation (e.g. δ_{CR} , K_W , $Q10_{CR}$). In general, many of the new parameters introduced in the Roots, Quality, or Microbes models are not well constrained. In Section 5.6.2 we evaluate how retrieved turnover parameters compare to literature studies.

Table 5.4 compares the log-likelihood for each of the models using the best fit parameter set retrieved from the parameter estimation. A higher log likelihood (closer to zero) indicates the model has a better fit with the data. The Roots and Quality models increased the overall log-likelihood from the Base model. With each model refinement (Roots, Quality, Microbes), additional parameters are introduced. Introducing these parameters to the model increases the degrees of freedom and may lead to a better model-data fit by overfitting the data. Hence one must ask if the increased log-likelihood

Table 5.3 continued

Parameter	Model		
	Base	Roots	Quality
Water-related parameters			
$W_{S,C}$ (cm water equivalent)	4.6 (4.7 \pm 0.2)	4.9 (4.8 \pm 0.1)	35.7 (35.3 \pm 0.7)
T_S ($^{\circ}\text{C}$)	0.06 (0.07 \pm 0.01)	0.06 (0.07 \pm 0.01)	0.09 (0.10 \pm 0.01)
f (no units)	0.13 (0.13 \pm 0.01)	0.13 (0.13 \pm 0.01)	0.15 (0.1 \pm 0.04)
Turnover parameters			
δ_L (yr^{-1})	0.077 (0.082 \pm 0.015)	0.087 (0.098 \pm 0.016)	0.063 (0.069 \pm 0.017)
δ_W (yr^{-1})	0.007 (0.040 \pm 0.035)	0.49 (0.35 \pm 0.30)	0.001 (0.029 \pm 0.026)
δ_{CR} (yr^{-1})		0.05 (0.18 \pm 0.25)	0.013 (0.11 \pm 0.12)
δ_{FR} (yr^{-1})		0.008 (0.26 \pm 0.28)	0.06 (0.04 \pm 0.06)
Microbe parameters			
θ_B (g C m^{-2})			9900 (9800 \pm 200)

The best value reports the parameter set that yielded the highest likelihood in the parameter estimation. The posterior mean and standard deviation determined from the distribution of each accepted parameter set during the optimization follows in parentheses.

Table 5.4. Model comparisons using the optimized parameter set retrieved from each model run.

Model	Base	Roots	Quality	Microbes
Log likelihood (LL):	-1466.5	-1427.9	-1436.2	-1671.0
NEE root mean square error:	0.19	0.19	0.19	0.18
ET root mean square error:	0.61	0.60	0.60	0.68
Number of data points (n):	4463	4463	4463	4463
Number of parameters (M):	17	23	23	24
BIC [†] :	3076	3049	3066	3543

Validation data were used to calculate these values. The root mean square error is calculated from the squared difference between the measured and modeled difference for NEE and ET . (†): The Bayesian information criterion (BIC) equals $-2LL + M \ln(n)$. A lower BIC indicates a model with greater support from the data.

associated with the Roots and Quality models truly represented a better model or an overfit of the data. The Bayesian Information Criterion (BIC) (*Schwartz, 1978*) is a way to assess this by introducing a penalty for each additional parameter introduced:

$$BIC = -2LL + M \ln(n), \quad (5.17)$$

where n is the number of data points used in the optimization, M is the number of parameters, and LL is the log-likelihood. A lower value of BIC indicates greater support for the model from the data (*Kendall and Ord, 1990*). Values of the BIC in Table 5.4 indicate that the Roots model had the greatest support from the data.

Figure 5.2 compares measured NEE to modeled NEE and measured ET to modeled ET for the Quality model using the best (e.g. highest likelihood) parameter set and the validation data. Similar results for the other models were obtained and hence are not shown. Figure 5.2 distinguishes between winter and summer time periods. For each year, summer was determined by the zero crossing of daily integrated NEE , indicating an ecosystem transition from a net source of CO_2 to a net sink of CO_2 .

During the winter, the Quality model predicts more net CO_2 uptake (more negative NEE) than observed and overestimates daytime ET (Figure 5.2c). During the summer this pattern is reversed, with the model predicting less net uptake (less negative NEE , Figure 5.2b) and less daytime ET and than measurements (Figure 5.2d). Similar results to the patterns in Figure 5.2 were found in *Sacks et al. (2006, 2007)*.

Figure 5.3 shows estimated values of NEE , GEE and TER for each of the model variants. Clearly, all models are able to generate consistent estimates of GEE and TER .

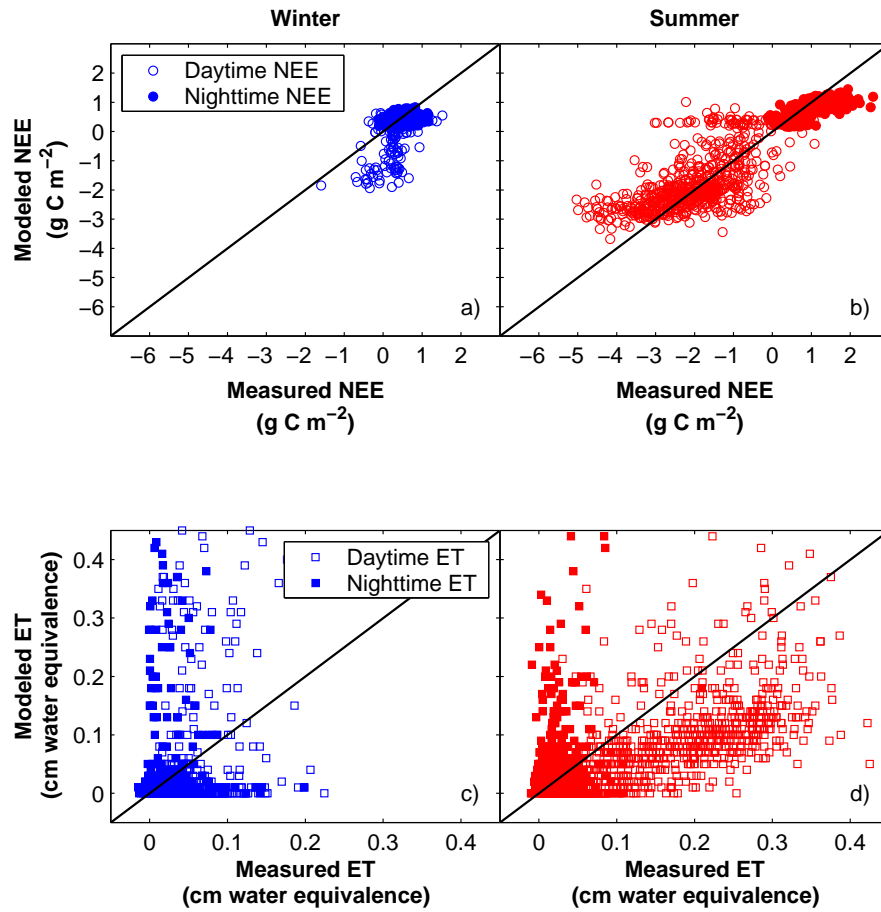


Figure 5.2. Comparison of measured and modeled *NEE* and *ET* fluxes using the validation data. Winter and summer are distinguished by a zero crossing of daily integrated *NEE* for a given year. Panels c-d) compare measured *ET* to modeled *ET*. Panels c-d) using the validation data.

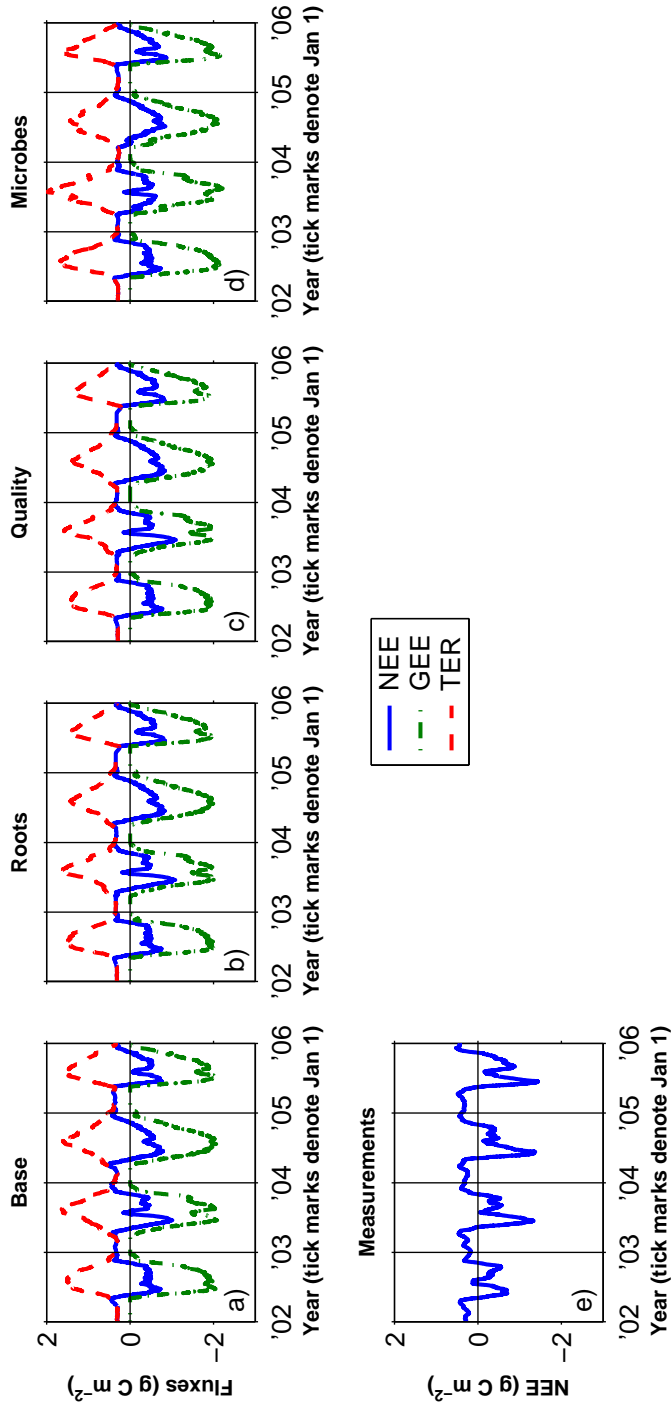


Figure 5.3. Comparison of modeled *GEE*, *TER*, and *NEE* for each of the model variants. Values shown are a running 28-day mean for the validation period only.

Figure 5.4a shows the twice daily values of measured and modeled NEE for the Roots model. Examination of the difference between measured and modeled cumulative NEE (Figure 5.4b) shows marked differences between the models not immediately evident when the twice-daily values of modeled NEE are examined in Figure 5.4a. The Base model eventually predicts less cumulative net uptake than the Quality and Microbes models. Since all models predict similar amounts of photosynthesis (Figure 5.3), we conclude that these differences arise from modeled values of respiratory fluxes. In addition, from Figure 5.4b one can infer that the Quality and Microbes models overestimate respiration, whereas the Base (and possibly the Roots) models underestimate respiration. No model could capture the increases in NEE due to drought during the summer of 2002 (Figure 5.3e).

Figure 5.5 shows values of R_{SOIL} (Figures 5.5a-d), R_{ROOT} (Figures 5.5e-f) and R_H (Figures 5.5g-j) for each of the model variants. Note that the Base model does not model root dynamics, hence R_{ROOT} and R_H are non-existent for this model. Estimates of R_{ROOT} for the Roots, Quality, and Microbes models all reached a maximum during summer months. This summer peak in root respiration agrees with seasonal trends shown in *Bond-Lamberty et al.* (2004b). Model estimates of R_H show summer-time decreases in the Roots and Quality models. These decreases are attributed to decreases in soil moisture, which reduce the amount of respiration. Suppression of heterotrophic, but not root, respiration during periods of soil moisture limitations is consistent with observations reported by *Scott-Denton et al.* (2006).

Figure 5.6 shows the distribution of values of R_{SOIL}/TER and R_{ROOT}/R_{SOIL} for each of the model variants. The Roots, Quality, and Microbes model have seasonal variation in the contribution of R_{SOIL} to TER and R_{ROOT} to R_{SOIL} , with wintertime values having R_{SOIL}/TER closer to unity. This seasonal variation arises from the assumption that foliar respiration only occurs when the air temperature is above a certain threshold, T_S , which for the Base, Roots, and Quality models was estimated to be 0.06 °C.

5.6 Discussion

It is necessary to evaluate model predictions of the different model variants (Base, Roots, Quality, Microbes). In order to make these evaluations, model estimates of the soil respiration and its components are compared to published empirical measurements of these fluxes. Additionally, model-estimated turnover rates are compared to published

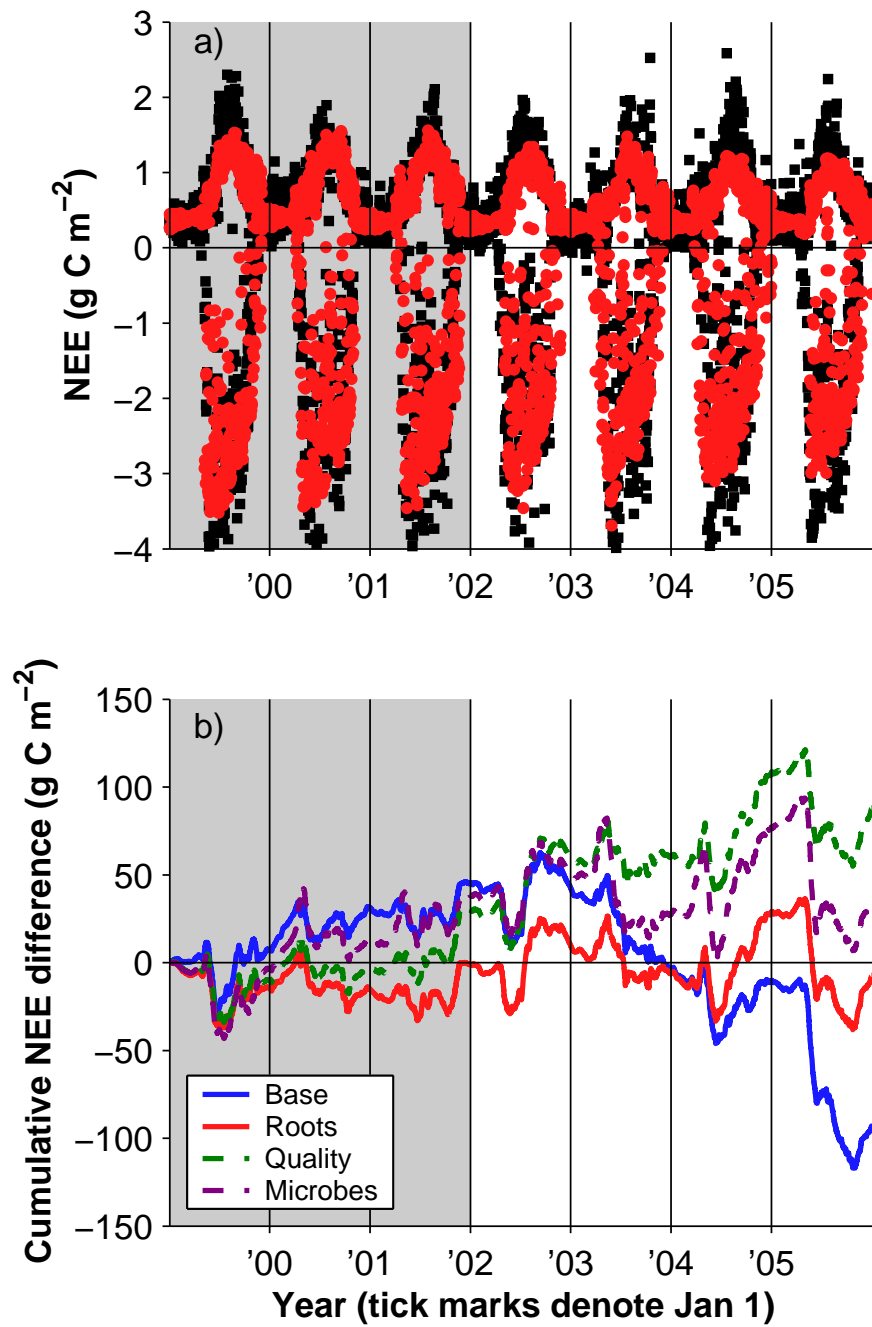


Figure 5.4. Comparisons of measured and modeled cumulative *NEE*. Panel a) shows comparison among twice-daily values of measured *NEE* and modeled *NEE* for the Roots model. Similar results for the other model variants were obtained. Panel b) shows the difference between measured and modeled values of cumulative *NEE* for each of the model variants. Gray-shaded panels in both plots represent the optimization period of fluxes used to estimate model parameters. Positive values indicate that the model is producing more negative values of *NEE* than measurements.

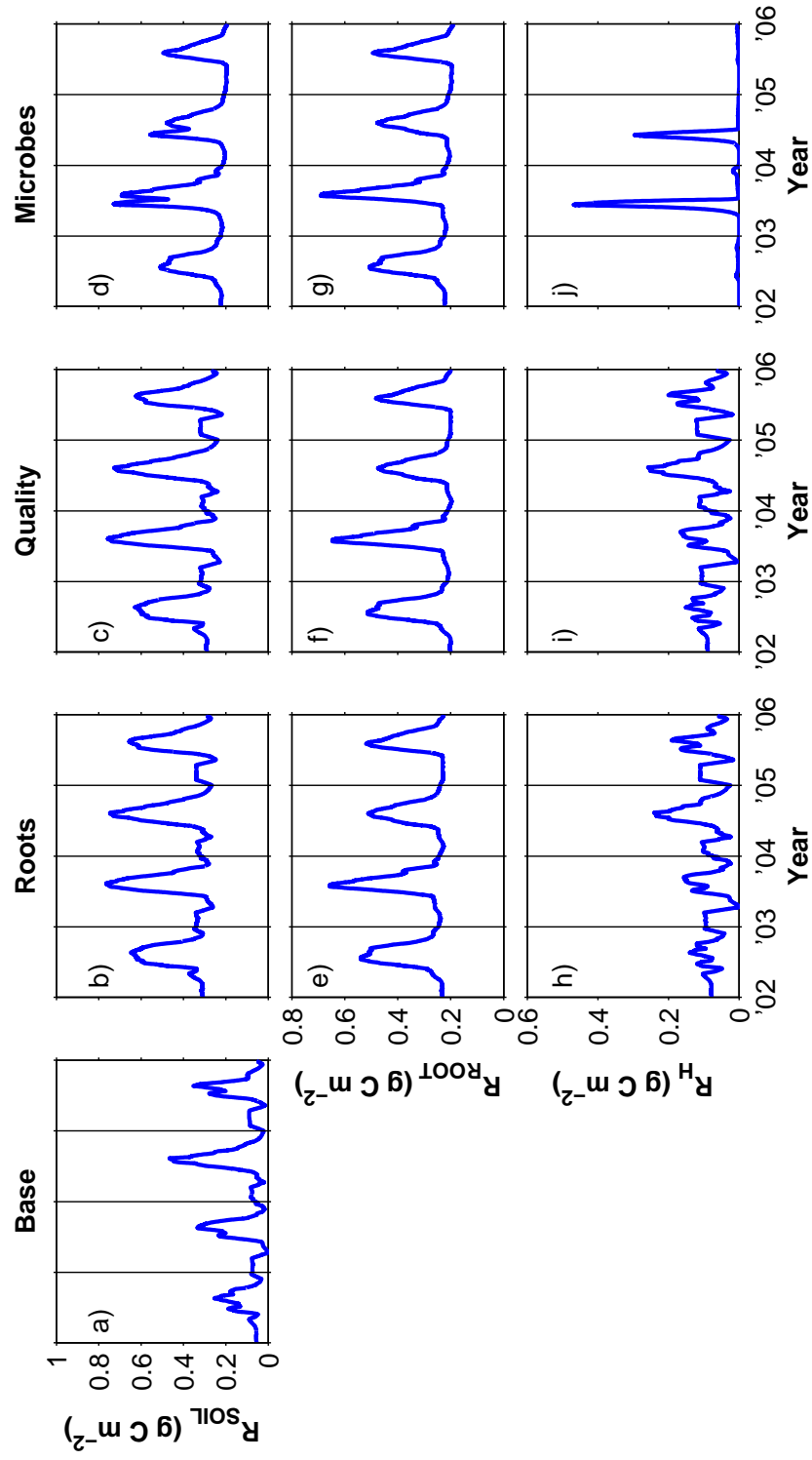


Figure 5.5. Comparison of modeled soil respiration fluxes for each of the model variants. Values shown are a running 28-day mean for the validation period. R_{ROOT} and R_H are not a component of the Base model.

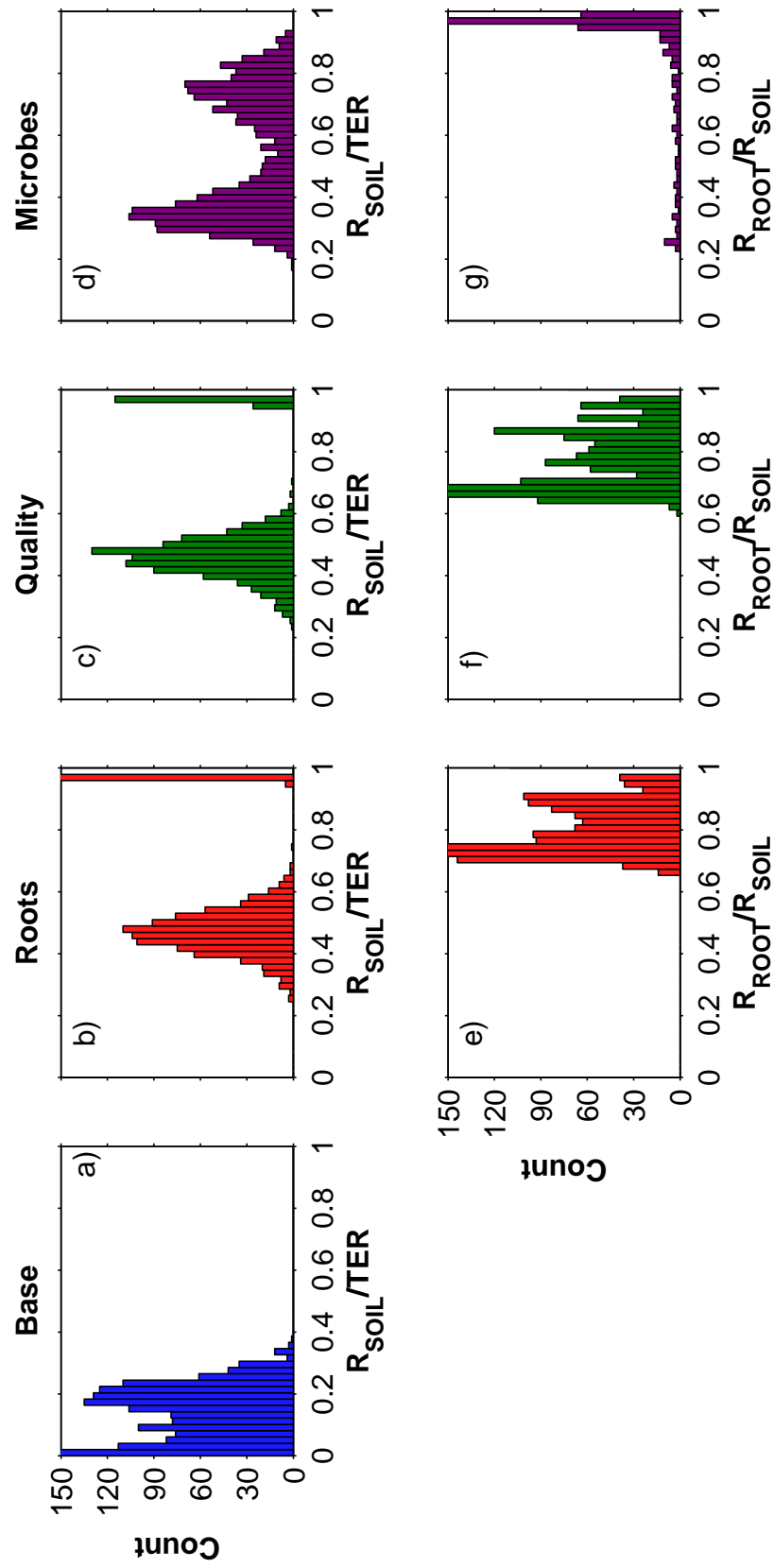


Figure 5.6. Histograms of the contribution of R_{SOIL} to TER (panels a-d) or R_{ROOT} to TER (panels e-g) for each of the model variants during the validation period. R_{ROOT} and R_H are not a component of the Base model.

estimates of these parameters. Finally, the BIC for each model variant (Table 5.4) is utilized to determine which model best reproduces measured fluxes (NEE and ET) without overfitting the data. From these comparisons we can conclude which model has the greatest success of capturing soil biological processes without large degrees of complexity.

5.6.1 Estimation of soil respiration fluxes

Past studies with SIPNET have been able to successfully partition NEE into GEE and TER (*Braswell et al.*, 2005; *Sacks et al.*, 2006, 2007), but had less success in partitioning TER into its autotrophic and heterotrophic components. Inclusion of (a) root carbon pools, and (b) structuring the soil carbon through a soil quality approach show improvements in the ability to match measured CO_2 and H_2O fluxes (Table 5.4).

Table 5.5 summarizes the estimated contribution of soil respiration to total ecosystem respiration predicted by the various models or from published studies. Mean values as an average across the validation period are reported, however we note that seasonal variation in soil respiration fluxes was found in the Roots, Quality and Microbes models (Figure 5.6). Model predicted values of R_{SOIL}/TER for the Roots, Quality, and Microbes models all fall within ranges of published studies at Niwot Ridge (*Monson et al.*, 2006a) or other literature studies (*Lavigne et al.*, 1997; *Law et al.*, 1999; *Janssens et al.*, 2001; *Davidson et al.*, 2006b). Note that the Base model significantly underestimates R_{SOIL}/TER . The mean values reported in Table 5.5 may be biased towards wintertime values, which were generally close to unity for the Roots and Quality models (Figures 5.6b-c). We argue these modeled values are overestimated; *Monson et al.* (2006a) estimated wintertime values of R_{SOIL}/TER at Niwot Ridge to be 0.35-0.48. As discussed in Section 5.5, these large values of wintertime R_{SOIL}/TER reflect the model assumption that foliar respiration is zero below a temperature threshold.

Modeled values of the contribution of R_{ROOT} to R_{SOIL} are approximately 0.8, with considerable variation (Table 5.5). These values are significantly higher than those reported in literature. A recent meta-analysis by *Subke et al.* (2006) showed that the contribution of heterotrophic respiration to soil respiration ranged between 0.4-0.7, implying that the contribution of R_{ROOT} to R_{SOIL} is approximately 0.3-0.6. Variation in this ratio may depend on forest age (*Bond-Lamberty et al.*, 2004b), time of year (*Bond-Lamberty et al.*, 2004b), plant phenology (*Davidson et al.*, 2006b), litter inputs (*Dehlin et al.*,

Table 5.5. Comparison of estimated respiration components to literature values

Parameter	Model/Literature reference	Value	Notes
R_{SOIL}/TER	Base	0.14 (0-0.37)	
	Roots	0.68 (0.25-1)	
	Quality	0.67 (0.25-1.0)	
	Microbes	0.53 (0.18-0.93)	
	<i>Monson et al.</i> (2006a)	0.35-0.7	Niwot Ridge study
	<i>Law et al.</i> (1999)	0.76	Ponderosa pine forest
	<i>Janssens et al.</i> (2001)	0.69 ± 0.35	Average across 18 Euroflux sites
	<i>Lavigne et al.</i> (1997)	0.48-0.71	Range across six coniferous boreal sites
	<i>Davidson et al.</i> (2006b)	0.5-0.8	
R_{ROOT}/R_{SOIL}	Base	N/A	
	Roots	0.81 (0.65-1.0)	
	Quality	0.78 (0.61-1.0)	
	Microbes	0.99 (0.88-1)	
	<i>Hanson et al.</i> (2000)	0.1-0.9	Review of published studies
	<i>Högberg et al.</i> (2001);	0.5-0.65	Forest girdling study
	<i>Bhupinderpal-Singh et al.</i> (2003)		
	<i>Bond-Lamberty et al.</i> (2004a)	0.3-0.5	Review of published studies from 54 sites
	<i>Bond-Lamberty et al.</i> (2004b)	0.05-0.4	Study across a black spruce chronosequence
	<i>Subke et al.</i> (2006)	0.3-0.6	Meta-analytical review of published studies
	<i>Wang and Yang</i> (2007)	0.5-0.8	Range across six temperature forests
	<i>Carbone et al.</i> (2007)	0.2 ± 0.03	^{14}C pulse-labeling study

Modeled values and literature studies of the contribution of R_{SOIL} to TER and R_{ROOT} to R_{SOIL} . Modeled values are given as a mean across the validation period followed by the minimum and maximum values in parentheses.

2006; *Cizneros-Dozal et al.*, 2007), nutrient cycling (*Brooks et al.*, 2004), or ecosystem type (*Subke et al.*, 2006). Methodological differences may have an effect on experimental estimates of R_{ROOT} and by association R_{ROOT}/R_{SOIL} ; these are discussed further in *Hanson et al.* (2000); *Hendricks et al.* (2006); *Jassal and Black* (2006); *Subke et al.* (2006).

Note how the Microbes model has particularly high values of R_{ROOT}/R_{SOIL} . This suggests that the Microbes model is incorrect or that microbial respiration does not have a large contribution to R_{SOIL} . Assuming microbial respiration does not have a large contribution to R_{SOIL} contradicts *Scott-Denton et al.* (2003), who showed that microbial biomass was a significant predictor of plot-level soil respiration measurements, whereas root biomass was not. Reasons for these low values of R_{ROOT}/R_{SOIL} are further discussed in Section 5.6.3.

The estimated contribution of R_{SOIL} to TER and R_{ROOT} to R_{SOIL} in Table 5.5 demonstrates that while these model refinements lead to better agreement with studies in partitioning R_{SOIL} from TER , additional work is needed to further partition R_{SOIL} into its constituent components R_{ROOT} and R_H . Biological mechanisms not accounted for in the different models (Roots, Quality, Microbes) may have a significant impact on the modeled fluxes. Studies have shown significant CO_2 fluxes from winter snowpacks (*Brooks et al.*, 2004; *Hubbard et al.*, 2005; *Monson et al.*, 2006b), with increased soil respiration rates during periods of snowmelt (*Hirano*, 2005; *Monson et al.*, 2006a). *Hirano* (2005) argued that increased respiration rates during snowmelt periods were due to a release of labile substrates from litter decomposition. *Scott-Denton et al.* (2006) observed similar respiration rates during late winter, but demonstrated that this respiration was stimulated from a pulse sucrose (potentially tree-derived) that stimulated respiration. In addition, physical, rather than biological, mechanisms, may lead to increased CO_2 fluxes from soils during winter. *Takagi et al.* (2005) made half-hourly CO_2 measurements belowground and in the snowpack itself and observed mixing of CO_2 into the snowpack during windy conditions. Not considering these physical mechanisms in SIPNET may lead to unrealistic values for the estimated parameters. Further modifications to SIPNET that incorporate these substrate linkages and models of pressure-pumping of CO_2 into snowpacks (*Massman et al.*, 1997; *Hubbard et al.*, 2005) could improve the ability to estimate R_{ROOT}/R_{SOIL} .

5.6.2 Evaluation of allocation parameters and estimated turnover rates

Table 5.6 summarizes turnover rate parameters estimated from the various models or from published studies. As discussed in Section 5.5, leaf turnover rate (δ_L) is a parameter well-constrained from the data assimilation. When these values are converted to litterfall rates, they compare favorably with literature values. Needle turnover rates in the range of 0.05-0.09 yr^{-1} correspond to leaf litterfall rates of 100-180 $\text{g C m}^{-2} \text{ yr}^{-1}$, assuming leaf biomass is approximately 900 g C m^{-2} and the fractional carbon content of leaves is 0.45. For our simulations, the final values of leaf biomass across all model variants range from 800-950 g C m^{-2} (results not shown). These litterfall rates are certainly within the range of values from a variety of ecosystems reported in *Davidson et al.* (2002). *Laiho and Prescott* (1999) reported annual litterfall input for *A. lasiocarpa* and *P. englemanni* forests to be 200 $\text{g C m}^{-2} \text{ yr}^{-1}$ and 240 $\text{g C m}^{-2} \text{ yr}^{-1}$ respectively. Assuming that half of the litter is foliage, this would correspond to leaf litter input rates of 100-120 $\text{g C m}^{-2} \text{ yr}^{-1}$.

The wood turnover rate parameter (δ_W) for the Base model is a well-constrained parameter, however this parameter is not well-constrained for any of the model variants. Assuming wood biomass is 5500 g C m^{-2} and a fractional carbon content of 0.5 (*Laiho and Prescott*, 1999), then wood turnover rates of 0.01-0.04 yr^{-1} correspond to wood litterfall rates of 110-440 $\text{g C m}^{-2} \text{ yr}^{-1}$. Woody litterfall input ranges derived from reported values in *Laiho and Prescott* (2004) were 100-120 $\text{g C m}^{-2} \text{ yr}^{-1}$; these measured values are near the low end of the modeled ranges. Hence we have reason to suspect that estimated values of δ_W for the Roots, Quality, and Microbes models may be too high.

Estimated fine and coarse root turnover rates have considerable variation among each of the model variants, suggesting that *NEE* and *ET* data alone could not adequately constrain these parameters. While there is considerable variation in the root turnover parameters, published literature values have considerable variation as well. *Gill and Jackson* (2000) reviewed 190 published studies and reported root turnover rates in temperate coniferous forests to range from 0.1-0.8 yr^{-1} . Additionally, *Gill and Jackson* (2000) reported greater fine root turnover rates than coarse root turnover rates. This variation may arise from methodological biases used to determine turnover rates (*Hendricks et al.*, 2006; *Subke et al.*, 2006).

The considerable variation in the model-estimated turnover parameters may reflect the simplistic way SIPNET treats turnover of particular carbon pools. Turnover rate

Table 5.6. Comparison of estimated turnover rate parameters to literature values

Parameter	Model/Literature reference	Value	Notes
δ_L (yr ⁻¹)	Base	0.077	
	Roots	0.087	
	Quality	0.091	
	Microbes	0.063	
	<i>Laiho and Prescott</i> (1999)	0.051-0.058 (†)	Separate <i>P. englemanni</i> and <i>A. lasiocarpa</i> study site
δ_W (yr ⁻¹)	Base	0.007	
	Roots	0.49	
	Quality	0.76	
	Microbes	0.001	
	<i>Laiho and Prescott</i> (1999)	0.009-0.01 (†)	Separate <i>P. englemanni</i> and <i>A. lasiocarpa</i> study site
δ_{CR} (yr ⁻¹)	Base	N/A	
	Roots	0.05	
	Quality	0.11	
	Microbes	0.013	
	<i>Arthur and Fahey</i> (1992)	0.056	Mixed <i>P. englemanni</i> and <i>A. lasiocarpa</i> forest
δ_{FR} (yr ⁻¹)	Base	N/A	
	Roots	0.008	
	Quality	0.002	
	Microbes	0.06	
	<i>Arthur and Fahey</i> (1992)	0.137	Mixed <i>P. englemanni</i> and <i>A. lasiocarpa</i> forest

(†): Derived from reported litterfall of 205 g m⁻² yr⁻¹ for *A. lasiocarpa* and 235 g m⁻² yr⁻¹ for *P. englemanni*, assuming that 50% of litter was needles and leaves (*Laiho and Prescott*, 1999). This number was then multiplied by the fractional C content of leaves (0.45) and wood (0.5) and dividing by leaves and wood biomass (assumed to be 900 and 5500 g C m⁻² respectively).

parameters represent not only loss from a particular carbon pool as litter, but also subsequent decay and release of that carbon into the soil carbon pool. Decay and subsequent release into the soil typically occurs at a much slower rate than litterfall, which would decrease the value a particular turnover parameter. For example, *Laiho and Prescott* (2004) reported values of coarse woody debris decay rates in coniferous forests to be much lower than input rates ($0.002\text{-}0.07\text{ yr}^{-1}$), with a mean rate approximately 0.02 yr^{-1} . In addition, *Johnson and Greene* (1991) reported values of decay rates of *P. englemannii* to be between $0.0025\text{-}0.0054\text{ yr}^{-1}$. Additionally, reported spatial variation of root turnover rates in the soil (*Gaudinski et al.*, 2001) challenges the use of a single model parameter to represent root turnover.

This study assumes a constant allocation to roots, leaves, and wood. This constant allocation assumption has broad support in the literature (*Raich and Nadelhoffer*, 1989; *Bond-Lamberty et al.*, 2004a; *Hendricks et al.*, 2006; *Subke et al.*, 2006). We derived values of α_{CR} and α_{FR} from an assumed relationship between TBCA and litterfall rate (*Raich and Nadelhoffer*, 1989). This relationship has been found to be highly uncertain, and perhaps larger, for forests not at steady state *Davidson et al.* (2002). Niwot Ridge is recovering from early twentieth-century logging (*Monson et al.*, 2002); hence applying the relationship from *Raich and Nadelhoffer* (1989) may underestimate α_{CR} and α_{FR} .

We chose a five-day time period between photosynthesis and structural allocation of carbon. This argues that there is a five day lag between when carbon is assimilated to when it could be potentially be respired. Past studies using (a) stable isotope tracers (*Ekblad and Högberg*, 2001; *Bowling et al.*, 2002; *Knobl et al.*, 2005; *Schaeffer et al.*, In preparation), (b) tree girdling to remove photosynthate supply (*Högberg et al.*, 2001), (c) radiocarbon tracing techniques (*Carbone et al.*, 2007), or (d) soil CO_2 measurements combined with measurements of *NEE* (*Tang et al.*, 2005) have estimated this lag to vary from 1-10 days. Hence our choice of a five day lag is appropriate but highly uncertain.

5.6.3 Evaluation of soil microbe models

The Quality model presented here is based on a discrete version (*Bosatta and Ågren*, 1985) of a continuous time-continuous quality model (*Ågren and Bosatta*, 1987; *Bosatta and Ågren*, 1991; *Ågren and Bosatta*, 1996). For simplicity, we assume that soil quality does not influence ingestion rates (μ_{MAX}), efficiency (ϵ), or respiration parameters (K_H or Q_{10H}). Previous modeling studies have argued that μ_{MAX} and ϵ should be an increasing

function of quality (*Ågren and Bosatta, 1987; Bosatta and Ågren, 1991; Ågren and Bosatta, 1996; Bosatta and Ågren, 1999*). Initial data assimilation tests showed that there was not enough information in the flux data to constrain μ_{MAX} or ϵ (results not shown). By association, any quality-dependent interactions would not be well-constrained.

Temperature may have an additional effect on soil parameters. There is current discussion in the literature over the temperature sensitivity of soil organic matter pools (*Knorr and Kattge, 2005; Reichstein et al., 2005a; Fierer et al., 2005, 2006; Subke et al., 2006; Davidson and Janssens, 2006*). *Bosatta and Ågren (1999)* used thermodynamic considerations to derive an Arrhenius type equation for microbe ingestion rate that was increasing function of temperature. *Hyvönen et al. (2005)* applied this model to soil samples collected from coniferous forests and found good agreement between model and theory. Temperature dependence in the ingestion rate (μ_{MAX}) or efficiency (ϵ) could generate different results than the ones presented here. *Fierer et al. (2006)* analyzed the temperature sensitivity of soil organic carbon from 77 different soil samples and found Q10 values to range from 2.2-4.6. Estimated soil temperature sensitivities from the Base (Q_{10S}) and Microbes (Q_{10B}) models fell outside this range, however the estimated value of Q_{10S} for the Roots and Quality model were approximately 2.9. In addition, Q10 functional responses are known to vary with temperature (*Tjoelker et al., 2001; Wythers et al., 2005; Davidson and Janssens, 2006; Fierer et al., 2006*). *Sacks et al. (2006)* found that including such seasonal variation in the Q10 and base soil respiration parameters improved the model-data fit. Because of the additional number of parameters added to each model refinement and the inability to adequately constrain these parameters from eddy flux data (Table 5.3), including additional affects of temperature in the model parameters would complicate the analysis.

For this study, litter and root exudates are quality dependent, leading to potential difference in the respiration from these different soil quality pools. The assumption of quality-dependent litter is supported in a recent study by *Dehlin et al. (2006)*, which found that microbial communities responded differently to mixtures of different substrates than when grown with individual substrates alone. Additionally, for this study, soil is always degraded to a lower quality with no delay between subsequent ingestion and release back to the soil. Subsequent degradation in soil quality may be valid for application of the quality model on longer timescales (decades to centuries, *Ågren and Bosatta (1987)*), but may not be appropriate for SIPNET on a twice-daily timestep. In addition, while a

key facet of continuous quality models is the continual degradation of the soil to more recalcitrant materials (*Ågren and Bosatta, 1987; Bosatta and Ågren, 1991; Ågren and Bosatta, 1996*), some fraction of soil of quality q_i could remain at that quality instead of being degraded to quality q_{i-1} .

One of the challenges of the soil quality model is parameterizing measurements of soil quality mathematically. The most general definition of quality is the accessibility of a substrate for decomposition (*Ågren and Bosatta, 1996*). Further expansions of the definition of soil quality could depend on physical parameters (e.g. water content, density), chemical factors (pH, total organic carbon), biological activity (microbial activity, presence of pathogens) (*Burns et al., 2006*), or radiocarbon content (*Trumbore, 2000*). *Bosatta and Ågren (1999)* utilize kinetic rate theory arguments to argue that quality should be related to the number of steps it takes for a microbe to ingest a molecule. Future studies should explicitly link these additional definitions of soil quality with measurements (e.g. soil temperature and moisture), or as we discuss in Section 5.6.4, association of resource availability.

While the Microbes model is able to reproduce expected patterns in ecosystem scale respiratory fluxes (namely GEE , TER , and R_{SOIL}), modeled values of R_H are almost always zero (Figure 5.5j). We argue that these unrealistic results arise from not correctly modeling resource limitations that would affect microbial biomass dynamics. Three related observations give support for this argument.

First, microbial parameters that are held constant (such as μ_{MAX}) may not be correctly determined. *Toal et al. (2000)* reviewed literature values of soil microbial maximal growth rates and determined a range for μ_{MAX} from 0.1-0.4 hr^{-1} . Experimental determinations of μ_{MAX} at Niwot Ridge are an order of magnitude lower (*Monson et al., 2006b; Lipson et al., In review*). This decrease may be explained by the low soil temperatures at Niwot Ridge. A study by *Buford Price and Sowers (2004)* found significant variation with temperature in the growth rate of microbes collected from a variety of ecosystems. That study reported ranges of μ_{MAX} to be from 0.01-0.1 hr^{-1} in temperature ranges of 0-30°. The mean soil temperature over the present study was 2.3°C and the μ_{MAX} of 0.04 hr^{-1} is within the ranges of values reported by *Buford Price and Sowers (2004)*. Furthermore, Niwot Ridge has lower productivity than most ecosystems (*Monson et al., 2002*) and soils are generally nitrogen limited (*Lipson et al., 1999*). Microbial communities in subalpine forests are sensitive to changes in moisture,

moisture, and nutrient availability (*Lipson et al.*, 1999; *Lipson and Schmidt*, 2004; *Brooks et al.*, 2004; *Withington and Sanford*, 2007; *Lipson*, 2007). Nitrogen and water constraints would lower the overall growth rate. Finally, the study by *Toal et al.* (2000) focused more on rhizosphere carbon dynamics. In general the rhizosphere is an area with high substrate availability that could support microbial populations with higher values of μ_{MAX} . The present study determines microbial growth kinetic parameters averaged over the entire soil, and hence we would expect μ_{MAX} to be lower.

Second, the retrieved value for K_B (0.03 hr^{-1}) is significantly higher than estimated K_S from the other model variants and one to two orders of magnitude higher than values reported in *Toal et al.* (2000). This high value of K_B led to immediate decreases in the microbial biomass pool. However if the value of K_B is reduced to in half (0.015 hr^{-1}), modeled microbial biomass values are more dynamic (dashed line in Figure 5.7a). The soil carbon pool sharply decreases as microbial biomass undergoes rapid increases (Figure 5.7b). The peaks in C_B in Figure 5.7a are due to root exudates, as they were not present when ϵ_R was set to zero (results not shown). These rapid increases in C_B additionally generated unrealistic values of R_H (Figure 5.5j). These model simulations suggest the strong sensitivity of the Microbes model to the value of K_B as well as its sensitivity to perturbations (e.g. root exudates).

Third, modeling of additional processes not accounted for in the Microbes model may be important. As previously discussed, for these subalpine soils, microbial biomass is strongly influenced by nutrient availability. Microbial biomass at Niwot Ridge ranges from approximately $0.4 \text{ mg C g}^{-1} \text{ soil C}$ in the summer to $0.6 \text{ mg C g}^{-1} \text{ soil C}$ in the winter (*Lipson and Schmidt*, 2004). This seasonal change in biomass is a combination of a variety of factors: (a) thermal insulation beneath snowpacks leading to microbial survival and growth beneath winter snowpacks (*Brooks et al.*, 1996; *Monson et al.*, 2006b), (b) greater substrate availability in winter soils (*Lipson et al.*, 1999; *Scott-Denton et al.*, 2006), and (c) seasonal differences in the microbial community species composition (*Lipson et al.*, 2000, 2002; *Lipson and Schmidt*, 2004; *Monson et al.*, 2006b; *Lipson et al.*, In review). Warming temperatures and changing substrate availability are assumed to be the cause for this community shift (*Lipson et al.*, 2000, 2002). For the Microbes model, the only nutrient considered is carbon. The function $g(C_S)$ in Equation 5.9 is the reduction in the ingestion rate due to substrate availability (namely C_S). If the value of $g(C_S)$ is near unity, then it is assumed that some resource other than carbon is potentially limiting.

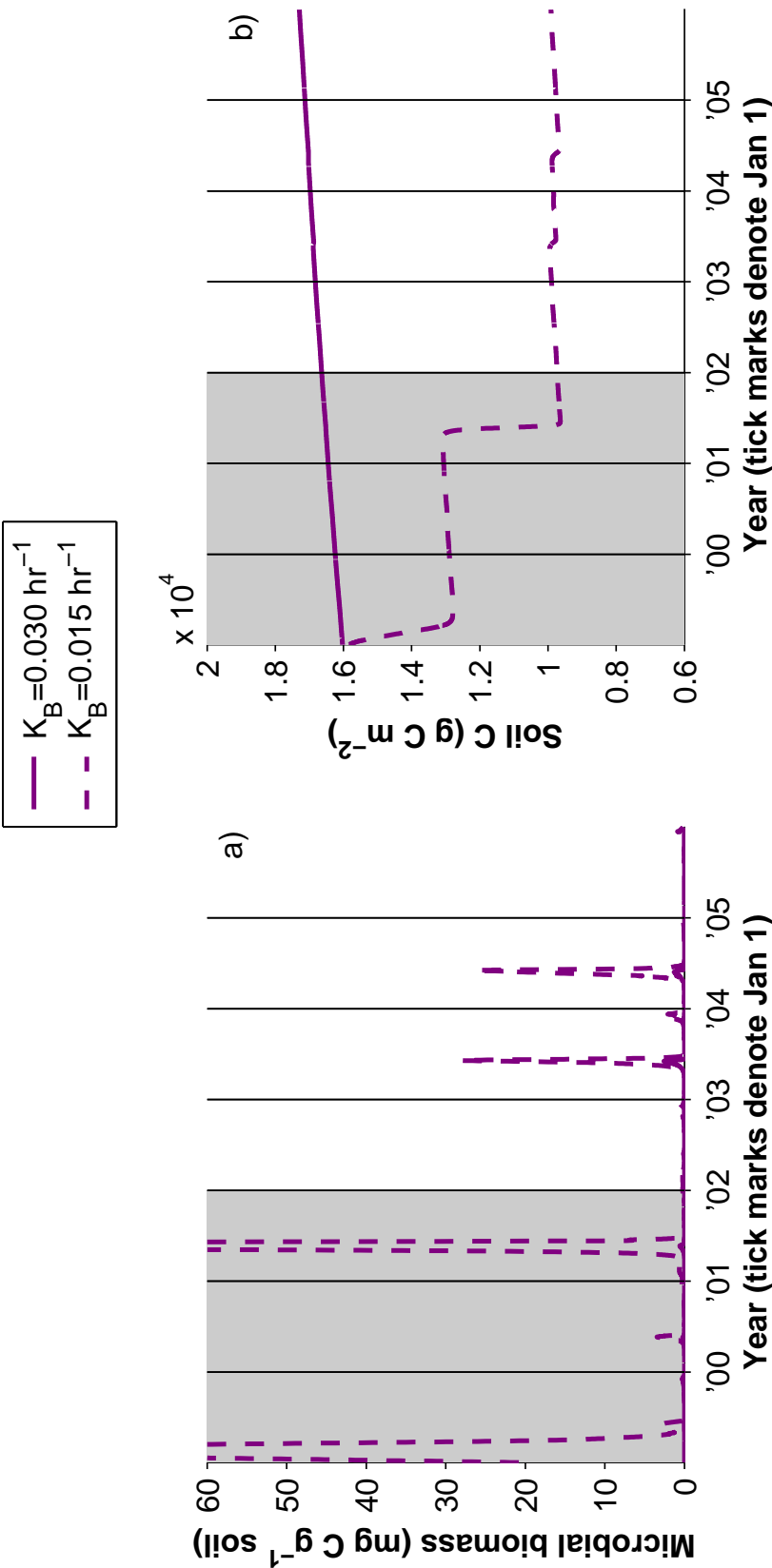


Figure 5.7. Comparison of modeled microbial biomass (panel a) and soil carbon (panel b) when $K_B = 0.03 \text{ hr}^{-1}$ (solid line) and $K_B = 0.015 \text{ hr}^{-1}$. Gray-shaded values indicate the optimization period.

Additional model refinements that incorporate Leibig's law of the minimum (*Leibig*, 1840) or stoichiometric considerations (*Loladze et al.*, 2000) may generate the patterns of the microbe biomass pool shown in Figure 5.7 without leading to sharp decreases in the soil carbon pool.

5.6.4 Overall model evaluation

Figure 5.4a shows that all the models could produce reasonable values of NEE that corresponded well with measurements. Overall, these soil carbon models did not detract from the ability of SIPNET to partition NEE into GEE and TER (Figure 5.3).

Figures 5.2a-b show how the Quality model predicts more net CO_2 uptake (more negative NEE , less respiration) than measurements during the winter and less net uptake (less negative NEE , more respiration) during the summer. This compromise between seasonal differences in respiration is influenced by the parameter estimation routine, which determines the best parameter set over *all* values simultaneously. In order to have a non-zero contribution to aboveground respiration during the summer, the parameter estimation routine would tend to favor decreased soil respiration parameters to match measured values of summertime NEE . However because aboveground respiration is significantly reduced during the winter, to match measured values during the winter, the parameter estimation would favor increased soil respiration parameters.

Table 5.5 shows that modeling of root dynamics is absolutely necessary to obtain reasonable values of the contribution of R_{SOIL} to TER , as the Base model significantly underestimated R_{SOIL}/TER . However the Roots, Quality, and Microbes models used in this study overestimated the contribution of R_{ROOT} to R_{SOIL} . Reasons for this have previously been discussed in Section 5.6.1.

The BIC from Table 5.4 shows that the model with the lowest BIC is the Roots model. The penalty for each additional parameter (the value of $\ln(n)$ in Equation 5.17) is approximately 9. Arguably the lower BIC from the Roots model is a marginal improvement over the Base and Quality models. The Roots, Quality, and Microbes models have at least 6 additional parameters than the Base model. If some of these additional parameters could be determined from direct experimentation, this would reduce the value of the BIC for the Roots and Quality and make the BIC comparison more robust.

Comparison of estimated parameters across the model variants shows that a given model structure can affect its estimated value. Biologically reasonable parameter estimates are not taken into consideration (but still important) when other model compar-

isons such as the BIC are utilized. For example, estimated Q_{10S} for the Base model was 6.5, whereas for the Quality model estimated Q_{10S} was 2.9. A Q_{10} of 6.5 is significantly higher than published reviews of Q_{10} values from soils (*Davidson and Janssens, 2006; Davidson et al., 2006a; Fierer et al., 2006*), which generally range from 2.2-4.6. These comparisons complicate the selection of a “best” model among the model variants.

Fundamental to the approach of SIPNET is the introduction of additional complexity only when needed in order to avoid overfitting data. The Roots and Quality models increase confidence in the ability of SIPNET to characterize soil respiration at the ecosystem scale. However additional modifications, such as consideration of multiple resource limitations, are needed. Yet we stress that this conclusion could not have been reached if a more complicated model was initially utilized. Furthermore, ecosystem-scale R_{SOIL} measurements would provide additional comparisons to potentially strengthen our conclusions. This could be achieved with plot-level measurements of R_{SOIL} , however care must be exercised when scaling these plot-level R_{SOIL} values to the ecosystem (*Lavigne et al., 1997; Dore et al., 2003*).

As previously discussed, a shortcoming of all the model variants (especially the Microbes model) is the incorrect model assumption that carbon is the only limiting resource. While carbon is the only resource considered in the Quality model, soil quality could be parameterized by the presence or absence of other soil nutrients. Hence the Quality model has implicit consideration of resource limitation. Future refinements to the Quality model could have more explicit linkages between soil quality and nutrient availability.

Many of the estimated soil parameters are not as well-constrained from the data (e.g. K_B , Q_{10S} , θ_B) as other parameters (e.g. A_{MAX} , T_{min} , T_{OPT}). Between the Microbes and Quality model we cannot recommend a best model for microbe biomass dynamics with this study alone. However, repeating this analysis with the inclusion of additional data streams in the data assimilation (such as measurements of R_{SOIL} appropriately scaled to the ecosystem) might better constrain some of the model parameters and indicate a more appropriate soil carbon model.

5.7 Conclusions

This study modified an established process-based ecosystem model and evaluated contrasting models for soil carbon processes. Model refinements included explicit modeling of root biomass dynamics and modeling of microbial biomass dynamics. Comparisons

of the original model to the model refinements found no noticeable difference on model predictions of GEE and TER . However, these model refinements strongly diverged from the original model in their estimates of soil respiration fluxes.

This study confirms that modeling of root biomass dynamics is absolutely critical to reproduce modeled soil respiration fluxes comparable to measured soil respiration fluxes. When compared to literature values, soil carbon models overestimated the contributions of R_{ROOT} to R_{SOIL} , even when the microbial influence (Quality and Microbes model) on R_{SOIL} was considered. These results prevent a recommendation of a particular soil microbe model.

In order to determine an appropriate soil microbe model for use with ecosystem-scale measurements of NEE , future studies should incorporate the following recommendations. First, the effect of multiple resource limitations on microbial dynamics is needed to obtain biologically realistic microbial biomass estimates. Second, inclusion of ecosystem-scale measurements of R_{SOIL} in the parameter estimation routine could potentially constrain process-level parameters and indicate which soil microbe model is best. Third, experimental determination of soil model parameters not constrained by the parameter estimation routine are needed.

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