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Nitrogen controls on ecosystem carbon sequestration: a model implementation and application to Saskatchewan, Canada

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Abstract

A plant–soil nitrogen (N) cycling model was developed and incorporated into the Integrated Biosphere Simulator (IBIS) of Foley et al. [Foley, J.A., Prentice, I.C., Ramankutty, N., Levis, S., Pollard, D., Sitch, S., Haxeltine, A., 1996. An integrated biosphere model of land surface process, terrestrial carbon balance and vegetation dynamics. *Global Biogeochem. Cycles* 10, 603–628]. In the N-model, soil mineral N regulates ecosystem carbon (C) fluxes and ecosystem C:N ratios. Net primary productivity (NPP) is controlled by feedbacks from both leaf C:N and soil mineral N. Leaf C:N determines the foliar and canopy photosynthesis rates, while soil mineral N determines the N availability for plant growth and the efficiency of biomass construction. Nitrogen controls on the decomposition of soil organic matter (SOM) are implemented through N immobilization and mineralization separately. The model allows greater SOM mineralization at lower mineral N, and conversely, allows greater N immobilization at higher mineral N. The model's seasonal and inter-annual behaviours are demonstrated. A regional simulation for Saskatchewan, Canada, was performed for the period 1851–2000 at a 10 km × 10 km resolution. Simulated NPP was compared with high-resolution (1 km × 1 km) NPP estimated from remote sensing data using the boreal ecosystem productivity simulator (BEPS) [Liu, J., Chen, J.M., Cihlar, J., Park, W.M., 1997. A process-based boreal ecosystem productivity simulator using remote sensing inputs. *Remote Sens. Environ.* 44, 81–87]. The agreement between IBIS and BEPS, particularly in NPP spatial variation, was considerably improved when the N controls were introduced into IBIS.

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1. Introduction

Much of current terrestrial ecosystem modelling is aimed at estimating ecosystem carbon (C) budgets and their future trends under a changing climate. Forest ecosystem modelling is of particular interest due to

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the fact that global forests account for 80–90% of terrestrial plant C and 30–40% of soil C, which totals about 2200 petagrams (Pg; 1 Pg = 10^{15} g) (Landsberg and Gower, 1997; Harvey, 2000). Although research has indicated that terrestrial ecosystems have been a C sink as large as 2–4 Pg C yr⁻¹ in the 1990s (Schimel et al., 2001), the role of global forests as a C sink is still under intensive investigation. This is not only because there exist considerable uncertainties in the magnitude of the global C sink in different regions (Schimel et al., 2001), but also because the future responses of forests to climate change are quite uncertain (as compared to many agricultural crops). It has been suggested that forest ecosystems may sequester more C with increasing atmospheric CO₂ concentration (Houghton et al., 1998), but some modelling work and field studies cast doubt on whether this increased sequestration would be sustained under stable CO₂ concentrations (Chen et al., 2000b; Schlesinger and Lichten, 2001; Luo et al., 2001).

One of the key factors creating uncertainties in estimating regional C sequestration and its spatial distribution is soil nitrogen (N) availability. Ecosystem carbon accumulation may be constrained by nutrients, particularly nitrogen (Nadelhoffer et al., 1999; Hungate et al., 2003). Poorter and Pérez-Soba (2001) reviewed several studies, which showed that low nutrient supply was found to reduce the proportional growth stimulation of elevated CO₂. Since N is generally the nutrient most limiting to tree growth, and often a limiting site factor in boreal ecosystems (e.g., Paavolainen, 1999; Hobbie et al., 2002), it is likely that any beneficial effects of elevated atmospheric CO₂ on net primary productivity (NPP) would be limited for these ecosystems—which include some 75% of Canada's forests.

Various strategies have been proposed to model the interactions between the C and N cycles, differing significantly in conceptualization, formulation, parameterization and data requirements (e.g., see Clein et al., 2000). Hungate et al. (2003) pointed out that models incorporating nutrient cycling predict significantly reduced CO₂ uptake when compared to models lacking these feedbacks. The main objective of this study was to build an appropriate model of ecosystem N cycling suitable for inclusion in the Integrated Biosphere Simulator (IBIS) of Foley et al. (1996) and Kucharik et al. (2000). A strict requirement of the N model was that it should be self-adjusting and maintain closed N bud-

gets, while observing the biological and biogeochemical principles of N cycling in terrestrial ecosystems.

There are basically three types of models that consider N limitation on C assimilation. (1) *Static soil nutrient level or leaf N concentration*: such models usually use a constant, site-specific soil fertility index or leaf N level to calculate NPP. The calculation of NPP is often represented in some detail, based on physical environmental variables driving a physiological process model, but usually omits the ecosystem N budget. These models are often quite successful in estimating NPP where soil fertility or leaf N contents are known. The 3PG model of Landsberg and Waring (1997), SIB2 (Sellers et al., 1996), CARAIB (Warnant et al., 1994) and BIOME3 (Haxeltine and Prentice, 1996) are examples of such models. (2) *Dynamic soil N limitation*: These models generally need a “potential” NPP (assuming no N limitation) and an N limitation factor that is based on plant N requirement and soil N availability. The limitation factor is used to scale down potential NPP to actual NPP, which drives new biomass production with a specified biomass C:N ratio. Such models can maintain stable ecosystem N budgets, allowing simulated NPP to fall into reasonable ranges while varying dynamically with soil N availability. The simplification is that leaf N is considered constant and/or N regulation of photosynthesis is treated as a black box. CENTURY (Parton et al., 1987; Schimel et al., 1996) and TREEDYN (Bossel, 1994) are examples of such models. (3) *Leaf N limitation*: These models are similar to the dynamic soil N limitation models but feature a further leaf-level N regulation of NPP. The common approach uses relative leaf N concentration to scale down proportionally either the leaf/canopy NPP or the maximum Rubisco (ribulose biphosphate carboxylase-oxygenase) carboxylation capacity, generally termed V_{\max} following Farquhar and coworkers (e.g., Farquhar et al., 1980). Example models of this type include HYBRID (Friend et al., 1997), FOREST-BGC and BIOME-BGC (Running and Coughlan, 1988; Running and Gower, 1991), InTEC (Chen et al., 2000a, 2000b), CenW (Kirschbaum, 1999), BEPS (Liu et al., 2002), and CLASS (Verseghy et al., 1993) as modified by Wang et al. (2001). In general, these models provide more realistic responses of leaf and canopy photosynthesis to environmental factors, and are thus favoured for climate change impact studies. A common failing of these models, however, is that they do

not address the role of N in controlling the conversion of carbohydrate to biomass. The HYBRID model, for example, allows leaf and fine root respiration to depend on N concentration, but N does not influence woody biomass construction. Many leaf N limitation models initially produce more carbohydrate than actually required for simulated biomass construction (after deducting dark respiration and growth respiration). Various strategies have been adopted to resolve this problem. In the Farquhar-Collatz model of photosynthesis (Collatz et al., 1991), which has formed the basis for several large-scale vegetation process models including SiB (Sellers et al., 1992), IBIS (Foley et al., 1996), and *ecosys* (Grant, 2001), a threshold of about 50% of V_{\max} was introduced to limit the capacity of the export or utilization of photosynthetic carbohydrates. In the CenW model, a biomass construction efficiency expressed as a function of water stress was introduced to scale down final biomass production. The InTEC model omits these additional limiting processes by simply downscaling initial NPP to a level proportional to soil available N. Our approach to modelling N limitation on C assimilation will be described in Section 2.

Recent research into soil organic matter (SOM) decomposition and nutrient cycling has revealed a relatively complex set of interacting processes. Many large-scale biogeochemical models use only simple SOM decomposition coefficients to represent the net effects of complicated soil processes. C–N cycles are simplified in these models in order to minimize the required input data and parameters, such that SOM decomposition rate is usually considered to depend mainly on temperature, moisture, and soil texture (BIOME-BGC (Running and Gower, 1991), PnET-BGC (Aber et al., 1997), TEM4.0 (McGuire et al., 1992, 1995), CENTURY (Parton et al., 1987), SAGE (Hanson et al., 1985), SOIL-N (Eckersten et al., 1995)). N controls for these models, if they exist, typically consider only the changes in SOM C:N ratios, rather than the rate. Cheng (1999) reviewed experiments and theories on the effects of elevated atmospheric CO₂ concentration on rhizosphere N concentration and SOM decomposition. He suggested the experimental results implied that SOM decomposition can be directly influenced by soil N status and is not unidirectional in its response (i.e., while decomposition rate in one SOM pool increases, it may decrease in another). Prescott et al. (2000) discussed

the dual effects of humus in northern forests on tree growth, demonstrating the complexity of SOM mineralization and N mobilization processes, and that soil microbes are often competing with plants for limited N resources. Cheng (1999) reviewed three hypotheses relating to soil N feedback effects on SOM decomposition: (1) the “*preferential substrate utilization effect*” (Merckx et al., 1987; Lekkerkerk et al., 1990; Liljeroth et al., 1990), which implies that soil microorganisms will increase SOM decomposition when soil N is insufficient; (2) the “*priming effect*” (Dalenberg and Jager, 1989; Nicolardot et al., 1994), where additional C input into the soil first reduces SOM decomposition because of N immobilization, but later stimulates SOM decomposition when N becomes limiting (with a similar result to preferential substrate utilization); and (3) the “*competition effect*” (Schimel et al., 1989; Ehrenfeld et al., 1997), which produces an effect opposite from the other two in that competition for N between roots and soil microorganisms will decrease SOM decomposition under N-limited conditions. These hypotheses and related experiments (Cardon, 1996; Kuikman et al., 1990; Hungate et al., 1997; Cheng and Johnson, 1998) are strong justifications for suggesting that two separate SOM decomposition controls, one for immobilization and another for mineralization, are needed to model soil N processes. Our SOM decomposition modelling approach will be described in Section 2.

IBIS is being used to investigate possible responses of Canada’s forest ecosystems to a changing climate at large spatial scales (El Maayar et al., 2001a). The IBIS model attempts to represent the major ecosystem processes that govern vegetation structure and function including plant physiology, land surface physics, canopy gas exchange, bio-geochemical cycling and competition among species. It has been applied at both regional and global scales (Ramankutty et al., 2002; Costa and Foley, 2000) as well as at eddy-covariance measurement sites forced by local meteorological data (e.g., El Maayar et al., 2001a; Delire and Foley, 1999). Detailed IBIS model descriptions are available at <http://www.sage.wisc.edu/pages/datamodels.html> and in Foley et al. (1996), and Kucharik et al. (2000). To date, IBIS has not contained a complete N cycle. Although soil N transformations are tracked in the soil biogeochemistry module reported in Kucharik et al. (2000), there are no soil N controls on vegetation productivity. El Maayar et al. (2001b) found this lack of N

control contributed to unrealistically large responses to elevated CO₂ when IBIS was applied to boreal ecosystems in Canada. To overcome this limitation they assigned constant leaf N levels (based on observations reported in the literature) to reduce V_{\max} for each boreal plant functional type. This was found to generally improve the simulation of vegetation productivity and distribution compared to available data.

In the model presented here, we retained as much as possible of the original IBIS representations of C and N cycling in litter and soil, but added new N feedback controls on both above-ground C assimilation and below-ground SOM decomposition, while imposing the requirement of a balanced N budget.

2. Model description

2.1. Model design

The design of the N feedback framework was based on currently available knowledge including models, hypothesis, or observations reported in the literature. For aboveground C assimilation, we propose an approach (termed *biomass construction limitation*) that considers limitations from both leaf N concentration and soil N availability. Briefly, leaf N operates as the primary control on leaf-level NPP (within a narrow control range) while soil N determines biomass construction efficiency (within a wide control range). The reasons for this are: first, leaf C:N and V_m (V_{\max} adjusted for N limitation effects beyond optimum leaf C:N) are relatively stable during the growing season (Cardoso-Vilhena and Barnes, 2001). Waring and Running (1998) pointed out that when nutrients are added to deficient soils, the growth rates of trees usually increase, often without inducing a change in foliar nutrient concentrations. This suggests that modelling approaches where leaf N concentration is regulated to match observed NPP and biomass increment are modelling simplifications. Our approach enables leaf N concentration and leaf-level regulation of V_m and NPP to operate within relatively narrow ranges, but can still capture long-term leaf N status and its impact on annual canopy-level NPP. Second, soil mineral N may have a direct influence on biomass construction. Not only are plant respiration rates related to nutrient uptake (Chapin et al., 2002; Lambers et al.,

1998), but also structural biomass formation needs N to proceed.

A Michaelis–Menten type of kinetics should be applicable to the processes controlling the rate of carbohydrate conversion to biomass because it is usually used to describe biochemical reactions limited by substrate concentration. The process of tissue formation at plant meristems (apices and cambia) requires both translocation of carbohydrates from within the plant, and N contained in cell proteins at the site of tissue construction. Hence, N available (from soil or within the plant) should be considered to impose a limitation on biomass formation, particularly in stems and roots. Evidence for this from the literature includes Poorter et al. (1997) who noted that enriched CO₂ increased the formation of non-structural carbohydrates (NSC), while having little effect on structural carbohydrate production—presumably because the increase in CO₂ was not accompanied by an increase in available N. If we treat structural carbohydrate as an N-rich organic material (compared to NSC which we assume has zero N content), then structural biomass formation is dependent on N availability, and Poorter's observation is supported. The NSC is treated in the model as an unstable product of NPP, which if not used soon after formation (i.e. more than the available N permitting), is treated as extra growth respiration, without contributing to plant biomass production.

For litter and belowground SOM decomposition, most biogeochemical models consider only soil temperature and moisture, but in the present model we also represent the effects of varying soil N levels. In this model, SOM decomposition is not unidirectional, which allows the three soil N feedback effects identified in the introduction to be represented.

A further development addresses a problem common to many large-scale spatial models of soil carbon dynamics, which is that decomposition rates are often treated as simple scalar functions of substrate pool size (albeit with temperature and moisture modifiers). This can often produce misleading results: at locations with high SOM densities (such as peatlands), rates of decomposition can be exaggerated, particularly at low water contents. Conversely, at sites with mineral soils containing little organic matter, the simulated low rates of decomposition generate mineralized N levels too low to support observed NPP. The TEM 4.0 model (VEMAP Members, 1995) dealt with high SOM levels

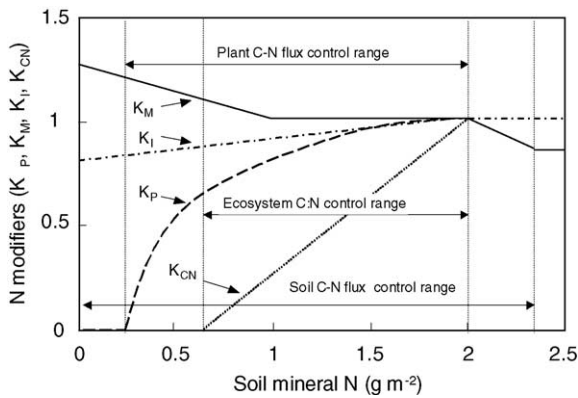


Fig. 1. Theoretical N limitation modifiers and their response curves with reference to soil mineral N. K_M , K_I , K_P are flux modifiers and K_{CN} is C:N modifier. K_P : decreases plant biomass production when N is limiting; K_I : decreases soil N immobilization when N is limiting; K_M : increases soil organic matter (SOM) mineralization when N is (more) limiting; K_{CN} : increases C:N ratios of all SOM fluxes and new biomass product when N is limiting, also lead to long-term ecosystem C:N ratio change.

by redefining a SOM pool to represent storage of reactive SOM instead of total SOM. We used the same approach in our model, where passive SOM is separated into two parts: “conserved passive” SOM that does not decompose, and “redeemable passive” SOM that decomposes normally. For sites where SOM contents are very low (or become very low due to simulated decomposition), an additional scalar factor (p) is activated to accelerate ecosystem the C–N cycle so that a positive feedback allow plant growth and SOM decomposition to continue at realistic levels.

In the design of N control, some major assumptions were made relating to N feedback ranges, such as maximum and minimum allowable C:N ratios and soil mineral N levels. A major objective was to ensure that the model captured negative N feedbacks while observing mass conservation rules for both C and N. Soil mineral N (N_M) is considered to be the primary indicator of N availability, reflecting its importance in field measurements as well as models. The main purpose of N control is that N_M determines both the ecosystem C flux and the C:N ratios of the different mass fluxes associated with growth, senescence and decomposition. A set of N control modifiers and their theoretical response curves and feedback ranges are defined for this modelling approach (Fig. 1). These modifiers differ from those in other models in several aspects: (1) K_P rep-

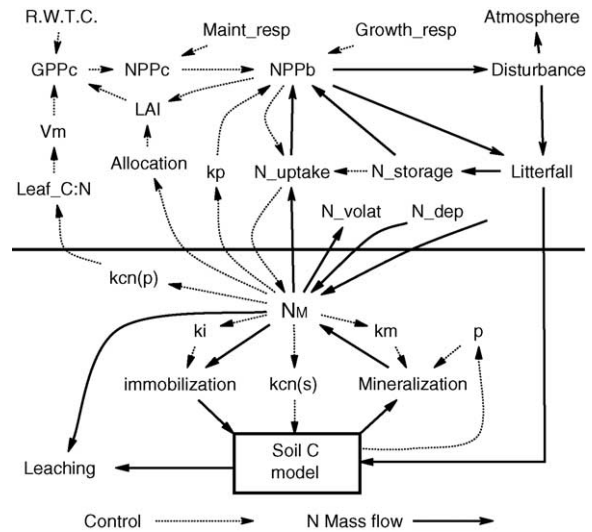


Fig. 2. Diagram of N cycle and N controls with IBIS. Dark solid arrows represent N mass flow, and light arrows indicate N control processes.

resents N limitation on biomass formation, rather than on NPP, interpreted as Michaelis–Menten kinetics. (2) K_{CN} controls new biomass and SOM C:N ratios as described in the CENTURY model. However, the lower threshold of K_{CN} was set higher than the lower threshold of K_P , so that biomass production can occur even at maximum leaf C:N. (3) K_I and K_M are two new scalars to modify the base soil C decomposition parameters, in addition to moisture, temperature and texture factors. These two scalars operate in opposite directions. In most models of SOM decomposition, such scalars adjust different SOM pools in the same direction at the same time, but here different SOM pools can increase or decrease decomposition rates according to N status.

The diagram of the overall N control and N budget is shown in Fig. 2. Foliar N concentration is represented by the leaf C:N ratio and denoted leaf_C:N, which is dynamically adjusted by a C:N modifier K_{CN} , which is in turn determined by N_M .

The environmental conditions RWTC (i.e., radiation, water, temperature and CO_2 concentration), the leaf area index, LAI, and the maximum Rubisco activity as limited by available N, V_m , determine canopy-level gross primary productivity (GPP_c). After deducting maintenance respiration (using the factor $Maint_resp$), GPP_c gives canopy-level NPP (NPP_c). At

this point, NPP_c represents the production of pure carbohydrate, rather than of new biomass C.

A fraction of NPP_c is consumed in growth respiration, with the remainder being converted to “stabilized” biomass NPP_b . Considering that the growth respiration ratio (Growth_resp) in IBIS is an empirical constant and does not allow for N limitation effects, this biomass production process was modified by adding the K_P modifier to represent N constraints on biomass conversion. Growth_resp and K_P combined imply a dynamic growth respiration ratio, or “biomass construction efficiency” ratio that relates canopy NPP (NPP_c) to the production of stabilized biomass (NPP_b). The NPP_b term therefore represents net biomass production, which is then allocated among the different C pools (leaves, roots and woody stems). NPP_b influences N uptake, and contributes to changes in leaf area index (LAI) and foliar N, thus determining leaf biomass, which in turn drives foliar litter production. Because the C:N of fresh leaf litter is higher than the C:N of living foliage, some foliar N is transferred to plant storage N whenever simulated litterfall occurs. Analogous, though typically smaller, N transfers occur with turnover of roots and woody material.

The N feedbacks on SOM decomposition are applied with separate N modifiers K_I , and K_M , which adjust N immobilization and SOM mineralization, respectively. Modifier K_{CN} , on the other hand, adjusts the C:N of SOM fluxes. In some very low SOM sites, decomposition may release only small amounts of N and thus limit plant growth. In such cases, the model can invoke a factor p to represent the stimulation of SOM decomposition, due to the priming effect. The N remaining in living plant tissues, after accounting for N lost in litterfall, is considered as internal N storage and hence provides an additional N supply available for plant development in the following growing season. In general, so long as net primary production is positive, there will always be some plant N going into internal storage at the end of each growing season, because the C:N of the litter is assumed always to be higher than that of living biomass, and mass conservation must be respected.

For the overall ecosystem N budget, the model also includes deposition of pollutant N, fixation of atmospheric N (by N-fixing bacteria and fungi), ammonia volatilization, mineral N leaching, and the effects of

disturbances such as wildfires on N transfers to atmosphere and soil. The representation of these effects follows earlier work and will not be discussed at length here.

2.2. Model equations

For simplicity, only the equations directly related to N budget and N control will be presented here. The symbols C and N represent carbon and nitrogen state variables, respectively, while subscripts i , j , or subscripted symbol names indicate specific C, N pools and fluxes. Table 1 lists the major variables and parameters used in this N model.

2.2.1. N feedbacks on NPP

Canopy NPP (NPP_c) is calculated using original IBIS equations derived from the models of Farquhar et al. (1980) and Collatz et al. (1991). In our modified model, the actual maximum carboxylation rate, V_m , varies from the notional unconstrained V_{max} , according to monthly fluctuations in simulated leaf C:N (B_L):

$$V_m = (B_{V_{max}}/B_L)V_{max} \quad (1)$$

where $B_{V_{max}}$ is the optimal foliar C:N (i.e., at which $V_m = V_{max}$). Eq. (1) indicates a simple feedback where increases in B_L due to N limitation cause V_m to decrease and hence reduce the maximum leaf photosynthesis rate.

The productivity of stabilized biomass, NPP_b , is calculated from the constant growth respiration ratio defined in IBIS, as modified by K_P . Here the term “stabilized” implies that the raw carbohydrate fixed in NPP_c is now converted to a quasi-permanent form that contributes to plant structure or metabolism or goes into internal storage. This provides the major N control on NPP in our model:

$$NPP_b = K_P NPP_c (1 - R_g) \quad (2)$$

K_P is calculated from N_M and two thresholds N_{Mmax} and N_{Mmin} , which constrain the range over which soil N feedbacks can occur. A quadratic equation is used to approximate the Michaelis–Menten kinetics while avoiding the need to determine a rate constant:

$$K_P = ((N_M - N_{Mmin})/(N_{Mmax} - N_{Mmin}))^{0.5} \quad (3)$$

Table 1
List of major variables and parameters of N cycle model

Variable	Definition	Units	Equation number
NPP_c	Daily canopy net primary productivity (in the form of carbohydrate)	$\text{kg m}^{-2} \text{ day}^{-1}$	– (IBIS original)
B_L	Simulated leaf C:N	kg C/kg N	– (see Eq. (9))
N_M	Soil mineral nitrogen concentration	g m^{-2}	– (see Eqs. (17) and (18))
V_m	Maximum Rubisco-limited carboxylation rate adjusted by leaf C:N	$\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	(1)
NPP_b	Daily biomass net primary productivity (C–N compound)	$\text{kg m}^{-2} \text{ day}^{-1}$	(2)
K_P	Modifier of plant biomass construction	–	(3)
K_M	Modifier of SOM mineralization	–	(4)
K_I	Modifier of soil N immobilization	–	(5)
K_{CN}	Modifier of ecosystem flux C:N	–	(8)
δ_{ij}	Identifier indicates whether a process absorbs or releases N	–	(6)
C_X	SOM C flux	$\text{kg m}^{-2} \text{ day}^{-1}$	(7)
B'	C:N of ecosystem organic matter fluxes	kg C/kg N	(9)
B_F	C:N of fresh litter	kg C/kg N	(10)
C_F	Annual fresh litterfall	$\text{kg m}^{-2} \text{ yr}^{-1}$	(11)
N_{ST}	Plant N storage	kg m^{-2}	(12)
N_{UP}	Plant N uptake	$\text{kg m}^{-2} \text{ day}^{-1}$	(13)
N_D	Atmospheric N deposition	$\text{kg m}^{-2} \text{ day}^{-1}$	(14)
N_{FX}	Plant N fixation	$\text{kg m}^{-2} \text{ day}^{-1}$	(15)
N_{LH}	Soil N leaching	$\text{kg m}^{-2} \text{ day}^{-1}$	(16)
dN	Ecosystem N budget	$\text{kg m}^{-2} \text{ yr}^{-1}$	(17)
dN_M	Soil mineral N budget	$\text{g m}^{-2} \text{ day}^{-1}$	(18)
Parameter	Definition	Units	Value/range
V_{\max}	Maximum Rubisco-limited carboxylation rate	$\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	25×10^{-6} (boreal leaf)
$B_{V_{\max}}$	Optimum leaf C:N when V_{\max} is reached	kg C/kg N	55 (boreal leaf)
B_{\max}	Maximum C:N of plant and soil components	kg C/kg N	65 (boreal leaf)
B_{\min}	Minimum C:N of plant and soil components	kg C/kg N	30 (boreal leaf)
$B_{F_{\max}}$	Maximum C:N of fresh plant litter	kg C/kg N	70 (boreal leaf)
$B_{F_{\min}}$	Minimum C:N of fresh plant litter	kg C/kg N	35 (boreal leaf)
$N_{M_{\max}}$	Maximum soil N_M threshold for N control calculation	g m^{-2}	2.0
$N_{M_{\min}}$	Minimum soil N_M threshold for N control calculation	g m^{-2}	0.2
R_g	Growth respiration ratio	–	0.3 (boreal leaf)
a_p	Biomass NPP allocation ratio for different plant components	–	0.3 (boreal leaf)
τ	Biomass turnover time	yr	2.5 (boreal leaf)
K	Specific C decomposition rate (day^{-1})	$\text{kg m}^{-2} \text{ day}^{-1}$	10^{-6} (slow SOM)
y	C decomposition efficiency	–	0.2 (passive SOM)
p	Factor to control SOM decomposition	–	If true: 5, else: 1
Subscript	Definition		
i, j	Numerical subscript for different ecosystem pools and fluxes. When used together i = source, j = target		

Note: Additional variables are explained in the text.

We set $N_{M\max}$ as 2 g N m^{-2} , below which N limitation on NPP_b is considered to occur, and set $N_{M\min}$ as 0.2 g N m^{-2} , below which plant biomass construction is assumed to be zero. Because of the limitations imposed by $N_{M\min}$ and $N_{M\max}$, K_P is confined to the range 0.0–1.0.

2.2.2. N feedbacks on soil C decomposition

The calculations of SOM flux modifiers K_M and K_I depend on different soil N conditions: (a) $N_M \geq N_{M\max}$, (b) $0.5 N_{M\max} < N_M < N_{M\max}$, (c) $N_M \leq 0.5 N_{M\max}$:

$$K_M = \begin{cases} 1.0 - (N_M - N_{M\max})/N_{M\max} & \text{(a)} \\ 1.0 & \text{(b)} \\ 1.0 + (0.5N_{M\max} - N_M)/N_{M\max} & \text{(c)} \end{cases} \quad (4)$$

$$K_I = 0.8 + 0.2N_M/N_{M\max} \quad (5)$$

K_M was confined to the range 0.8–1.5, and K_I to 0.8–1.0. These ranges were selected to impose relatively small negative N feedbacks on the SOM decomposition rates simulated by the standard IBIS model. It should be noted that the shapes of the K_P , K_M and K_I curves (Fig. 1) represent dynamic nutrient competition between soil microbes and plants. The soil will have a greater nutrient competition advantage over the plants when N is limiting because K_P decreases faster than K_I . Conversely, SOM decomposition could be decreased under moderate soil N limitations because K_I decreases and K_M remains constant; although this can reverse because K_M will increase at very low mineral N levels.

The net N fluxes related to litter or SOM decomposition processes (i.e., microbial N uptake or release) are given by

$$\delta_{ij} = 1/B_i - y_{ij}/B_j \quad (6)$$

where B_i , B_j indicate the C:N ratios of the source and target pools (such as live foliage and foliage litter), respectively, and y_{ij} is the yield coefficient when C is transferred from source i to target j . If $\delta_{ij} > 0$, the process releases N, and conversely if $\delta_{ij} < 0$, the process absorbs N.

The actual soil decomposition rate is then adjusted by

$$C_X = \begin{cases} d_s y_{ij} K_i p K_I C_i, & \delta_{ij} \leq 0, \\ d_s y_{ij} K_i p K_M C_i, & \delta_{ij} > 0 \end{cases} \quad (7)$$

where d_s , y_{ij} and K_i belong to the original IBIS model, of which d_s is the coefficient representing soil moisture and temperature effects on decomposition and K_i the fixed base decomposition rate of each SOM pool. The new K_M and K_I factors thus represent the effects of N on decomposition rate. The factor p is described in next section.

2.2.3. SOM stock size and SOM decomposition

We introduced empirical schemes to simulate SOM decomposition when stocks were either high enough to create unrealistically high rates of soil C loss or low enough to limit N available to plants. In the case of cold wet sites where very high SOM stocks accumulate, “conserved” and “redeemable” passive SOM pools were identified. This was because the passive SOM pools could be very large at such sites, so adopting a universal passive SOM decomposition ratio and applying it to the whole passive SOM pools would cause these pools to decompose rapidly and cannot remain at a realistically high stock level. [Note: They will not cause the pool to disappear because as the material decomposes, the pool gets smaller and net C loss decreases.] Conserved SOM is assumed to remain inactive in the decomposition process, whereas redeemable SOM has a decomposition rate comparable to that used by most biogeochemical models. In the model, redeemable SOM is assumed to be 10 kg C m^{-2} if the total passive SOM is greater than 10 kg C m^{-2} . If passive SOM exceeds this level, only 10 kg C m^{-2} is available for decomposition. This threshold is a notional value based on the observation that C content of most temperate region forest soils (top 30 cm) is less than 10 kg C m^{-2} , while most estimates of SOM decomposition rates were obtained for such soils. If the redeemable SOM falls below this level, then the shortfall is replaced by a simple transfer from the conserved passive SOM. Conversely, if redeemable SOM exceeds 10 kg C m^{-2} , the excess is transferred to the conserved passive pool.

At sites of very low SOM, the scalar factor, p , was introduced (Eq. (7)). Based on the work of Bailey et al. (2003), Cheng et al. (2003) and Hoosbeek et al. (2004), the p factor represents the “priming effect”, where very high C inputs to the soil can stimulate SOM decomposition. For this study high C input is relative to the SOM stock. A threshold input was defined such that the soil capacity for accepting additional C was

limited to the previous year's SOM (excluding litter) plus 5% of annual NPP. If during the daily simulation of soil C dynamics, SOM exceeds 110% of the calculated capacity, faster decomposition will occur.

2.2.4. Ecosystem C:N

The ecosystem component fluxes (among vegetation biomass, litter and soil carbon pools) are considered in the model to possess dynamic C:N ratios that are updated by flux C:N modifiers at each time step. Soil organic matter C:N dynamics are modelled similarly to those in CENTURY (Schimel et al., 1996), in which a linear relationship between N_M and SOM flux C:N was assumed. Plant tissue C:N follows a similar method, where the C:N modifier is a function of N_M :

$$K_{CN} = (N_M - 2N_{M\min}) / (N_{M\max} - 2N_{M\min}) \quad (8)$$

This equation indicates that K_{CN} will become zero at $2N_{M\min}$, which will typically occur before $K_P = 0$. This implies that even at maximum C:N, some plant growth can still take place.

The C:N ratios associated with the C fluxes are calculated using

$$B'_i = B_{i\max} - K_{CN}(B_{i\max} - B_{i\min}) \quad (9)$$

where i represents any carbon pool (foliage, wood, roots, microbial biomass, protected slow C, non-protected slow C, or passive soil C). Fluxes with dynamic C:N ratios lead to changes in both C and N pool, allowing the model to represent C:N dynamics in each of the biomass and soil pools.

The C:N of fresh litterfall is assumed proportional to the living plant C:N at the end of each year:

$$B_{Fi} = B_{Fi\min} + (B_i - B_{i\min}) / (B_{i\max} - B_{i\min}) \times (B_{Fi\max} - B_{Fi\min}) \quad (10)$$

Here the subscript F indicates fresh litterfall and i the foliage, wood or roots.

2.2.5. N input, N loss and N budget

Annual litterfall C is calculated using the following equation modified from the original IBIS model for explicit solutions of both the C and N budgets:

$$C_{Fi} = C_i(1 - e^{-1/\tau_i}) + a_{p_i} \text{NPP}_b(1 - \tau_i(1 - e^{-1/\tau_i})) \quad (11a)$$

where a_{p_i} is the NPP allocation fraction, and τ_i the time constant for turnover, of each biomass pool i , respectively. The calculation of litterfall N uses an analogous equation, where the NPP term is divided by the appropriate C:N ratio to obtain N content for each pool:

$$N_{Fi} = N_i(1 - e^{-1/\tau_i}) + a_{p_i} \text{NPP}_b(1 - \tau_i(1 - e^{-1/\tau_i})) / B_i \quad (11b)$$

The net flux of N into annual plant N storage, N_{ST} , is then calculated as the difference between N in the portion of biomass that is lost to turnover each year, and the N actually contained in annual litterfall:

$$N_{ST} = \sum (C_{Fi} / B_i - C_{Fi} / B_{Fi}) \quad (12)$$

The amount N_{ST} will be available from storage at the beginning of the next growing season to reduce the plant's initial dependence on soil N.

Daily N uptake is determined from N demand and N storage. Two possible conditions are considered to exist: (a) $N_{ST} \leq 0.5 \text{NPP}_b / B_A$, and (b) $N_{ST} > 0.5 \text{NPP}_b / B_A$. Here B_A is the C:N ratio of NPP_b , so NPP_b / B_A is the N required by the plant for biomass construction. Under condition (a), stored N will be used up, whereas under condition (b), only half of the N required for new biomass construction will be taken from N storage (typically in early spring). Hence, net N uptake is given by

$$N_{UP} = \begin{cases} \text{NPP}_b / B_A - N_{ST}, & N_{ST} \leq 0.5 \text{NPP}_b / B_A, \\ 0.5 \text{NPP}_b / B_A, & N_{ST} > 0.5 \text{NPP}_b / B_A \end{cases} \quad (13)$$

In the modified model, the deposition of atmospheric N (including pollutants) is calculated according to a simple approach used in the InTEC model (Chen et al., 2000b) where N deposition (N_D) is related to greenhouse gas emissions (G):

$$N_D = N_{D0} + (G - G_0) / (G_C - G_0) (N_{DC} - N_{D0}) \quad (14)$$

where N_D and G without subscript refer to the current simulation year, and the subscripts 0 and C represent the assumed first year of industrial N deposition (1901) and a calibration year (determined as the average of

measurements during the period 1983–1994), respectively. Eq. (14) produces annual N deposition values up to $2.0 \text{ g N m}^{-2} \text{ yr}^{-1}$ at some locations in Canada where the calibration measurements showed very high deposition in the 1990s, but for most of Canada deposition rates are typically less than $0.5 \text{ g N m}^{-2} \text{ yr}^{-1}$.

The representation of N fixation also follows the approach of InTEC where N fixation is related to three driving variables: precipitation, mean soil temperature and soil microbial biomass carbon (C_{MB}).

$$N_{\text{FX}} = c_1 \times 2^{(T_s + c_2)/10} P(0.5C_{\text{MB}} + 0.5) \quad (15)$$

where c_1 and c_2 are constants calibrated to apply to the whole area of Canada, T_s is the annual average soil temperature and P the annual precipitation. This equation typically gives annual N fixation rates in the range $0.5\text{--}1.0 \text{ g N m}^{-2} \text{ yr}^{-1}$.

The total of mineral and organic N leaching is calculated as

$$N_{\text{LH}} = f(N_{\text{M}} + N_{\text{MB}}) \quad (16)$$

where f is a leaching fraction calculated from drainage water in the original IBIS model. N_{MB} is soil microbial biomass N.

The current IBIS model calculates losses of biomass carbon due to fire and other disturbances using fixed fractions. For the C and N budgets, we assumed 50% of the disturbed C and N (N_{X}) are released to the atmosphere, with the remainder transferred to the soil as raw leaf, root and stem litter. There is also an N volatilization term (N_{VL}) in the model that removes 0.001% of N_{M} each day.

The annual ecosystem N budget is the sum of all N inputs and outputs

$$dN = N_{\text{D}} + N_{\text{FX}} - N_{\text{LH}} - N_{\text{VL}} - N_{\text{X}} \quad (17)$$

where N_{X} is calculated annually and the remaining terms are calculated daily. It is clear that soil mineral N concentration (N_{M}) is updated every time step by its net daily change rate (dN_{M}) in the model. The daily budget of soil mineral N includes some internal N redistribution

$$dN_{\text{M}} = N_{\text{D}} + N_{\text{FX}} + N_{\text{MI}} - N_{\text{IM}} - N_{\text{LH}} - N_{\text{UP}} - N_{\text{VL}} \quad (18)$$

where N_{MI} and N_{IM} are mineralized N and immobilized N, respectively.

2.3. Input data

For spatial tests of the modified IBIS model, a gridded data set (10 km resolution on the Lambert Conformal Conic projection) was used to provide a subset coverage of the Province of Saskatchewan, with 5987 land pixels. The Soil Landscapes of Canada (SLC) survey data were rasterized from the Canadian Soil Information System (CanSIS) data set and aggregated. Soil properties included clay content, sand content, and total soil C. Climate variables used by IBIS include monthly mean temperature and diurnal range, total precipitation, relative humidity, wind speed and wet days per month, which are used to drive a version of the Richardson WGEN weather generator for diurnal forcing conditions. Baseline climate data were interpolated from Meteorological Service of Canada (MSC) 1961–1990 station normals, while inter-annual variations for the period 1951–2070 were taken from an interpolated Canadian General Circulation Model (CGCM2) simulation forced by the IS92A GHG + A emissions scenario (Price et al., 2001). Deposition of atmospheric N (reference year 1994) was correlated to historical greenhouse gas emissions following the approach used in the InTEC model (Chen et al., 2000b). InTEC used the same soil data as IBIS, but in the climate were taken from the UK Climatic Research Unit CRUTS 0.5 degree data set (Versions 1.0 and 1.1) (New et al., 2000), interpolated to 1 km. Vegetation classification was taken from a simplification of the Natural Resources Canada LCC95 land cover map of Cihlar et al. (1996).

2.4. Experiments

The sensitivity of simulated NPP, NEP, and C stocks to variations in climate and CO_2 concentration were explored for a single representative grid cell in the present-day boreal zone of Saskatchewan, focusing on the N controls imposed by K_{P} , K_{I} , K_{M} , and K_{CN} . Three experiments were carried out: (a) constant atmospheric CO_2 concentration of 280 ppm with simulated N controls, and the priming factor, p set to 1.0; (b) increasing CO_2 concentration following the IPCC IS92A emissions scenario with simulated N controls, and dynamic p factor; and (c) IPCC IS92A CO_2 concentration increase without simulated N controls, but with dynamic p factor.

Modelled estimates of NPP were also compared with the NPP output of the boreal ecosystem productivity simulator (BEPS) of Liu et al. (1997, 2002) for the year 1994. The BEPS result was derived from advanced very high-resolution radiometer (AVHRR) remote sensing imagery at $1\text{ km} \times 1\text{ km}$ resolution, and validated against eddy-covariance measurements made at flux towers operated during the BOREAS experiment (Sellers et al., 1996). BEPS output reveals clear NPP spatial patterns within and beyond the Saskatchewan study region, with a pronounced north–south gradient in NPP (Fig. 5a). The objective was to determine whether IBIS could reproduce the broad spatial patterns in NPP distribution generated by BEPS while maintaining soil C densities (kg C m^{-2}) close to the levels reported in the SLC data set (recognizing that these are highly aggregated and idealized data).

3. Results

3.1. Model behaviour

According to data provided in the Soil Landscapes of Canada (SLC) database, soil C stocks in Saskatchewan range from 3 to 150 kg C m^{-2} . Soil C for the test pixel was reported to be 33 kg C m^{-2} , a relatively high carbon density for a mineral soil in a region where values above 50 kg C m^{-2} indicate peatland ecosystems. Fig. 3a shows the variations in simulated soil mineral N over a one-year period. Soil mineral N availability increases during spring and late autumn, a seasonal variation that depends on the simulated N feedbacks. Without the limitation on biomass conversion imposed through K_P , soil N almost disappears during the summer. With the K_P limitation, however, soil N was maintained at a higher level because of reduced N uptake. The feedbacks operating through N mineralization and immobilization (K_M and K_I) contributed to controlling soil mineral N levels to reduce the intra-annual variation, although they generally caused only small changes compared to the K_P effect.

Simulated NPP dynamics were seen to respond realistically to the simulated variations in mineral N availability—mainly those imposed via K_P . When the K_M and K_I N controls were introduced, however, simulated NPP at this pixel increased initially as in the

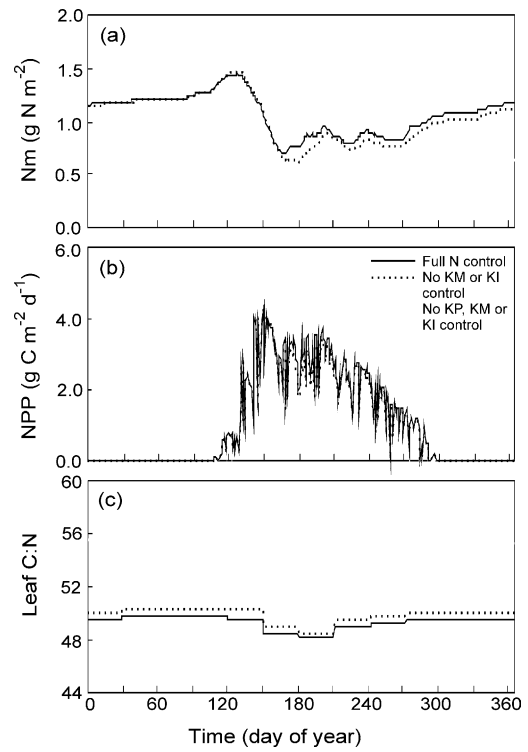


Fig. 3. Seasonal variations of soil mineral N, NPP (daily time step), and leaf C:N (monthly time step) at a test pixel in boreal eco-region.

standard model, but subsequently preceded at a significantly lower rate for the remainder of the growing season (Fig. 3b). The initial non-N limiting phase was due to the simulated high soil N and the utilization of internal plant storage N. In addition, the K_M and K_I controls also contributed to a slightly higher NPP than when they were excluded.

The model updates leaf C:N on a monthly time step (Fig. 3c). The simulation predicts that the average ecosystem foliar C:N changes within a range of s (48–51), decreasing in spring and early summer but gradually increasing from mid-summer onwards. This is because in spring the model provides a relatively rich supply of N, from both soil and plant storage, which serves to increase foliar N (and hence slightly reduce C:N), such that NPP increases relatively rapidly when environmental conditions are non-limiting. When N controls were turned off, simulated leaf C:N was appreciably higher (about 54–56 in the test pixel), related to the higher simulated NPP and lower soil N during the growing season. It should be noted that IBIS does

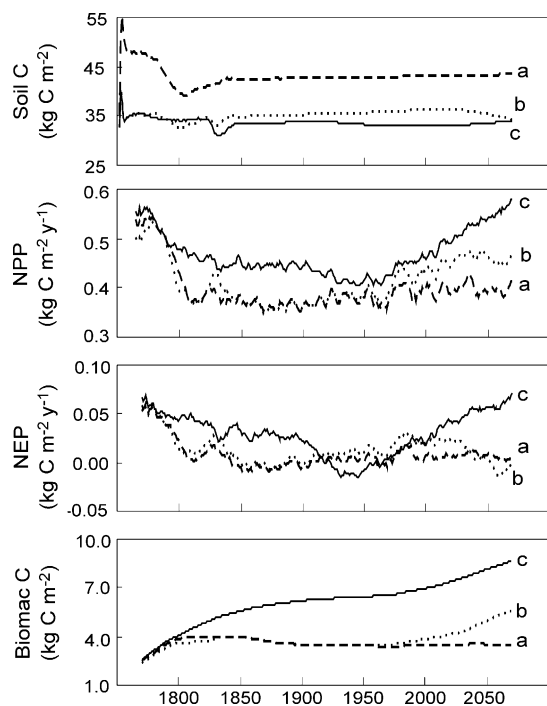


Fig. 4. Simulated long-term trends of soil C, biomass C, NPP, and NEP of a test pixel in the boreal eco-region in Saskatchewan: (a) assuming constant atmospheric CO₂ concentration and with N controls on NPP and soil decomposition; (b) with CO₂ concentration following IPCC IS92A emissions scenario and with N controls; (c) as (b) but with no N controls.

not explicitly simulate the annual phenology of deciduous foliage (leaf expansion, senescence and fall), so the simulated C:N outside the growing season is unrealistic—at least for deciduous species. In keeping with the modelling philosophy of IBIS, however, a portion of deciduous foliar N can be considered to be conserved elsewhere in vegetation biomass rather than completely lost in litterfall.

The long-term model behaviours are represented by three model experiments (experiment (a)–(c) as described in Section 2.3) running for the period 1751–2070, including a 100-year accelerated soil C spin-up (approximating 3500 years of soil C cycling) to bring the soil C pools to equilibrium and another 50 years of adjustment prior to 1901. The monthly anomalies derived from the CGCM2 IS92A emissions scenario also imposed a warming trend for the period from 1990 to 2070 in all three experiments.

It can be seen from Fig. 4 that simulated soil C in all three experiments stabilized after spin-up (by the simulated year 1850). In experiment (a) the p factor was set as constant 1.0 so the soil C stabilized at a higher level than in the other two experiments. This is because the p factor in the model is designed to increase SOM decomposition. With dynamic p , experiments (b) and (c) (both with simulated increases in CO₂ concentration) stabilized at lower soil C levels that were much closer to the observed value (33 kg C m⁻²). Moreover, these two runs showed somewhat greater variation in soil C than experiment (a) after 1850, which indicates the model was actively responding to the simulated changes in climate and increasing CO₂ concentration.

As for mean annual NPP, NEP and biomass C accumulation, experiment (c) gave higher values because there was no N limitation imposed on photosynthesis and biomass construction (consistent with the results obtained by El Maayar et al., 2001b). When N controls were introduced (experiment (b)), the simulated effects of increasing atmospheric CO₂ were clearly limited by available N, such that NPP and biomass C accumulation in this run were both lower than in experiment (c), but still higher than those obtained in the constant CO₂ experiment (a). Experiment (b) also showed a tendency toward decreasing soil C towards the end of the simulation, where NPP stabilized but NEP decreased towards 0. This suggests that if an N limitation to ecosystem productivity exists, ecosystem C sequestration (even allowing for effects of CO₂ enrichment and climate warming) will reach equilibrium sooner than in an ecosystem that is not N-limited.

3.2. Model calibration and application to Saskatchewan

The province of Saskatchewan was chosen for model tests because of its large spatial extent (approximately 600,000 km²) and its central location in Canada's prairie and boreal regions. The south–north climatic gradient, extending from warm and dry in the grassland region to cool and moist in the tundra, is reflected in soils that vary from predominantly mineral (though with significant organic content) in the south, to mixtures in the forest region and highly organic soils and peatlands in the north. Hence, soil nutrient availability is expected to vary greatly, both spatially and temporally, over the study region.

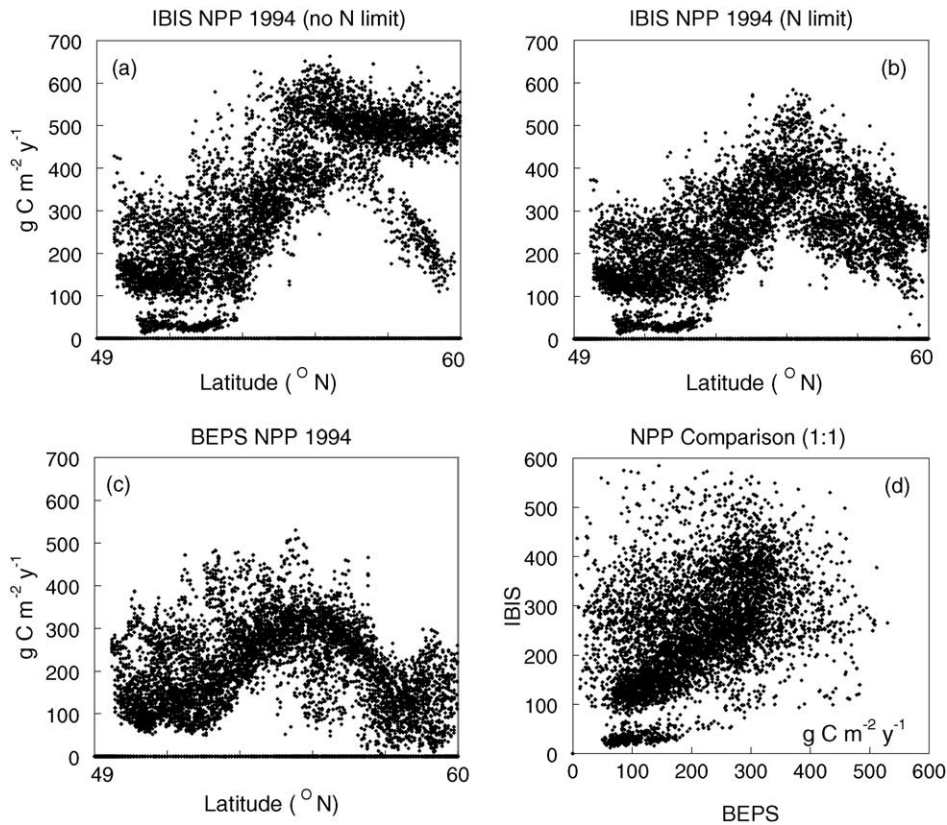


Fig. 5. Regional NPP comparison of BEPS and IBIS model outputs of 1994.

Fig. 5 shows the estimated NPP of the two models for all the geographically matched 10 km pixels in the study region. It can be seen that the two models produced broadly similar ranges of NPP values. The NPP spatial patterns generated using BEPS were captured by IBIS, although IBIS reported a systematically higher NPP than BEPS, particularly when N controls were not implemented (Fig. 5a). Introducing N limitations into IBIS reduced simulated NPP for much of northern Saskatchewan (Fig. 5b) as compared to the non-N limitation output—as well as bringing the two models into closer agreement (Fig. 5c).

Some exceptional regions in southern Saskatchewan exhibited very low NPP (under $50 \text{ g C m}^{-2} \text{ yr}^{-1}$) when compared to BEPS output. Such differences between the two models are not surprising, considering the fundamental differences in their methods of estimating NPP. BEPS utilizes remote sensing observations of

present-day spatial distribution of vegetation, which also integrate the effects of past fire and insect disturbances. The vegetation distribution created by IBIS, however, is determined mainly by simulated responses to soil and climate data, with the disturbance history superimposed on this statistically (i.e., as an annual fraction disturbed in each $10 \text{ km} \times 10 \text{ km}$ grid cell). Close agreement between the two models cannot be expected, which explains the broad scattering in simulated NPP around the 1:1 line (Fig. 5d).

The spatial patterns of NPP simulated by the two models are displayed in Fig. 6. The biomass growth limitation varies spatially with N status (K_P). Many boreal regions appear to be highly N-limited due to immobilization where soil C pool sizes are large. Simulated mineral N was more available in the southerly grassland biome, but simulated NPP was lower than elsewhere due to the relatively dry climatic conditions in this region.

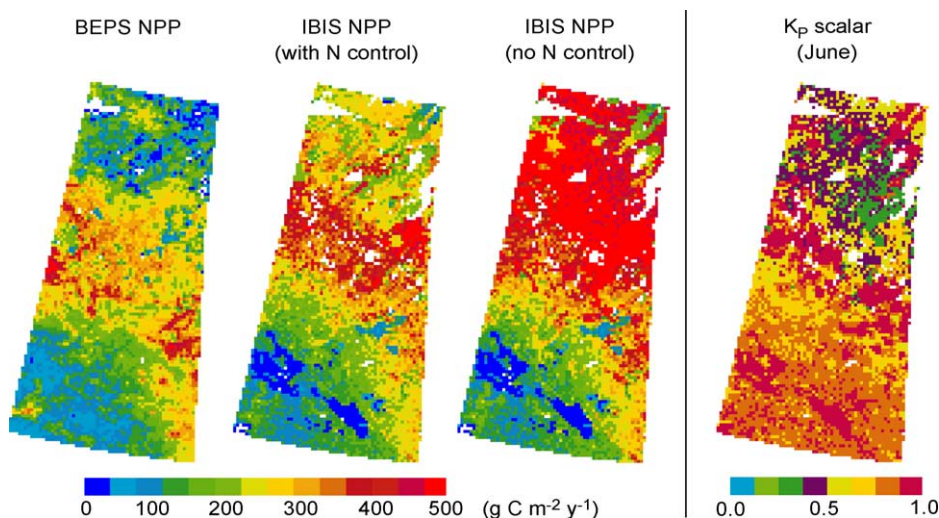


Fig. 6. Spatial NPP comparison of BEPS and IBIS, and spatial pattern of relative N limitation simulated from IBIS (1994).

4. Discussion

The overall objective of this work was to provide a relatively simple representation of the effects of N limitations on productivity of boreal forests that would be computationally efficient while also responding realistically to spatial and temporal variations in climatic drivers. Compared to other large-scale biogeochemical models, the modified version of IBIS reported here differs in three major respects.

Firstly, the calculation of NPP and biomass production is limited not only by foliar N concentration effects operating on Rubisco activity, V_m , but also by N constraints on the conversion of non-structural carbohydrates to structural biomass. Variations in leaf N and V_m are constrained to a relatively narrow range so that leaf-level NPP is more stable. At the same time, a nitrogen limitation factor is used to modify biomass construction efficiency so that NPP is adjusted immediately according to the available N. The effect is that aboveground N controls on plant growth have both fast and slow responses to soil N limitation.

A second feature of the modified IBIS is the representation of N feedbacks on SOM decomposition. Many biogeochemical models use coefficients to allow a baseline SOM decomposition rate to respond to changes in soil temperature, moisture content, and in some cases, spatial variations in soil texture and other

physical properties. Our approach, based on hypotheses in the recent literature, also considers the role of N controls in SOM decomposition processes. In particular, N limitation effects are allowed to operate independently for different soil C pools. This means that under particular combinations of conditions, decomposition of one SOM pool (e.g., lignins) may slow down, while another (e.g., the slow SOM pool) may accelerate. Eq. (7) has a similar form to those used in CENTURY, BIOME-BGC and other models, but it includes two sub-functions and three more control factors (K_M , K_I , and p) that operate dynamically on SOM decomposition rates. The net effect is that the soil system becomes more self-regulating and buffered in its responses to external changes.

The third feature is the regulation of SOM stock size and decomposition rates. We defined “conserved passive” and “redeemable” SOM to simulate C decomposition at sites with large stocks of SOM. This is analogous to creating an additional pool with a very slow decay rate. For sites with very low SOM content, an empirical “priming factor”, the p scalar, was introduced to accelerate C decomposition at low soil N availability. These controls enable high SOM accumulations to persist without decaying unrealistically, while sites with low SOM contents can support reasonable NPP when normal SOM decomposition rates does not provide enough N.

The detailed parameterization of our N control model remains to be addressed. Nevertheless, using parameter values derived from observations reported in the literature to define reasonable ranges and limits, the model appears to respond realistically to seasonal and longer-term changes in key environmental factors. Simulated levels of N in soil and plant tissue are maintained within appropriate ranges and provide limitations to simulated large-scale NPP that are more consistent with observations and the results of another (independently tested) spatial model, BEPS, driven by remote sensing inputs. The strength of the modified version of IBIS is that it can be used to investigate effects of future changes in climate for regions where soil N is likely to limit positive growth responses. Such simulations cannot be performed using remote sensing inputs alone.

Two aspects of soil–plant N cycle modelling were addressed here:

(1) Negative N feedback and N limitation

Because the model is self-regulating with its negative N feedbacks, it is not strictly necessary to predetermine the constant allocation ratio of soil mineral N to SOM decomposition and to plant uptake. By using globally fitted SOM decomposition coefficients (Kucharik et al., 2000) and using relatively broad plant and soil C:N ranges, the model achieves stability of both C:N ratios and simulated C and N fluxes within and among the various ecosystem carbon pools. Because the model observes mass conservation, the N budget is closed (allowing for inputs from deposition and losses due to volatilization and drainage), so the C cycle, including both primary production and heterotrophic decomposition processes, becomes more realistic and controllable than models without N control. In reality, of course, N control is far more complicated in many details and the N is only one of the many possible limiting elements in ecosystem.

(2) The relationship of C sink to N sink, and the controls on ecosystem C:N

The model presented here supports the general view that the potential benefits of increased atmospheric CO₂ on plant primary production (“CO₂ fertilization effect”) would be limited by N availability. Theoretically, within a closed ecosystem (no external N input and output), increased NPP

will raise ecosystem C:N but stabilize at a certain level because increased foliar C:N will reduce NPP per unit leaf area (Chen et al., 2000a, 2000b). With an open ecosystem (i.e., with external inputs such as N deposition and losses such as leaching and ammonia volatilization), the net C uptake is surely related to N inputs, N uptake, and N loss, so that an increased N sink will generally result in a larger C sink. Because leaves and fine roots turn over faster than highly lignified material such as stemwood and coarse roots, the major “long-term” N sinks are actually in soil organic matter and woody biomass. If the soil C pool and C:N ratio stabilize, then it can be expected that long-lived woody biomass will consume only a small amount of N because the allowable woody biomass C:N range is 300–900. That means the potential accumulation of woody biomass would not lead to significant soil N-depletion, hence the productivity of ecosystem will not be obviously limited by N resources. On the other hand, if soil C is to accumulate, it would likely immobilize much more N than woody biomass because SOM C:N is typically as low as 10–20. This means we may not expect too much C fixation in soil where soil N availability is low. The model suggests that under N limiting conditions, biomass C could not accumulate to very high levels while maintaining SOM with stable pool sizes and C:N ratios. Test simulations showed that total net ecosystem C sequestration (i.e., in both vegetation and soil) will be limited by N availability and pool C:N ratios. Because the modelled ecosystem C:N ratios shift gradually based on the soil nutrient indicator (mineral N concentration), different equilibria in C and N pools, and hence in their C:N ratios will occur over time. More realistic simulation of C–N dynamics will require more precise C:N parameters and perhaps more specific equations of C:N responses to soil mineral N.

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