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Nitrogen mineralization drives the response of forest productivity to soil warming: Modelling in *ecosys vs.* measurements from the Harvard soil heating experiment

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ABSTRACT

Effects of climate warming on ecosystem productivity are strongly influenced by those on mineralization and uptake of key soil nutrients, particularly N. Models used to project these effects must therefore include a comprehensive and fully coupled N cycle which has undergone rigorous testing. Key hypotheses governing the response of the N cycle to warming in the terrestrial ecosystem model *ecosys* were tested against changes in ecosystem C and N stocks measured during 7 years of 5 °C soil heating in the Harvard soil heating experiment. These hypotheses enabled the model to simulate gains in plant C stocks that rose from 50 to 200 $g\,C\,m^{-2}\,y^{-1}$ driven by increased N mineralization and uptake as the soil heating experiment progressed. However these gains were offset by continuing losses of soil C stocks from 125 to 250 $g\,C\,m^{-2}\,y^{-1}$ driven by increased heterotrophic respiration, so that total C stocks changed little with soil heating. Both gains and losses in the model were consistent with those measured in the soil heating experiment. The changes in N cycling with soil heating on which these model results were based were further corroborated by comparing modelled *vs.* measured increases in soil N mineralization rates, foliar N contents and reductions in root phytomass, and by comparing modelled increases in CO_2 fluxes and net primary productivity with those reported in meta-analyses of warming effects on ecosystem productivity. However when the model was run under gradual climate warming by 5 °C per century, these modelled changes in N cycling drove gains in ecosystem C stocks that rose gradually to *ca.* 165 $g\,C\,m^{-2}\,y^{-1}$ after 100 years. The greater gain in ecosystem C modelled under gradual climate warming *vs.* sudden soil heating was attributed to much smaller losses in soil C stocks.

1. Introduction

The direction and magnitude of terrestrial feedback to atmospheric CO_2 concentration (C_a) during climate change is highly uncertain. Most current modelling studies indicate a positive feedback in which increases in autotrophic and heterotrophic respiration (R_a and R_h) from rising air temperatures (T_a) exceed increases in gross primary productivity (GPP) from rising C_a (*e.g.* Friedlingstein et al., 2006; Gregory et al., 2008). However these model findings are inconsistent with experimental studies which show that warming hastens R_h and thereby soil N mineralization, causing commensurate increases in plant N uptake and hence plant growth, particularly in cooler climates (Rustad et al., 2001). Soil warming studies have indicated that gains in plant C from increased mineralization alone may largely offset losses in soil organic C (SOC) from increased R_h (Melillo et al., 2011). Soil warming under elevated C_a may further hasten soil N mineralization and plant N uptake through priming of humus decomposition from increased microbial activity driven by greater litterfall (Drake et al., 2011; Phillips et al., 2011; Schleppi et al., 2012). The magnitude and possibly the direction of the terrestrial feedback from climate change are therefore determined by the extent to which increases in GPP from rising C_a and N uptake offset increases in R_a and R_h from rising T_a.

This offset from rising N uptake on GPP during climate warming was not represented in models included in the meta-analyses of the C⁴MIP intercomparison by Friedlingstein et al. (2006) and Gregory et al. (2008) because these models lacked a fully coupled N cycle so that changes in N cycling with warming were not simulated. All models in these meta-analyses projected declines in global ecosystem C stocks with climate change, and hence large positive feedbacks to C_a, because C losses with rising T_a were larger than C gains with rising C_a. In contrast, some more recent studies

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using models with coupled C—N cycles have given much smaller C losses, or even C gains, with rising T_a because of increased N mineralization, particularly in cooler ecosystems (Sokolov et al., 2008; Thornton et al., 2009; Zaehle et al., 2010). However these coupled models vary in the extent to which N availability reduces C losses with rising T_a and reduces C gains with rising C_a, and hence in the extent to which gains offset losses. In some models, this offset is greater than that from models lacking an N cycle, causing a smaller positive feedback, or even a small negative feedback, to C_a (Thornton et al., 2009). In others, however, this offset is smaller, increasing the positive feedback to C_a (Zaehle et al., 2010).

In all coupled C—N models, N cycling had important effects on terrestrial feedbacks to C_a simulated during climate change so that effects of warming on N cycling must be accurately modelled when projecting these feedbacks. The inclusion of a robust and well tested N cycle is therefore vital to reduce uncertainty and improve confidence in model projections. However to date models used in these studies have been subjected to at best limited testing against results from controlled warming experiments. To represent N cycling effects in climate change studies, a comprehensive, process-based N cycle has been incorporated in the terrestrial ecosystem model *ecosys*, with detailed simulation of decomposition, mineralization, adsorption, nitrification, denitrification and leaching as affected by soil temperature (T_s) and soil water content (θ). This model has undergone detailed testing with results from controlled experiments under contrasting temperature (Grant et al., 2011), N fertilizer (Grant et al., 2010b), irrigation (Grant et al., 2007) and C_a (Grant, 2013). A PC version of *ecosys* with GUI is available at https://portal.ales.ualberta.ca/ecosys/default.aspx.

Changes in soil and plant C stocks, and in N mineralization measured in the Harvard Forest soil heating experiment (Melillo et al., 2011) provide a unique opportunity to extend testing of model hypotheses for T_s effects on coupled N and C cycles because the spatial and temporal scales of this experiment (30 m × 30 m and 7 years) approach those at which changes in ecosystem N and C cycling with warming can be most fully observed. These changes were therefore used to test whether these model hypotheses could explain the extent to which gains in forest C stocks through increased GPP from N mineralization offset losses in soil C stocks through increased R_h during soil heating.

However heating in such experiments is imposed as a sudden increase in soil temperature rather than as a gradual increase in soil and air temperatures expected with climate warming. The effects of heating on C and N cycling observed in these experiments may therefore be artefacts of this sudden increase, and so may differ from those of gradual climate warming, limiting the extent to which climate warming effects can be inferred from such experiments. To evaluate this difference, C and N cycling modelled with sudden soil heating of 5 °C over 7 years were compared against those with gradual climate warming of 5 °C over 100 years.

2. Model description

The key algorithms governing the simulation of C and N transformations in *ecosys* are described in the Supplement to this article, in which equations and variables referenced in the Results below are described and listed in Appendices A through H. Algorithms representing biological processes in soil (Appendices A, G and H), physical processes driving soil–plant–atmosphere water transfer (Appendix B), biological processes in plants (Appendices C and F), and chemical processes governing soil solute transformations (Appendix E) were solved at an hourly time step driven by hourly changes in atmospheric boundary conditions. Algorithms representing physical processes driving soil water, heat, gas and solute transfers (Appendix D) were solved at a 4-min time step assuming constant boundary conditions within each hour. All parameters in these algorithms remained unchanged from those in earlier studies of forests, crops and grasslands cited in the Introduction. The key model hypotheses for the effects of soil warming on N and C cycling are described in further detail below with reference to equations in the Supplement.

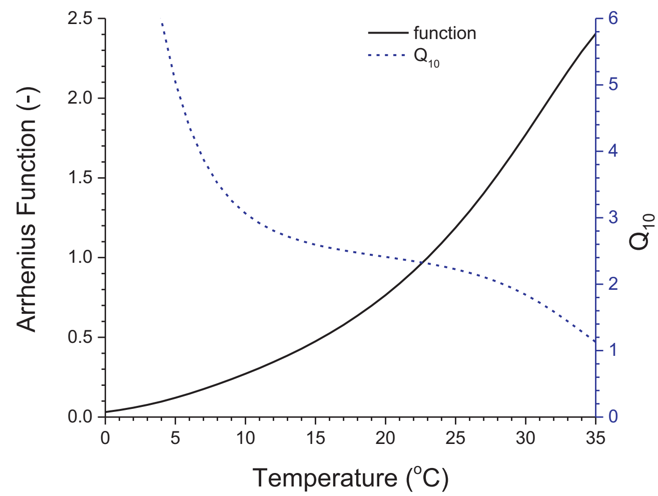

Fig. 1. Arrhenius function used in *ecosys* (Eq. (1) in text and Eq. [A6] in Supplement) with derived Q_{10} values.

2.1. Model hypotheses for changes in N and C cycling with soil warming

2.1.1. Decomposition

Organic transformations in *ecosys* occur in five organic matter–microbe complexes (coarse woody litter, leaf and fine non-woody litter, animal manure (if present), particulate organic matter (POM), and humus), each of which consists of five organic states consisting of C, N and P (three decomposition substrates – solid organic matter, sorbed organic matter, and microbial residue, their decomposition products – dissolved organic matter (DOC, DON and DOP), and the decomposition agent, active microbial biomass (M)) in a surface residue layer and in each soil layer. The rates at which each of the three substrates decompose in each complex are first-order functions of M in diverse heterotrophic microbial functional types, including obligate aerobes (bacteria and fungi), facultative anaerobes (denitrifiers), obligate anaerobes (fermenters), heterotrophic (acetotrophic) and autotrophic (hydrogenotrophic) methanogens, and aerobic and anaerobic heterotrophic diazotrophs (non-symbiotic N_2 fixers) [A1, A2], modified by an Arrhenius function of T_s [A6]. This function was parameterized from basic studies of oxidation–reduction kinetics, and tested under controlled changes in T_s and water potentials (Grant and Rochette, 1994). The inclusion of terms for low and high temperature inactivation enabled this function closely to resemble the Gaussian function found best to represent T_s effects on R_h in a meta-analysis by Tuomi et al. (2008) (Eq. (1); Fig. 1).

$$f_{tgl} = \frac{T_{sl}\left\{e^{\left[B - H_a/(RT_{sl})\right]}\right\}}{\left\{1 + e^{\left[(H_{dl} - ST_{sl})/(RT_{sl})\right]} + e^{\left[(ST_{sl} - H_{dh})/(RT_{sl})\right]}\right\}} \quad (1)$$

where f_{tgl} is the temperature function for microbial growth respiration in layer l, T_l is the soil temperature in layer l (K), B is the parameter such that f_{tgl} = 1.0 at T_{sl} = 298.15 K (26.235), H_a is the energy of activation (65 × 10^3 J mol^{-1}), H_{dh} is the energy of high temperature deactivation (225 × 10^3 J mol^{-1}), H_{dl} is the energy of low temperature deactivation (197.5 × 10^3 J mol^{-1}), R is