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Forest soil carbon and nitrogen cycles under biomass harvest: Stability, transient response, and feedback

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ABSTRACT

Biomass harvest generates an imbalance in forest carbon (C) and nitrogen (N) cycles and the nonlinear biogeochemical responses may have long-term consequences for soil fertility and sustainable management. We analyze these dynamics and characterize the impact of biomass harvest and N fertilization on soil biogeochemistry and ecosystem yield with an ecosystem model of intermediate complexity that couples plant and soil C and N cycles. Two harvest schemes are modeled: continuous harvest at low intensity and periodic clear-cut harvest. Continuously-harvested systems sustain N harvest at steady-state under net mineralization conditions, which depends on the C:N ratio and respiration rate of decomposers. Further, linear stability analysis reveals steady-state harvest regimes are associated with stable foci, indicating oscillations in C and N pools that decay with time after harvest. Modeled ecosystems under periodic clear-cut harvest operate in a limit-cycle with net mineralization on average. However, when N limitation is strong, soil C–N cycling switches between net immobilization and net mineralization through time. The model predicts an optimal rotation length associated with a maximum sustainable yield (MSY) and minimum external N losses. Through non-linear plant–soil feedbacks triggered by harvest, strong N limitation promotes short periods of immobilization and mineral N retention, which alter the relation between MSY and N losses. Rotational systems use N more efficiently than continuous systems with equivalent biomass yield as immobilization protects mineral N from leaching losses. These results highlight dynamic soil C–N cycle responses to harvest strategy that influence a range of functional characteristics, including N retention, leaching, and biomass yield.

1. Introduction

Soil biogeochemical cycles and biomass production are closely linked processes in managed ecosystems. Soils supply plants with essential nutrients through a complex of biogeochemical processes mediated by soil organic matter (SOM) and decomposers. In turn, soil biogeochemical processes are affected by harvest management practices that determine the relative amounts of organic material (e.g., carbon (C) and nitrogen (N) ratios) and nutrients applied to the soil or harvested from the ecosystem. In particular, microbially-mediated decomposition of plant residues and associated N mineralization and immobilization fluxes control soil carbon–nitrogen (C–N) cycling and N availability after harvest (Vitousek and Matson, 1985; Prescott, 1997). Improved quantitative understanding of soil C–N cycles in response to harvest is one challenge associated with sustainable management of soil, water, and ecosystem resources (Porporato and Rodriguez-Iturbe, 2013; Porporato et al., 2015).

The coupled ecosystem C–N cycle can be understood as a complex system of plant and soil compartments linked through the dynamics of plants, SOM, and soil decomposers (Figs. 1 and 2). Under management for food or timber production, harvest and associated management practices impose two changes to the structure of this dynamical system. First, management practices may take the form of an external forcing to the system, as in the export of harvested biomass or the addition of N fertilizer. Secondly, the balance of harvest export and residue application, which depends on the quality and quantity of harvested biomass, changes the plant litter flux. The plant litter flux is integral to decomposer-SOM feedback and long-term soil N availability (Vitousek and Matson, 1985; Manzoni and Porporato, 2007). In these ways, biomass harvest alters the inputs and outputs as well as the internal dynamics of ecosystem C–N cycles.

There is no shortage of studies that quantified the impact of biomass harvest on soil C and N storage and associated soil

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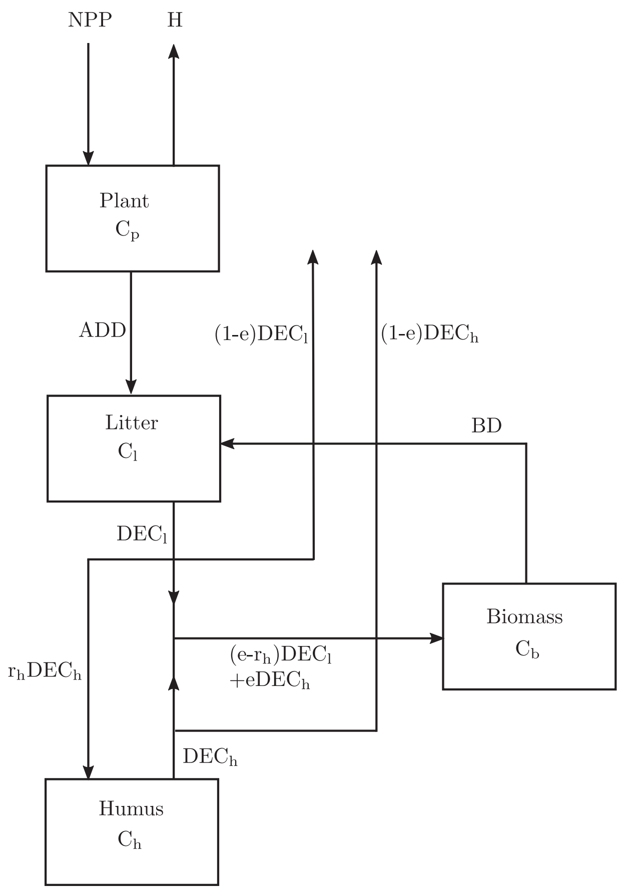

Fig. 1. Carbon balance model schematic. Fluxes are: net primary productivity (*NPP*), litter and humus decomposition (DEC_l and DEC_h), biomass harvest (*H*), litterfall (*ADD*), decomposer turnover (*BD*). Pools are: plant (*p*), fast-cycling litter (*l*), slow-cycling humus (*h*), and decomposers (*b*). The fraction of decomposed litter partitioned to humus is r_h and the heterotrophic carbon use efficiency is *e*.

biogeochemical process rates. However, while biomass harvest inevitably intensifies ecosystem C and N losses, there is little consensus on the magnitude and direction of the aggregate effects on soil C storage, soil C and N fluxes, and primary production. In a meta-analysis of 73 studies, Johnson and Curtis (2001) found no change in soil C and N storage after harvest, although individual studies showed positive or negative changes. In contrast, a meta-analysis of 432 studies in temperate forests showed harvesting decreased forest floor C storage by 30% on average (Nave et al., 2010). Although many studies demonstrated soil C losses under harvest, full recovery of C storage is common after several decades (Covington, 1981; Guo and Gifford, 2002; Peng et al., 2002; Wei et al., 2003; Yanai et al., 2003; Nave et al., 2010). With regard to N fluxes, clearcut harvest was found to increase N availability, nitrification, and mineralization across more than 54 studies (Jerabkova et al., 2011). Similar to changes in C storage, these effects disappeared 10–15 years after harvest. In general, soil biogeochemical impacts after harvest were attributed to harvest type (i.e., whole-tree, stem-only), species, fertilization, and the time of post-harvest sampling. In addition to the large amount of uncertainty in these results, the time-dependence of post-harvest ecosystem function underscores the importance of identifying the time-scales of transient disturbance responses in harvested ecosystems with models.

Many previous studies modeled the soil biogeochemical cycle response to management practices (e.g., Aber et al., 1982; Rolff and Agren, 1999; Thornley and Cannell, 2000; Peckham et al., 2013; Dangal et al., 2014) and a subset purposely analyzed the relation between harvest and the internal dynamics of soil C–N cycles (Dewar and McMurtrie, 1996a,b; Corbeels et al., 2005; Tian et al., 2012; Wang et al., 2014). These modeling studies noted residue removal and increased soluble inorganic nitrogen leaching after harvest as primary sources of N loss in harvested ecosystems, which may reduce primary production over time. Because harvest residue constitutes the main source of organic N to decomposers and the pool of inorganic N available for leaching results from the balance of plant and decomposer N demand, it is anticipated such modeling results are sensitive to the underlying modeling structure. Recent advances in the modeling of C–N cycle dynamics emphasized the strength of nutrient competition between plants and decomposers and the coupling of decomposer population dynamics to the decomposition rate (Johnson, 1992; Schimel and Bennett, 2004; Manzoni and Porporato, 2007). Further understanding of these processes in harvested ecosystems may yield new insight regarding the management of soil C–N cycles to reduce N losses (Goulding et al., 2008).

To make progress on this topic, the impact of ecosystem management practices on soil C–N cycles is studied in a model ecosystem of intermediate complexity. Specifically, we consider the plant–soil C–N cycle feedbacks and the balance of N mineralization and immobilization during SOM decomposition in response to N fertilization and harvest intensity, defined as the quantity (i.e., mass), quality (i.e., C to N ratio (C:N)), and frequency of harvest. We present analytical, steady-state solutions to a simplified system harvested at a continuous and constant rate as well as numerical simulations of systems subject to repeated clear-cut harvest and regrowth. Continuous harvest is analogous to the selection method, in which a small fraction of the forest is harvested and replaced at short intervals (Smith et al., 1997). From these model results, harvested ecosystem function is discussed with respect to ecosystem services including biomass yield, standing biomass, and soil biogeochemical cycling.

2. Model of coupled plant–soil carbon–nitrogen dynamics

The model developed here combines the soil C–N cycling schemes proposed by Porporato et al. (2003) and Manzoni and Porporato (2007) coupled to a model for the plant C–N dynamics. This coupled plant–soil C–N model has nine pools as state variables: four carbon and five nitrogen pools. The soil model describes three soil organic matter pools (litter, humus, and decomposer biomass), each with associated C and N, and one mineral N pool.

Several model assumptions are employed to parameterize C and N fluxes and to reduce model complexity. Decomposition follows a flexible scheme that merges the mineralization-immobilization turnover (MIT) and direct assimilation (DIR) hypotheses (Manzoni and Porporato, 2009). Further, three decomposition functions are tested to evaluate the consequences of coupling substrate and decomposer dynamics. The model assumes a constant C:N for the plant, humus, and decomposer pools and a variable litter C:N, which reduces the number of state variables from nine to six. The model is applied at the annual time-scale and inter-annual variations in climate are ignored. The model, with additional assumptions, is described below and depicted in Figs. 1 and 2.

The C balance equations for plant (C_p), litter (C_l), humus (C_h), and decomposer biomass (C_b) are:

$$\frac{dC_p}{dt} = NPP - LF - H, \tag{1}$$

$$\frac{dC_l}{dt} = ADD + BD - DEC_l, \tag{2}$$

$$\frac{dC_h}{dt} = r_h DEC_l - DEC_h, \tag{3}$$