Boom and bust carbon-nitrogen dynamics during reforestation

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ABSTRACT

Legacies of historical land use strongly shape contemporary ecosystem dynamics. In old-field secondary forests, tree growth embodies a legacy of soil changes affected by previous cultivation. Three patterns of biomass accumulation during reforestation have been hypothesized previously, including monotonic to steady state, non-monotonic with a single peak then decay to steady state, and multiple oscillations around the steady state. In this paper, the conditions leading to the emergence of these patterns is analyzed. Using observations and models, we demonstrate that divergent reforestation patterns can be explained by contrasting time-scales in ecosystem carbon-nitrogen cycles that are influenced by land use legacies. Model analyses characterize non-monotonic plant-soil trajectories as either single peaks or multiple oscillations during an initial transient phase controlled by soil carbon-nitrogen conditions at the time of planting. Oscillations in plant and soil pools appear in modeled systems with rapid tree growth and low initial soil nitrogen, which stimulate nitrogen competition between trees and decomposers and lead the forest into a state of acute nitrogen deficiency. High initial soil nitrogen dampens oscillations, but enhances the magnitude of the tree biomass peak. These model results are supported by data derived from the long-running Calhoun Long-Term Soil-Ecosystem Experiment from 1957 to 2007. Observed carbon and nitrogen pools reveal distinct tree growth and decay phases, coincident with soil nitrogen depletion and partial re-accumulation. Further, contemporary tree biomass loss decreases with the legacy soil C:N ratio. These results support the idea that non-monotonic reforestation trajectories may result from initial transients in the plant-soil system affected by initial conditions derived from soil changes associated with land-use history.

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1. Introduction

Ecosystem transitions between agricultural and forest land uses occur across the globe and are associated with transient changes in biogeochemical cycling. It is estimated that 64% of the world's forests are regenerating from disturbance caused by human activities (FAO, 2010). Land use legacy effects originating from such transitions include altered species composition, water fluxes, soil chemistry, soil carbon and nitrogen storage, and ecosystem nitrogen cycling (Richter et al., 1994, 2000; Guo and Gifford, 2002; Farley et al., 2005; Berthrong et al., 2009; Bain et al., 2012; Bernal et al., 2012; Vadeboncoeur et al., 2012).

Several modes of transient forest recovery after disturbance have been recognized. Peet (1981) summarized biomass recovery trajectories across a gradient of increasing time lag between recruitment and mortality: saturating growth to steady state (no lag), overshoot of and subsequent decay to steady state (moderate lag), and multiple oscillations around the steady state (long lag) (Fig. 1a). Consistent with Peet's (1981) "asymptotic yield" curve with no lag, reforestation trajectories are commonly characterized by a monotonic, saturating approach to a relatively stable live tree biomass (Fig. 1b) (e.g., Odum 1969; Dewar 1991; Dewar and Cannell, 1992; Ryan et al., 1997; Amiro et al., 2000; Williams et al., 2012; Wang et al., 2014). In contrast, many stands exhibited non-monotonic reforestation trajectories with overshoot or oscillations (Fig. 1c) (e.g., Peet and Christensen, 1987; Aakala and Keto-Tokoi,
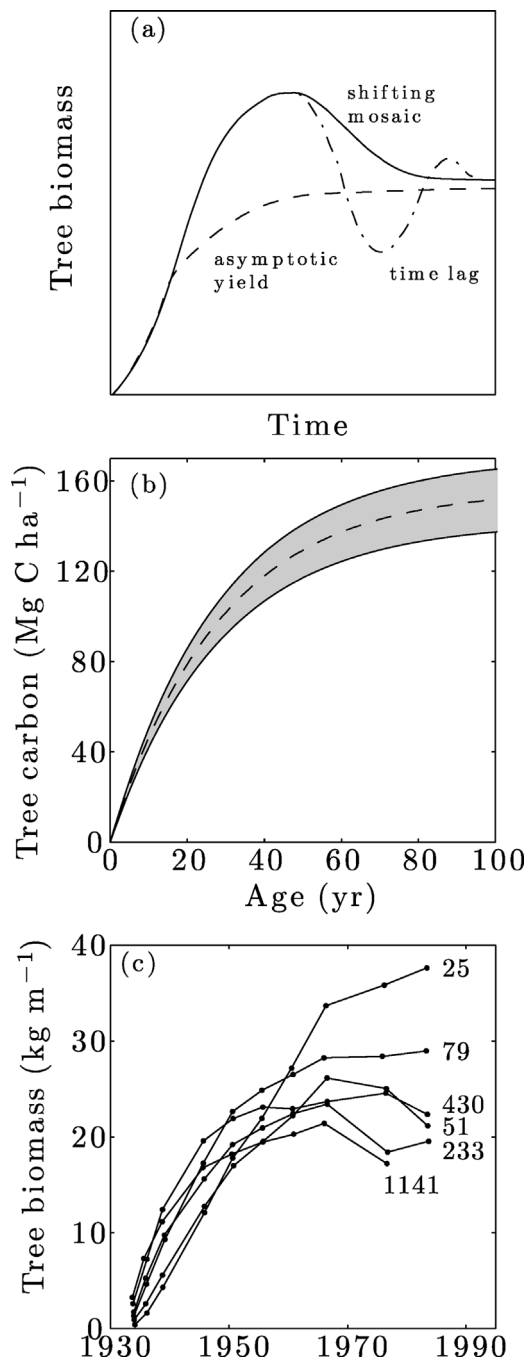
Fig. 1. Alternative perspectives on reforestation dynamics: (a) three hypothesized reforestation trajectories, including asymptotic yield, shifting mosaic, and time lag (redrawn from Peet, 1981); (b) monotonic, saturating reforestation trajectory fit to the USFS Forest Inventory and Analysis dataset for Slash Pine in the Southeast US (Williams et al., 2012); and (c) observed biomass change over 60 years at Duke Forest exhibiting both saturation and overshoot (redrawn from Peet and Christensen, 1987). In (c), the numbers correspond to initial planting density (stems per 0.1 acres).

2011; Mobley 2011), often termed "boom-and-bust cycles" in other complex systems (Brander and Taylor, 1998; Rodrigues et al., 2009).

Proposed mechanisms that underlie non-monotonic, boom-and-bust reforestation trajectories include temporal changes in age-structure and soil resource availability. The "shifting mosaic" hypothesis contends that planted even-aged stands grow to a peak biomass that is greater than that of the steady-state mixed-aged stand (Bormann and Likens, 1979; Peet and Christensen, 1987). The transition from peak even-aged biomass to the lower all-aged

steady state biomass occurs as age-related mortality in the original cohort is offset by heterogeneous gap recruitment and regeneration. Secondly, changes in soil nutrient availability over time (e.g., Richter et al., 2000) imply that the strength of nutrient limitation of productivity may also change with forest age (Peet 1981). In the Duke Forest, volume of 44-year old loblolly pine was strongly positively correlated with site index, determined by A horizon depth and B horizon plasticity (Peet 1981). Stands with high site index exhibited monotonic increases in tree volume, whereas stands with low site index exhibited a peak and subsequent losses of tree volume (Peet 1981).

The flow of carbon and nitrogen in ecosystems may capture how soil resource availability affects reforestation trajectories. Forest biogeochemical cycles are complex, multi-dimensional systems composed of abiotic-biotic interactions tightly coupled through the stoichiometric requirements of autotrophic and heterotrophic metabolism. In particular, the carbon-nitrogen ratio (C:N), an index of soil organic matter (SOM) quality, is a soil property that integrates the cycling of these essential elements between plants and soil (Manzoni et al., 2010). Plant-soil trajectories during reforestation arise from internal feedbacks regulated by SOM quality, which include plant nutrient uptake, canopy re-translocation, litterfall, mortality and other biomass turnover, and nitrogen mineralization through decomposition of plant residue and SOM. As in any system with a large number of interacting states, such feedback interactions between plants and soil may produce complex, non-monotonic dynamics, even in the absence of external oscillatory forcing or excitation (Murray, 2002; Bechhoefer, 2005) (e.g., disturbance or climate extremes). Indeed, consumer-resource oscillations have been noted in bacteria- or decomposer-substrate systems (Zelenev et al., 2000; Manzoni and Porporato, 2007; Raupach, 2007; Sanchez-Vila et al., 2013), but have not been extended to coupled plant-soil systems.

Models can be used to distill the complexities of reforestation mechanisms and outcomes (Neubert and Caswell, 1997; Baisden and Amundson, 2003; Wang et al., 2014). From a systems perspective, biomass overshoot and oscillations indicate an interaction exists between at least two ecosystem components. As noted above, either forest age structure or soil resource availability provides the additional degree of freedom that allows biomass to vary in a non-monotonic way. Therefore, at a minimum, a quantitative description of the three hypothesized reforestation trajectories depicted in Fig. 1 must couple the dynamics of tree biomass to forest age structure or a soil resource.

A logical starting point for a quantitative analysis of reforestation dynamics is an aggregated, stand-level forest model that does not explicitly represent age structure. While age-structured models are useful in many situations, they are represented as systems of coupled partial differential equations that are not easily analyzed (Friend et al., 1997; Moorcroft et al., 2001; Strigul et al., 2008). Stand-level models, on the other hand, can be represented as systems of ordinary differential equations (e.g., Parton et al., 1988; Thornton et al., 2002) with opportunity for detailed mathematical analysis. Stand-level models are commonly used in the study of harvest impacts on reforestation and some are known to produce non-monotonic reforestation trajectories (Neubert and Caswell, 1997; Baisden and Amundson, 2003; Wang et al., 2014), which is why they are selected for the starting point of the analysis. Finally, ecosystem processes aggregated at the population level, such as productivity, are related to age structure (van Straalen, 1985; Moorcroft et al., 2001), providing a link between the results of stand-level and age-structured models.

In this paper, models of coupled plant-soil carbon and nitrogen cycles are developed and used to identify mechanisms intrinsic to forest carbon-nitrogen cycles that may lead to alternative asymptotic, overshoot, and oscillation reforestation trajectories. In a case