Accomplishments

**Activities, objectives, significant results, and key outcomes:**

Based on our work with the Multiple Element Limitation (MEL) model (Rastetter et al. 2013), we are developing a new theory of ecosystem recovery from disturbance. The essence of the theory derives from the observation that mature terrestrial ecosystems rely almost exclusively (>95%) on N, P, and probably other nutrients recycled within the ecosystem. To achieve this degree of closure, nutrients must accumulate in the ecosystem over many years. Thus, early in primary succession, the nutrients supporting primary production are derived almost exclusively from outside the ecosystem (weathering of parent material, N fixation, and deposition). As the ecosystem matures, these nutrients are entrained into ecosystem cycles and accumulate predominantly in soils and vegetation (Fig. 1). For this accumulation to occur, a balance has to be maintained between soil and plant processes; soil organic matter (SOM) cannot accumulate without the litter produced by vegetation and the vegetation cannot grow and continue to produce organic matter without the nutrients mineralized from the SOM. In addition, the accumulation of nutrients has to be synchronized; N cannot accumulate in the ecosystem unless P and other vital nutrients also accumulate and vice versa. Disturbance disrupts the plant-soil balance and the synchronization among nutrient cycles, often resulting in a net loss of nutrients from the ecosystem and usually resulting in a redistribution of nutrients from vegetation to soils in slash, ash, and debris.

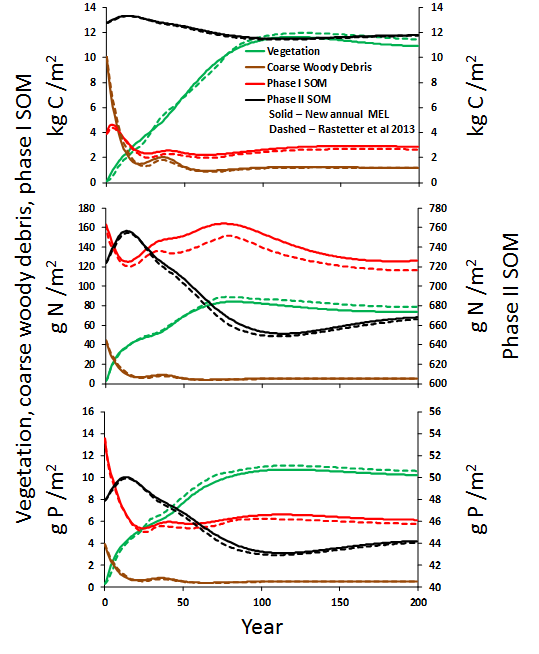


Figure 2: Comparison of the new annual time-step MEL model and the daily time-step MEL model used in Rastetter et al. (2013). The simulation is for the recovery from a bole-only, clear-cut harvest, the base simulation in our 2013 paper.

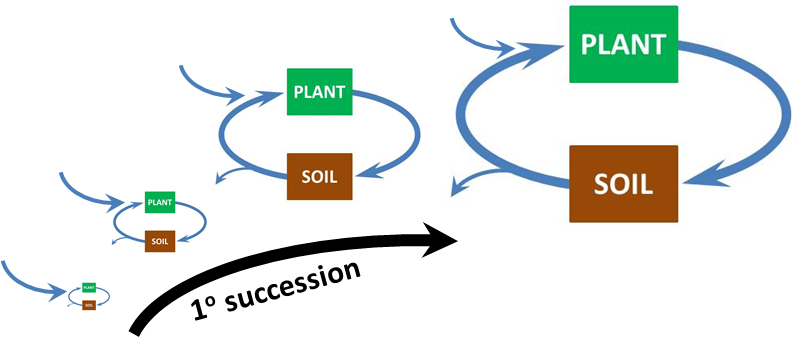


Figure 1: Entrainment of nutrients into the internal ecosystem cycle during primary succession and the progressively stronger reliance of the ecosystem on internally recycled nutrients.

To analyze the long-term dynamics of primary and secondary succession, we needed a model that was easier to implement and less computationally intensive than the daily time-step version of the MEL model (version IV) we used for the analysis in Rastetter et al. (2013). We therefore developed an annual-time-step version of the MEL model (version V) and calibrated it to the same data for Hubbard Brook used in our 2013 paper. The annual time-step model captures the long-term dynamics of the daily time-step model well (e.g., Fig. 2 for a bole-only harvest).

Using this model, we ran simulations of primary succession and secondary succession following a bole-only, clear-cut, harvest; both simulations were run under present-day N and P supply rates. We also ran simulations of primary and secondary succession for a factorial N and P fertilization where the concentrations of available N and/or P were held at concentrations that saturated both plant and microbial uptake kinetics (109 g m-2).

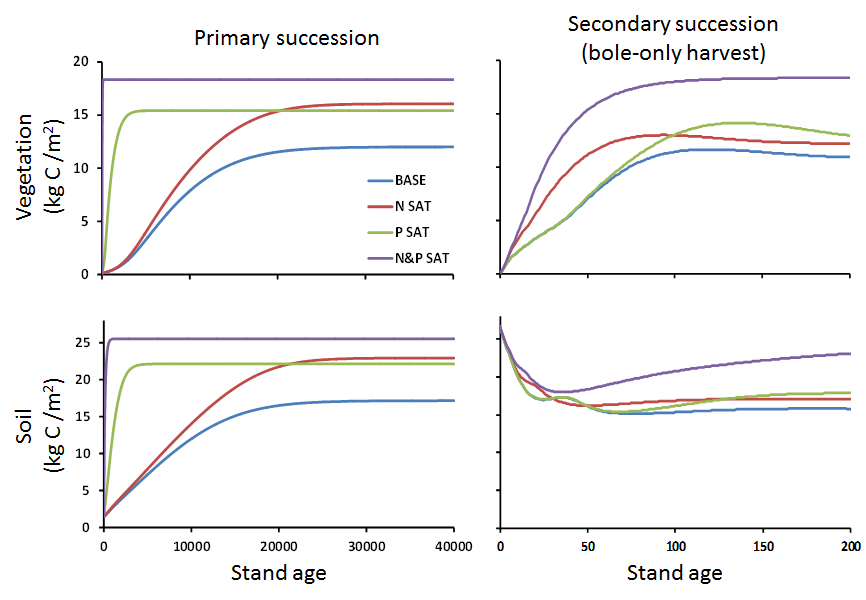


Figure 3. Simulation of a N-P factorial fertilization for primary and secondary succession. In the fertilized simulations, N and/or P were held at saturating concentrations (109 g m-2).

The nature of limitation differs between the two sets of simulations (Fig. 3). Because of the slow external supply of P relative to N in our simulations, primary succession is initially P limited. Even with N supplied in excess, the ecosystem requires 20,000 years to reach maximum vegetation and soil mass because of this slow P supply. This mass-accumulation rate is slow relative to actual accumulation rates (this landscape is only 14,000 years old); we hypothesize that the post glacial landscape had much higher rates of P supply than the present-day weathering estimates we are using in our simulations (consistent with Walker and Syers 1976). In the post glacial landscape there would have been glacial flour and till and freshly exposed parent material that could have been a readily available supply of P; with a faster P supply rate the vegetation and soil mass could accumulate in 2000 years; with both faster P and N supply (e.g., N fixation), the vegetation can accumulate in about 100 years and the soil in less than 1000 years.

In contrast to the slow P-limited accumulation in primary succession, the recovery of vegetation in our simulation of secondary succession requires only 100 years and is clearly N limited. The reason for this fast recovery, of course, is the large stock of nutrients remaining in the soils, a nutrient subsidy that gives the ecosystem a head start over primary succession. Most of the vegetation recovery is fueled by a transfer of nutrients from the pre-disturbance soil plus nutrients added to the soil in the disturbance as slash. Even with this redistribution of nutrients, the ecosystem only recovers to about 92% of its pre-disturbance C, N, and P mass in 200 years. Only about a fourth of the total N and P loss occurs in the disturbance itself; the remaining three fourths occurs during the recovery because plant and soil processes are not in balance (e.g., mineralization is in excess of plant demand early in recovery) and the element cycles are not synchronized (e.g., early N limitation means that mineralized P is susceptible to loss). To recover the remaining 8% of the ecosystem N and P capital requires a much longer time, more in line with the time scales of primary succession.

In summary, because of the slow external supply of nutrients during primary succession, plant and soil processes can continuously adjust to one another and the two can remain in balance. Because of this balance between plant and soil processes, the ecosystem retains nutrients and they are entrained into the ecosystem cycle. Disturbance disrupts this balance, initiating a two phase recovery in secondary succession (Fig. 4). During the first phase of recovery, nutrients are redistributed from soil to vegetation. This redistribution is imperfect because plant and soil processes are not in balance and the nutrient cycles are not fully synchronized. There are therefore nutrient losses during recovery in addition to the losses during the disturbance. Nevertheless, this redistribution accelerates vegetation recovery and reestablishes the balance between plant and soil processes. When this balance is reestablished, the ecosystem can again accumulate nutrients and secondary succession converges to the trajectory of primary succession.

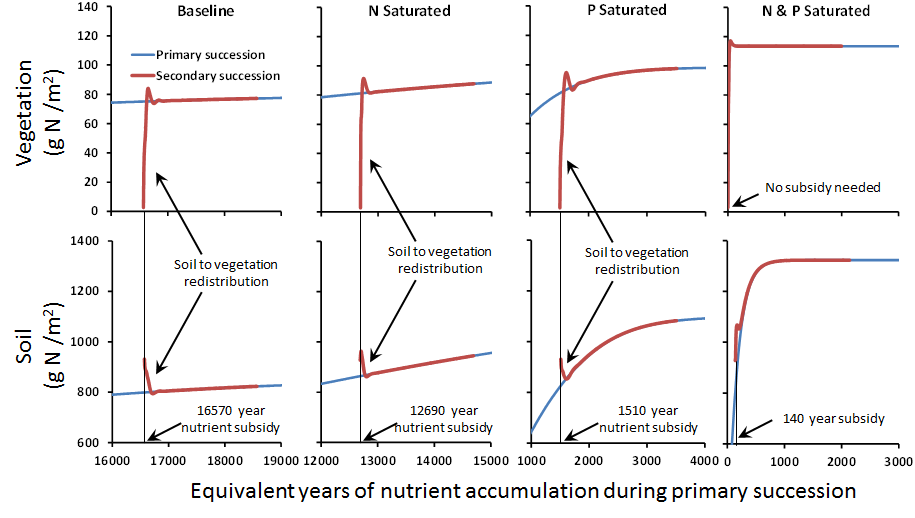


Figure 4: Trajectories of primary and secondary succession. The major biogeochemical difference between 1o and 2o succession is that the ecosystem starts with a major nutrient subsidy during 2o succession.

Because of the slow progression of 1o succession, a balance is maintained between plant and soil processes. Disturbance disrupts that balance. During recovery from disturbance, nutrients are first redistributed from soil to vegetation, which reestablishes the balance between plants and soils. The trajectory of 2o succession therefore converges to the trajectory of 1o succession.

This two-phase recovery can be illustrated more clearly in a plant nutrient-soil nutrient phase-plane plot (Fig. 5). Assuming negligible nutrient content in ecosystem components other than vegetation and soils (here soils include woody debris, forest floor, and all the soil layers), the isopleths of total nutrient in the ecosystem are diagonal lines in this plot. The trajectory of primary succession in the plot proceeds up and toward the right as the ecosystem accumulates nutrient. The exact trajectory will depend on the local environmental conditions (climate, parent material, topography, potential biota), but because of the slow rate of nutrient accumulation, the plant and soil process will remain in balance.

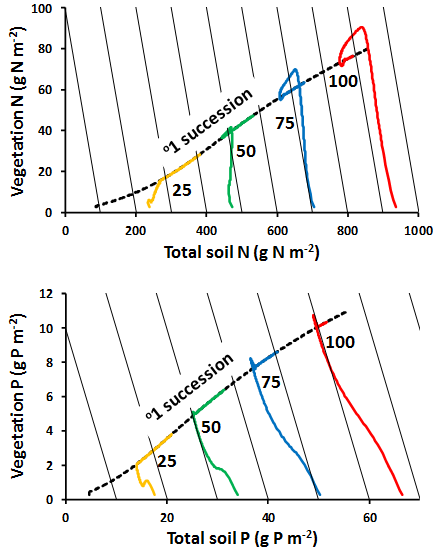


Figure 6. Phase plane plots for N and P in simulations with soil stocks equal to 100%, 75%, 50%, and 25% of the soil stocks in the bole only harvest simulation (Fig. 2).

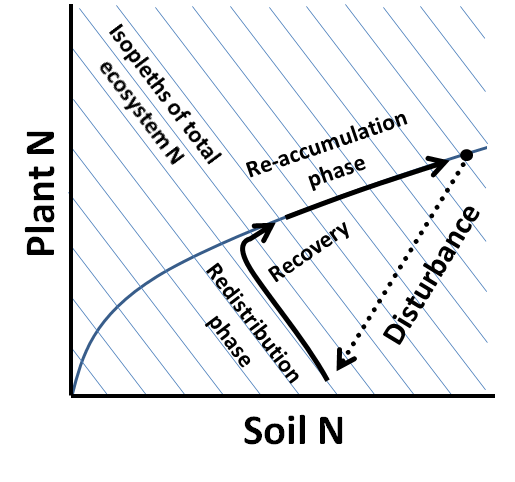


Figure 5: Plant N soil N phase plane plot illustrating trajectories of primary and secondary succession.

A disturbance might directly result in net nutrient losses or gains for soils, but will typically result in nutrient losses from the vegetation. In any case, the disturbance will displace the ecosystem from the primary succession trajectory, that is, from the trajectory that represents a balance between plant and soil processes for the particular environment. Immediately after the disturbance, we postulate a redistribution phase where there is a net release of nutrients from soil and net accumulation by plants. If the nutrient is limiting to growth during the recovery, the recover trajectory will parallel the isopleths of total ecosystem nutrient or be slightly above and to the right of those isopleths if nutrient is also accumulated in the ecosystem as a whole. If the nutrient is not limiting during recovery, there will tend to be a net loss from the ecosystem and the recovery trajectory will be below and to the left of the isopleths of total ecosystem nutrient. This redistribution trajectory will approach the primary succession trajectory as plant and soil processes come back into balance. The location on this plot where the primary and secondary succession trajectories converge will depend on the amount of nutrient lost in the disturbance and during the recovery before a plant-soil balance can be reestablished. Once the balance is reestablished, the ecosystem will be more effective at entraining and retaining nutrients in the ecosystem cycle. From that point on, the recovery trajectory should coincide with the primary succession trajectory.

We used this phase-plane plot to analyze the recovery of the forest following a harvest with different amounts of soil and detritus remaining (Fig. 6). As a baseline, we used the same bole-only harvest simulation discussed above (Fig. 2 and baseline simulations in Figs. 3 & 4). We also simulated recovery with coarse woody debris and Phase I and Phase II SOM all reduced to 75%, 50% and 25% of that in the baseline simulation. The recovery trajectories of both N and P start off with a slope that is below and to the left of the isopleths of total ecosystem nutrient, indicating losses of both N and P. This early nutrient loss is the result of high net mineralization rates but plant uptake rates that are limited by the photosynthetic capacity of an as yet poorly developed canopy. For N, this early loss is very short lived (barely noticeable in the 100% simulation), then the ecosystem begins to slowly accumulate N. Because the first 2-80 years of recovery are N limited, P is lost from the ecosystem during this period. However, late in the recovery as the vegetation and soils converge on the pre-disturbance stoichiometry of the ecosystem, this P lost early in recovery has to be matched by a proportional loss of N later in recovery (as discussed in Rastetter et al. 2013). Eventually both the N and P recovery trajectories converge on that of primary succession and a balanced entrainment of N and P into the ecosystem can proceed.