

Findings for MBL MEL Project DEB-0108960

Findings

Findings are listed by paper, the citations for which can be found in the citations section.

Herbert et al. 2003: We applied MEL to secondary growth in the Amazon Forest in both a C-N and a C-P configuration to assess limitation by N and P after pasture abandonment. Our analysis indicates that the early stages of re-growth are N, rather than P, limited because a large amount of N is lost from these forests when they are cut and burned. The forest reverts to P limitation later in succession.

Herbert et al. 2004: We analyzed competition for light and nutrients across a nutrient gradient to assess the effect on species diversity. Diversity was highest at intermediate total community biomass but increased monotonically with both productivity and nutrient supply. The highest diversity was also found at intermediate values of the ratio of community leaf area to root length, indicating a condition where the community as a whole was co-limited by light and nutrients.

McKane et al. 2002: Support from this project helped in the interpretation of a ¹⁵N labeling experiment designed to assess plant niche partitioning based on NH₄, NO₃, glycine as sources on N, early versus late season uptake, and shallow versus deep soil N foraging. Productivity among species increased as the pattern of uptake of various sources on N by the species approached the pattern of supply of those sources in the soil.

Rastetter et al. 2001: We used the MEL model to derive an equation to predict the conditions under which symbiotic N fixation should be favored: high CO₂, high light, open canopy, low available soil N, and a soil volume fully exploited by roots. The equation provides a quantitative means to combine the relative contributions of these five factors. Simulations are generally consistent with observations. This analysis explains why symbiotic N fixation does not persist late in succession even though N remains limiting to plant production.

Rastetter and Ågren 2002: Based on our work on competition with the MEL model, we reassessed the R-star model and its predictions of coexistence i.e., one species per limiting resource. We found that this prediction is an artifact of the assumptions in R-star, in particular the assumption of both growth and biomass turnover being proportional to biomass. If the model is modified so that growth is a monotonically increasing, concave downward function of biomass, any number of species can coexist with just one limiting resource. We argue why growth should be a concave downward function of biomass rather than proportional.

Rastetter 2003: Funding from this project help support participation in the Cary Conference on Models in Ecosystem Science. I assessed what can be learned from comparisons of ecosystem models. Most such comparisons are frustratingly unenlightening because the data were not taken AFTER the model comparison and therefore were not designed to discriminate among the alternate hypotheses represented by the models. The comparison does however serve to guide future data collection (but the guidance is rarely followed).

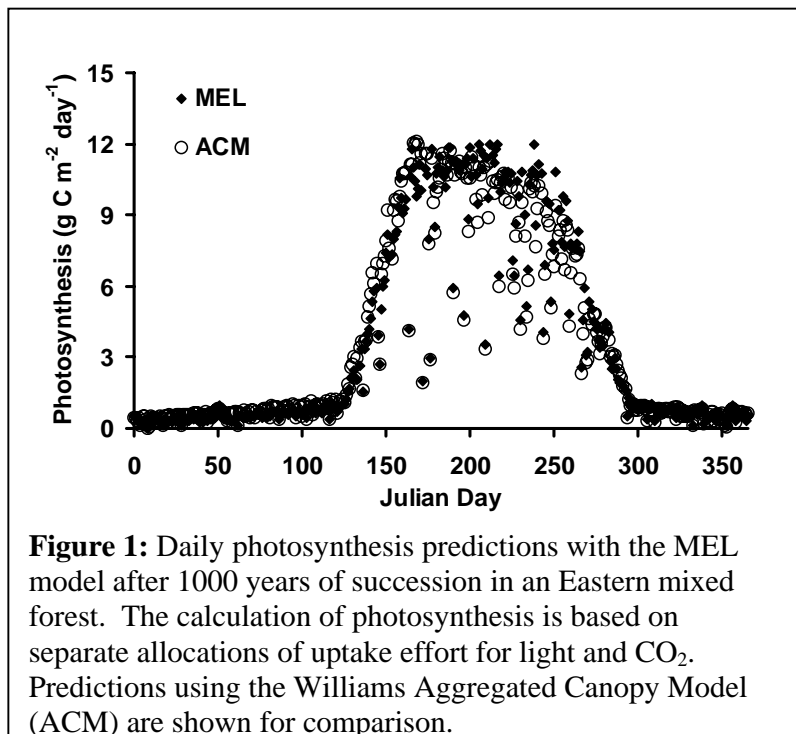
Rastetter et al. 2004: We used MEL's sister model GEM to assess the role of down-slope water and nutrient fluxes in the Response of Arctic hill slopes to climate change. Down-slope locations are more productive mostly because running water breaks down the nutrient diffusion

gradient around roots. In response to elevated CO₂, warming, and increased rainfall, upslope locations had a higher proportional increase in stored C, but down-slope locations had a higher absolute increase

Rastetter et al. 2005: We used the MEL model to assess the importance of DON losses on the response of terrestrial ecosystems to elevated CO₂ and warming. Assuming DON is unavailable to plants, its concentration in soil solution cannot be depleted by increased N demand as the vegetation responds to elevated CO₂. Therefore, unlike DIN losses, DON losses do not decline with elevated CO₂. Because a decline in N losses results in higher N accumulations, ecosystems will respond more strongly to CO₂ if most of the losses are as DIN than if the losses are as DON. Warming amplifies this difference.

Rastetter et al. 2005: To be able to make use of isotope data, we developed a stable isotope simulator that can be coupled to mass-balance models like MEL. The simulator used the output from the mass-balance model and, with information on initial isotope distributions, isotopic signatures of the inputs, and the fractionation for processes in the model, predicts the time course of isotopic signatures for all the model component pools and processes. The software will be published in Ecological Archives so that other modelers can make use of it with their models.

Rastetter et al. In prep.: We now have a version of the MEL model that can simulate interactions among more than two resources, including non-element resources (e.g., light and water), and among substitutable resources (e.g., NH₄ or NO₃ as sources of N). The approach is general enough that the model can now be extended to any number of element and non-element resources and to any number of substitutable resources. The specific form of the model that we have implemented has eight resources: CO₂, PO₄, H₂O, light, NH₄, NO₃, DON, and N₂-fixation, the last four of which are substitutable sources for N. In addition, we have converted the model from an annual to a daily time step so that we can examine changes in phenology (Fig. 1) and seasonal changes in resource availability, and can tie losses of dissolved materials (NH₄, NO₃, DON, DOC, PO₄) to a daily soil-water budget.



Allocation of Uptake Effort: We refer to the internal assets (biomass, proteins, carbohydrate...) allocated toward the acquisition of a resource as the uptake effort for that resource. We assume that the total uptake effort that can be expended toward the acquisition of all resources is limited, but increases with the vegetation biomass. The fraction of the total effort that is allocated toward the uptake of resource i is represented by the variable V_i (no units), which can change through time as the availability of, or requirement for, resource i changes. Because V_i represents a fraction of the total uptake effort, the sum of the V_i for all resources must be 1, which implies

that $\sum_{i=1}^n \frac{dV_i}{dt} = 0$; where n is the number of resources represented in the model and t is time (i.e.,

increases in one V_i must be exactly compensated by a net decrease in sum of the other V_i). We assume that the total uptake effort increases in proportion to the active biomass (leaves plus fine roots), which we calculate as an allometric function of total biomass.

The form of the specific uptake functions depends upon the resource (e.g., Michaelis-Menten function). However, for all resources the rate of uptake increases as V_i or active biomass increases (but not necessarily proportionally) and is zero if either V_i or active biomass is zero.

The heart of the MEL model is the dynamic algorithm for allocating plant uptake effort among resources (i.e., calculation of dV_i/dt). In the past, the MEL model has only been applied to two elements at a time and the allocation of effort was based upon the deviation of the ratio of these two elements in the biomass from some optimum ratio. For example, if the biomass C:N ratio was below the optimum, effort would be reallocated toward C acquisition and away from N acquisition. If the C:N ratio was above the optimum, the opposite allocation pattern would occur. This allocation scheme might be generalized to more than two elements by using optimum element concentrations (e.g., g per g dry weight) rather than ratios. However, it cannot be used for non-element resources (e.g., light) because it is impossible to specify a biomass concentration for such resources. Therefore, in the new version of the model, the allocation scheme has been reformulated based on a resource requirement. The resource requirement changes with the allometry of the vegetation, as maintenance and growth requirements change, and with the consumption of the resource as part of the cost of the uptake of other resources:

$$R_i = R_{im} + R_{ig} + \sum_{j=1}^n \phi_{ji} U_j$$

where R_i is the requirement for resource i (resource i $m^{-2} \text{ day}^{-1}$), R_{im} is the requirement associated with maintenance (resource i $m^{-2} \text{ day}^{-1}$), R_{ig} is the requirement associated with growth plus any associated costs (e.g., growth respiration; resource i $m^{-2} \text{ day}^{-1}$), U_j is the uptake rate for resource j (resource j $m^{-2} \text{ day}^{-1}$), ϕ_{ji} is the amount of resource i consumed per unit uptake for resource j (resource i resource j^{-1}), and the summation calculates the amount of resource i consumed in uptake of all resources. For example, the C cost of N_2 fixation (i.e., ϕ_{ij}) is about 23 g glucose per g N fixed or 9.2 g C g^{-1} N and the C cost of NO_3 reduction is about half that. To put the growth requirement (R_{ig}) on an equal footing with maintenance and uptake costs, it is assessed based only on growth to replace biomass lost in tissue turnover; a biomass increment only arises when uptake exceeds that needed to meet the full requirement R_i .

To account for differences in the phenology of uptake among resources, the allocation of uptake effort is calculated based on the 365-day running means of the requirement and the actual acquisition of the resource:

$$\frac{dV_i}{dt} = a \ln \left(\Phi \frac{\overline{R_i}}{\overline{U_i}} \right) V_i$$

where a is a rate parameter (day^{-1}), $\overline{R_i}$ and $\overline{U_i}$ are the running means of R_i and U_i over the previous 365 days, and Φ is a variable that is selected to ensure that the dV_i/dt sum to zero:

$$\Phi = \prod_{j=1}^n \left(\frac{\overline{U_j}}{\overline{R_j}} \right)^{V_j}$$

At steady state, all the dV_i/dt equal zero, which can only occur if

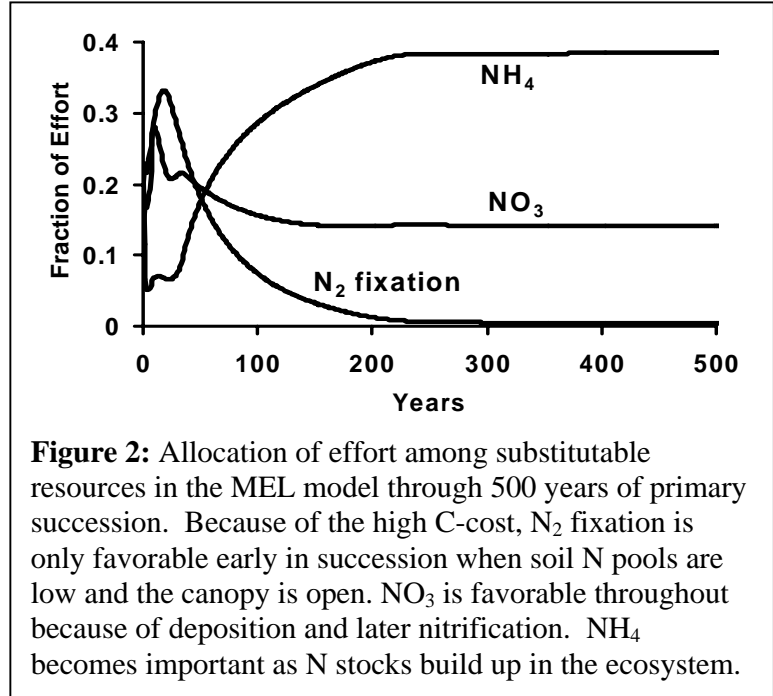
$$\frac{\overline{U_i}}{\overline{R_i}} = \Phi; \text{ for all } i$$

That is, the ratios of acquisition to requirement for all resources are equal (but not necessarily equal to one). It is in this sense that all resources are equally limiting at steady state.

Substitutable Resources: Substitutable resources in the context of the MEL model are resources that satisfy the same plant requirement (e.g., N requirement satisfied by NH_4 or NO_3 uptake or by N_2 -fixation). To allocate effort, this requirement must be partitioned among the substitutable resources (Fig. 2). We base this partitioning on the uptake return per unit effort allocated, which we call the yield. However, the effort allocated toward resource i includes not only the effort allocated directly to the uptake of resource i (i.e., V_i), but also the effort allocated toward the uptake of other resources that are consumed during the uptake of the resource i (e.g., $\phi_{ij} = 9.2 \text{ g C g}^{-1} \text{ N}$ cost of N_2 fixation, $\phi_{ij} = 4.6 \text{ g C g}^{-1} \text{ N}$ cost of NO_3 uptake and reduction). The yield is the uptake of resource i divided by this total allocated effort:

$$y_i = \frac{U_i}{V_i + \sum_{j=1}^n \left(U_i \phi_{ij} \frac{V_j}{U_j} \right)}$$

To optimize resource acquisition, the allocation of effort should favor substitutable resources with a high yield over those with a low yield; otherwise it would be possible to increase production by reallocating effort from low-yield to high-yield resources without an increase in total effort allocated toward any set of substitutable resources (Fig. 2). For a resource that decreases in concentration as plant uptake increases (a "depletable resource"), the yield will tend to decrease with time because the uptake per unit effort will decline as the resource concentration declines. Thus, the simulated plant will first tap the substitutable resource with the highest yield. That yield will decline until it matches the next highest yield, at which point the



plant will tap the top two substitutable resources. Those yields will decline until they match the third highest yield etc. until the total requirement is met. This successive tapping of substitutable resources with successively lower yields will stop as soon as the yields of the depletable resources match the yield for any non-depletable resource because the supply of a non-depletable resource is effectively infinite.

Sample Simulation: We have applied the model to 14 thousand years of primary succession at Hubbard Brook assuming no disturbance. Although it is impossible to corroborate the predicted time series, the model produces a reasonable reconstruction of the P dynamics for the site (Fig. 3). However, to achieve this result, we had to incorporate a feedback on primary mineral weathering that increased weathering when plant demand for P was high (V_{PO_4} high). We imposed a C cost on the plant for this stimulation of weathering and interpret it in terms of either the cost of producing acids excreted by roots or the cost of feeding mycorrhizae to mine mineral P.

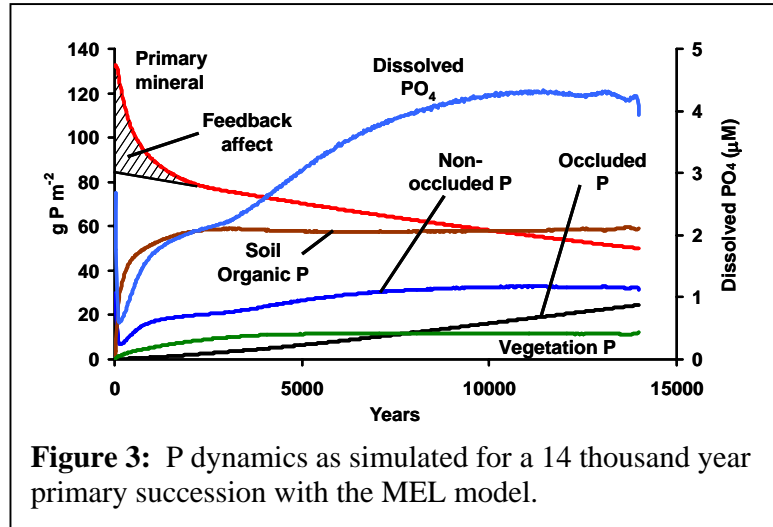


Figure 3: P dynamics as simulated for a 14 thousand year primary succession with the MEL model.