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Nutrient limitation on terrestrial plant growth – modeling the interaction between nitrogen and phosphorus

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Summary

- Growth of plants in terrestrial ecosystems is often limited by the availability of nitrogen (N) or phosphorous (P) Liebig's law of the minimum states that the nutrient in least supply relative to the plant's requirement will limit the plant's growth. An alternative to the law of the minimum is the multiple limitation hypothesis (MLH) which states that plants adjust their growth patterns such that they are limited by several resources simultaneously.
- We use a simple model of plant growth and nutrient uptake to explore the consequences for the plant's relative growth rate of letting plants invest differentially in N and P uptake.
- We find a smooth transition between limiting elements, in contrast to the strict transition in Liebig's law of the minimum. At N : P supply ratios where the two elements simultaneously limit growth, an increase in either of the nutrients will increase the growth rate because more resources can be allocated towards the limiting element, as suggested by the multiple limitation hypothesis. However, the further the supply ratio deviates from these supply rates, the more the plants will follow the law of the minimum.
- Liebig's law of the minimum will in many cases be a useful first-order approximation.

Introduction

Stoichiometric relations in and differences between various components of ecosystems lead to powerful constraints on ecosystem development (e.g. Sterner & Elser, 2002; Sardans *et al.* 2012). Nitrogen (N) and phosphorus (P) are the two elements considered as limiting autotroph (plant) growth in most ecosystems. However, the increasing use of N and P fertilisers, as well as the formation of reactive N in various combustion processes, are increasing their availability in the biosphere. We should expect this to modify the stoichiometric constraints on plants in many ecosystems; possibly shifting ecosystems from N to P limitation (Peñuelas *et al.*, 2012). In a review on responses of plants to N and P additions across marine, aquatic, and terrestrial ecosystems, Elser *et al.* (2007) showed that simultaneously adding both nutrients gave a much stronger response than either of them alone. Harpole *et al.* (2011) reached similar conclusions in a study of factorially designed experiments with N and P. In both studies, the authors concluded that ecosystems are frequently both N and P limited (co-limited), which challenges the conventional view that plants are generally limited by one nutrient at a time (Liebig's law of the minimum). Harpole *et al.* (2011) also suggest that we distinguish between simultaneous co-limitation, when both N and P have to be added simultaneously to get a growth response, and independent co-limitation, where a response is obtained when either N or P is added but the simultaneous addition may or may not add up to the two individual responses.

Davidson & Howarth (2007) criticised Elser *et al.*'s (2007) conclusions about co-limitation on the basis of how nutrient doses were applied and what time scales the different experiments covered. They further noted that there currently does not exist a mechanistic understanding of how co-limitation would function in the studied systems. Saito *et al.* (2008) suggested that co-limitation could be classified in three categories:
(1) Independent nutrient co-limitation; the limitation caused by one nutrient is independent of the other (this is similar, but not identical, to the definition by Harpole *et al.*, 2011),
(2) Biochemical substitution co-limitation; different nutrients can 'fill in' for each other, and
(3) Biochemically dependent co-limitation, uptake of one nutrient depends on the availability of another nutrient; the latter two categories of co-limitation have no direct correspondence in the scheme by Harpole *et al.* (2011).

Saito *et al.* (2008) suggest possible biochemical mechanisms for each of the three cases. We propose a fourth mechanism (described in detail later): (4) serially linked nutrients, where the rate control on growth by one nutrient depends on the rate control by another nutrient of another process. Note that this is not a serial co-limitation in the terminology of Harpole *et al.* where the response to two nutrients depends on the order in which they are added.