

Comment on "Ecosystem Properties and Forest Decline in Contrasting Long-Term Chronosequences"

Wardle *et al.* (1) studied six long-term chronosequences in Australia, Sweden, Alaska, Hawaii, and New Zealand and found that in the absence of major ecosystem disturbance, a transient peak in forest biomass is commonly followed by a forest decline phase. They ascribed the decline of forest biomass to the decline of soil phosphorus (P) availability. With increasing substrate age, nitrogen to phosphorus (N:P) ratios of fresh litter and humus increased in the majority of chronosequences. The authors concluded that similar phases of forest decline occurred widely, from tropical to temperate to boreal forest ecosystems. I argue that their conclusion is premature and that their forest dynamics model does not take the function of species diversity into consideration.

Wardle *et al.* (1) report that forest decline is associated with increased P limitation relative to N and a reduced release of P from decomposing litter. Geochemical changes in soil phosphorus fractionation during long-term soil development have been well established (2). Subsequent biogeochemical studies using the Hawaiian Islands as a model system have proven the shift of N limitation in net primary productivity in the

developing phase to P limitation in the retrogressive phase (3–5). However, the decline of soil P availability cannot necessarily be translated to ecosystem processes elsewhere (6). I argue that the rise and decline of forest biomass is peculiar only to the biomes where regional tree-species diversity is impoverished. Unlike the Hawaiian model and the forest ecosystems studied in (1), conspicuous forest decline does not occur in the mainland tropics.

A meta-analysis of rain forests in the mainland tropics demonstrates that fresh-litter N:P ratios can vary widely, but that aboveground biomass does not drastically decline (Fig. 1). All sites far exceed the litter N:P ratio of 16 (the Redfield ratio), beyond which Wardle *et al.* argue that P is limiting biological processes relative to N. Aboveground biomass of mainland tropical rain forests increases with increasing leaf-litter N:P ratios for lowland sites or is more or less constant for montane sites; either case is inconsistent with the six chronosequences presented in (1). Moreover, Wardle *et al.* used basal area as an index of biomass, but this cannot be justified because tree height and not diameter is often a more decisive indicator of forest biomass.

In the case of Borneo, three tropical rain forests located approximately 1800 m above sea level (asl) and close to each other, but with contrasting soil P availability, do not drastically differ in forest biomass (7–9). Unlike a chronosequence, soil P availability in these forests differs as a result of geology. Nevertheless, the three sites form a gradient of soil P availability, which is in effect comparable to a chronosequence. In spite of six-fold differences in the pool of labile inorganic P and/or total P, the magnitude of the decline of forest biomass is small because of the displacements of P use by efficient species. In this soil P gradient, the fresh-litter N:P ratio more drastically increases with decreasing soil P pool than in the six chronosequences in (1).

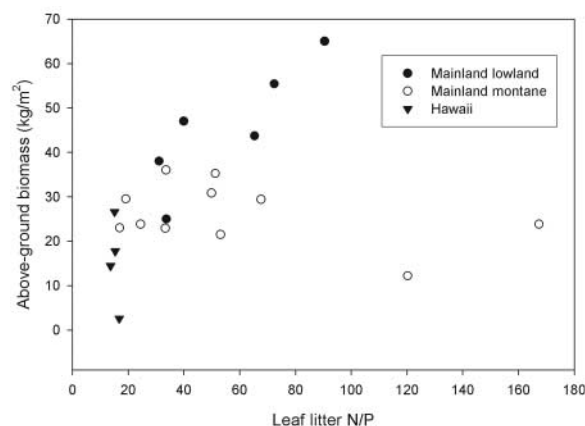


Fig. 1. N:P ratios of fresh leaf litter and aboveground biomass of rain forests in the mainland tropics (8, 10, 12–15) and in Hawaii (5). Tropical rain forests of the mainland are divided into lowland sites (below 1000 m asl) and montane sites (1000 to 2700 m asl) because of the possible interaction of air temperature and nutrients (P). For instance, plants need different amounts of P for a unit of photosynthesis under different air temperatures. The sites where both aboveground biomass and litter N:P are measured are included.

Why forest biomass does not drastically decline in the mainland tropics is an intriguing question. I argue that regional (not plot basis) tree-species diversity is two to three orders of magnitude greater in the mainland tropics than in the six chronosequences and that proportionately more tree species of high P-use efficiencies occur in the mainland tropics. Beta diversity of tree species across all six chronosequences is extremely low, which suggests that either the same taxon or relatively few taxa occur throughout each of the six chronosequences despite drastically different soil P pools [see species compositions in table S1 in (1)]. An extreme case is the Hawaiian chronosequence, where a single species, *Metrosideros polymorpha*, dominates the entire chronosequence. The ability of a single tree species to adapt to a wide range of phosphorus levels is limited relative to the adaptability of a collection of different species. The decline of forest biomass in response to reduced soil P availability is thus more dramatic in a monodominant system. In Southeast Asia, tropical rain forests can maintain an extremely large biomass (65 kg/m²) on infertile soils where litter N:P ratios exceed 90, which suggests a limitation of P relative to N (10). This clearly suggests that P-use-efficient species (11) maintain the biomass. Such plants probably use the labile P that is replenished from organic P on deeply weathered tropical soils. (6). The Wardle *et al.* study ignores the important role of biodiversity in terms of its community structure and function.

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References

1. D. A. Wardle, L. R. Walker, R. D. Bardgett, *Science* **305**, 509 (2004).
2. T. W. Walker, J. K. Syers, *Geoderma* **15**, 1 (1976).
3. T. E. Crews *et al.*, *Ecology* **76**, 1407 (1995).
4. P. M. Vitousek, H. Farrington, *Biogeochemistry* **37**, 63 (1997).
5. D. A. Herbert, J. H. Fownes, *Ecosystems* **2**, 242 (1999).
6. A. H. Johnson, J. Frizano, D. R. Vann, *Oecologia* **135**, 487 (2003).
7. K. Kitayama, N. Majalap-Lee, S. Aiba, *Oecologia* **123**, 342 (2000).
8. K. Kitayama, S.-I. Aiba, *J. Ecol.* **90**, 37 (2002).
9. K. Kitayama, S.-I. Aiba, M. Takyu, N. Majalap, R. Wagai, *Ecosystems* **7**, 259 (2004).
10. J. Proctor, J. M. Anderson, P. Chai, H. W. Vallack, *J. Ecol.* **71**, 237 (1983).
11. P. M. Vitousek, *Ecology* **65**, 285 (1984).
12. P. J. Edwards, P. J. Grubb, *J. Ecol.* **65**, 943 (1977).
13. E. V. J. Tanner, *J. Ecol.* **65**, 883 (1977).
14. E. V. J. Tanner, *J. Ecol.* **68**, 573 (1980).
15. P. J. Edwards, *J. Ecol.* **70**, 807 (1982).

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