

The importance of nutrient pulses in tropical forests

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Attention to the significance of pulsed nutrient release has focused recently on tropical forest ecosystems. Pulsed nutrient mineralization can result from sudden additions of organic matter, leaching from epiphytes, or lysis of microbial biomass. Wetting and drying cycles can dramatically affect detrital food chains leading to pulses of nutrient mineralization, but the differences between pulsed and steady-state systems has not always been appreciated¹. Where one or more mineral elements are limiting to the growth of plants and microbial decomposers (a condition found in certain tropical forests as well as some temperate ecosystems), pulsed nutrient mineralization may be particularly important. Drying-rewetting cycles can accelerate the replenishment of available soil nitrogen (N) pools from microbial, recalcitrant or physically protected N pools^{2,3}. If the availability of nutrients is limiting to plant growth, then the synchrony between nutrient mineralization and plant uptake can be especially critical for maximizing plant nutrient accumulation and preventing losses of limiting elements such as N from the ecosystem^{4,9} or phosphorus (P) from the biologically available pools¹⁰. Furthermore, fluctuations in soil nutrient availability and moisture may increase the uptake of limiting nutrients by plants by causing periodic crashes in populations of their potential competitors, the soil microbial biomass⁵.

Pulsed nutrient release

Wetting and drying cycles

Recent papers show that fluctuations in the availability of soil nitrogen are especially marked in seasonally dry, humid tropical forests^{4,7,11}. Luizao *et al.*¹¹ found that rewet&g of a seasonally dry Amazonian forest soil resulted either in N immobilization or a large pulse of N mineralization, depending on how preceding conditions affected the status of the soil microbial biomass and labile carbon (C) pools. In seasonally dry Indian⁷ and Mexican forests⁴, rewetting of dry soils resulted in a large pulse of N mineralization attributed primarily to the lysis of soil microbial biomass. In temperate ecosystems with drought-prone soils, microorganisms accumulate intracellular solutes to retain moisture¹², which then cause them to lyse upon rewetting^{2,13}. In the tropical monsoon forests of India, the fluxes of N and especially P mineralized from microbial biomass in the first four weeks of the rainy season (32 and 13.2 kg ha⁻¹, respectively) were greater than the total flux of N and P mineralized from litterfall over the entire rainy

Recent research shows that nutrient fluxes are often pulsed in tropical forests, and that pulsed versus gradual inputs have different effects on the fates of nutrients in the ecosystem. Synchrony of nutrient mineralization with plant uptake can lower competition between microbes and plants for limiting nutrients while maintaining tight nutrient cycling, whereas asynchrony can lead to losses of nutrients from the system. Thus, nutrient pulses may play a critical role in maintaining productivity in tropical forests with tight nutrient cycling.

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season (25 and 10 kg ha⁻¹, respectively)^{7,8}. Studies of soils in India with a tropical monsoonal climate showed that in forest, cropland, mine spoils and grazed and protected savanna, the storage of C, N and P in microbial biomass was significantly higher during the dry summer, and lower during the rainy season, within each habitat^{9,14,15}. The drop in microbial biomass at the beginning of the rainy season was attributed to lysis, while maintenance of low biomass during the wet season was attributed to greater microbivory (consumption of microorganisms)^{7,14}.

In contrast to the other studies in Indian forest with a monsoon climate, Behera *et al.*¹⁶ found greater fungal biomass with increasing soil moisture, especially

in the upper soil horizons. One possible explanation for this discrepancy is that fungi and bacteria might respond differently to changes in soil moisture in these seasonally dry tropical forests. In a study on the effects of natural rainfall and irrigation on leaf litter microbes in a moist Panamanian forest, the numbers of bacterial colonies that were cultured increased whereas microfungus colonies decreased in response to increases in litter moisture¹⁷. The fungi growing in tropical moist forest litter may have optimal growth at low water potentials and may therefore have a negative response to moisture. However, it is not clear whether colony counts of microfungi in this study reflect total fungal biomass because forest litter is often dominated by basidiomycetous fungi, which are difficult to culture with the methods used.

In wet tropical forests with no marked dry season, the occasional dry spell is most effective in causing lysis of microbial biomass. Sparling and his collaborators had previously found in New Zealand that extractable soil P increased in air-dried soils from constantly wet but not from dry habitats, and that the amount of increased P was correlated with, and likely derived from, microbial biomass¹². No dramatic increases in extractable P were observed when soils from dry environments were air-dried¹². Recent studies in a non-seasonal wet forest on Puerto Rico in the Caribbean⁵, a moderately seasonal humid forest on Hainan Island in China¹⁸ and a moderately seasonal Amazonian forest^{11,19} show that fungal^{5,18} and total microbial biomass^{11,18,19} can fluctuate widely and rapidly in direct response to available moisture. In the wet Puerto Rican forest, fungal biomass in litter increased as much as three times or decreased by half in as little as two weeks, and was directly related to the frequency of days in the preceding week with enough rain to reach the forest floor,

rather than the total amount of rainfall in the preceding week⁵. A recent study in a temperate forest showed a ten-fold increase in soil microbial N over a two-month period; half of the increase occurred in a ten-day interval²⁰. Such fluctuations in microbial biomass may result in microbial immobilization and conservation of nutrients against leaching during the rainy periods^{5,16,18,20} and pulses of mineralization in response to drying^{5,12,21}.

Pulses of nutrient mineralization from leaf litter in seasonal dry forest can occur when the first wet-season rains initiate synchronous decomposition of all litter accumulated over the dry season¹⁷. However, dramatic pulses of nutrient mineralization from leaf litter may also occur in some non-seasonal wet tropical forests because of the susceptibility of the litter fungi to drying, and because nutrients may be recycled and stored at high concentrations by litter fungi where nutrient availability is limited^{5,22}. Recycling of nutrients by fungi from partially decomposed litter into fresh litter may be the primary mechanism responsible for increases of 110-160% above the initial N, P or calcium (Ca) content of leaf litter during the early stages of decomposition in some wet tropical forests in the Amazon²³, Puerto Rico⁵ and Hong Kong²⁴. Nutrient recycling in litter by fungi is apparently not restricted to wet forests in the tropics, since a similar increase of approximately 25% above the original content of N, P and Ca was also found for bamboo leaf litter in a dry savanna in India²⁵.

Less is known about the impact of cycles of wetting and drying on nutrient pulses associated with throughfall. Throughfall (precipitation passing through the forest canopy) contains a high proportion of biologically available C (Refs 26,27); it is often richer in base cations²⁸, N and P (Ref. 29) than ambient precipitation; and it is known to stimulate microbial growth and activity in temperate³⁰ and tropical forests³¹. Coxson *et al.*²⁶ recently described the pulsed release of sugars and polyols from bryophytes growing within the canopy of a tropical montane rainforest in Guadeloupe exposed to severe desiccation during one-third of the year. These organic compounds are used in maintenance of osmotic pressure within the bryophytes during periods of desiccation, and are released in a large pulse during rewetting. They estimated that bryophytes are releasing 122 kg ha⁻¹ yr⁻¹ of sugars and polyols, with concentrations up to 50mg l⁻¹ (Ref. 26). An unknown proportion of these compounds is probably absorbed by bryophytes²⁶ and epiphyllic microorganisms³¹ in the lower canopy. However, in Guadeloupe, the lower canopy epiphytes were also exposed to desiccation a few days each year, and at such times they may augment the flux of C in throughfall that reaches the forest floor. If a significant fraction of C and nutrients that are flushed from the epiphytes reaches the forest floor, this would represent a major flux of labile organic matter.

Pulsed inputs of labile C in throughfall were found to enhance fungal growth and increase nutrient mineralization by soil fungal communities in a temperate forest³⁰, and to increase respiration rates of the soil microbial biomass in tropical forests^{5,18}. In addition to the effects of nutrients reaching the forest floor, pulses of nutrients and C leached from canopy epiphytes can significantly affect nutrient cycling through their effects in the lower canopy. In a Panamanian forest with abundant epiphylls in the understory (as in the cloud forest on Guadeloupe studied by Coxson *et al.*²⁶), pulsed inputs of labile organic matter stimulated asymbiotic N-fixation by epiphyllic microbes³¹. Understory leaves obtain some of the N fixed by their epiphylls during drying-rewetting cycles³¹.

Tropical storms

Hurricanes and tropical storms can cause sudden, massive deposition of nutrients in green litter onto the forest floor, resulting in major shifts in nutrient cycling pathways⁶. In 1988, Hurricane Gilbert caused leaf litter deposition that was 1.5 times annual leaf litterfall in sub-deciduous dry tropical forest in Mexico³². Similarly, Hurricane Hugo in 1989 caused leaf litter deposition during 24 h that was 0.8-1.6 times the mean annual leaf litterfall rates in wet sub tropical and lower montane rainforests in Puerto Rico^{6,33,34}. Additions of N and P in leaf litterfall resulting from hurricane damage to these forests were 1.3-2.5 times the mean annual fluxes of N in leaf litterfall and 1.4-4.1 times the mean annual fluxes of P in leaf litterfall^{6,32-34}. Even tropical storms that do not reach hurricane strength are responsible for disproportionately large nutrient pulses in litterfall, because nutrient concentrations in green leaves (especially N and P) can be greater than in senescent leaves after nutrient retranslocation has occurred³⁵.

Implications for plant-microbe competition

Microbial biomass in soil or litter can act as either a source or a sink of plant-available nutrients^{15,20}. Sparling *et al.*¹² had previously found that the contribution of microbial biomass to what are generally considered the labile P pools in temperate New Zealand soils varied from 4% to 76%, depending on the vegetation and climate. In tropical monsoon forest and a teak plantation in India, the mean total microbial biomass accounted for 9-12% of the soil organic P (Ref. 15). In another tropical monsoon forest in India, Rhaghubanshi⁹ found that mean microbial biomass N and P accounted for 4.5-9.6% of the total soil N, 9.4-10.2% of the total soil P, and probably a greater fraction of the labile nutrient pools. Changes in nutrient immobilization may be more important than mean immobilization values in determining the availability of nutrients to plants. In a subtropical wet forest in Puerto Rico, the percentage of total P that was immobilized in fungal biomass alone varied from 3% to 85% in the litter layer, and the percentage of labile P extracted from soil (Olsen, sodium bicarbonate extraction from air-dried soil) that could be accounted for in fungal biomass ranged from 0.8% to 20%.

Periodic crashes in microbial populations may release nutrients from microbial biomass and also play an important role in reducing nutrient competition with plants⁵ (Box 1). If the abundance of labile organic matter and environmental conditions are not limiting to microbial growth, then saprophytic microorganisms usually outcompete higher plants, and the decomposers obtain the largest share of limiting nutrients^{20,36}. This principle appears to explain recent results from Puerto Rico, where slower rates of canopy recovery and litterfall production were observed in forest plots where woody debris from Hurricane Hugo was left on the forest floor, as compared to plots where debris was removed shortly after the hurricane⁴⁷. Presumably, the massive deposition of organic matter carbon on the forest floor stimulated microbial nutrient immobilization, reducing the availability of N and possibly other nutrients to trees. In the Zimmerman *et al.* study³⁷, the rates of litterfall in plots receiving complete fertilization were equal to or greater than those in the plots where debris was removed, suggesting that fertilization released the trees from nutrient competition with decomposers.

Fate of pulsed nutrient releases

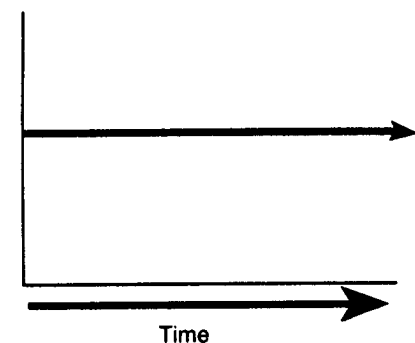
Close competition between plants and microbes often results in tight nutrient cycling in tropical ecosystems. In

Box 1. The effects of fluctuating environments on nutrient release, and the availability of nutrients to decomposers and plants

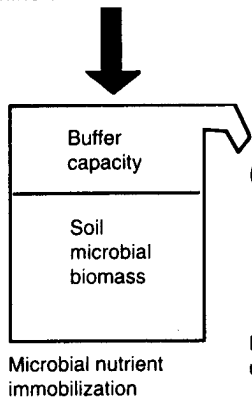
Fluctuations in environmental conditions can induce pulses of nutrient mineralization and fluctuations in microbial populations that affect the fate of nutrients in forest ecosystems. Drying or rewetting in tropical forests causes crashes in soil microbial populations and induces pulses of nutrient release from epiphytes^{26,29} and dead microbial biomass^{7,8}.

Microbial populations

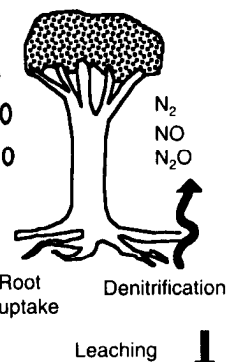
With a constant environment



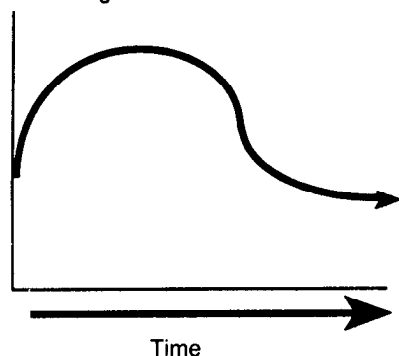
Nutrient mineralization



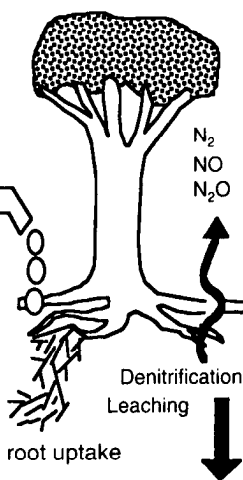
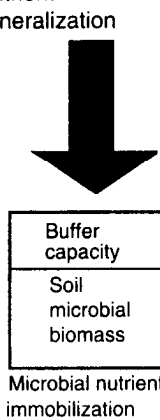
Plant uptake and productivity



With pulse dynamics in a fluctuating environment



Nutrient mineralization



Decomposers outcompete plants for limiting nutrients in forests where abundant energy is available to microbes from organic matter, and plants primarily obtain nutrients that are in excess of microbial demand^{20,36}. In addition to the ability of soil microorganisms to immobilize nutrients by increasing their biomass, they can rapidly increase their P concentrations by several times^{15,22}. The capacity for rapid growth and increased sequestering of nutrients give the microbial biomass an additional 'buffer capacity' to immobilize nutrient pulses, with the size of the buffer reflecting the size and composition of the microbial biomass.

Fluctuations in moisture induce pulses of available nutrients which often coincide with crashes in microbial biomass. When this occurs, a greater proportion of the mineralized nutrients may overflow the reduced buffer capacity of the microbial biomass and become available to plants. As a result, forest productivity under fluctuating environment and nutrient supply may exceed productivity under constant conditions. Nutrient pulses may be taken up by plants if they are synchronized with the proliferation of fine roots^{4-9,38,39}, but they can also be lost from the ecosystem if they are not synchronized with plant or microbial uptake^{6,41,42}. Pulses of N can be lost via leaching and denitrification in such situations^{4,41}, and pulses of P can accelerate loss of P from biologically available pools¹⁰.

by Kavanagh and Kellman³⁸ suggests that the proximal cue for root proliferation was soil moisture rather than nutrient concentrations. In the Amazonian forest studied by Luizao *et al.*¹⁹ soil microbial biomass and fine roots in the upper soil horizon increased and decreased together in response to seasonal moisture, but tight nutrient cycling was maintained by the activity of roots in the deep soil horizons during the dry season. Not all pulsed nutrient releases, however, are retained within the ecosystem, and they may be lost as gaseous or hydrological efflux (**Box 1**). The flush of N mineralization in the Mexican forest studied by Davidson *et al.*⁴, for example, was associated with losses of N from the ecosystem via denitrification. Hydrological export can represent a significant loss of nutrients from tropical forests, especially following the pulsed inputs associated with disturbance. McDowell and Asbury⁴⁰ showed that N export from three montane watersheds in Puerto Rico under typical hydrological conditions was two to four times as much as inputs from atmospheric deposition. At those sites, a large pulse of N and labile C was added to the forest floor in green leaf litter by Hurricane Hugo³³. Nitrogen was initially immobilized and disappeared from stream water⁷, but there was subsequently a large pulse of N mineralization, which stimulated nitrification and denitrification and increased the loss of nitrate (NO₃⁻) in streams^{6,40,41}. An unusual and extreme drought may have uncoupled nutrient mineralization from plant uptake, by causing the sudden release of N from microbial biomass, and at the same time con-

tributing to massive mortality of fine roots^{6,40-42}. Nutrient pulses can result in large gaseous losses of N. At the Puerto Rican site, losses of nitrous oxide (N₂O) increased 15-fold with the large litter inputs and increases in soil nitrification and N mineralization rates induced by Hurricane Hugo⁴¹. Simple wetting and rewetting cycles can also result in enhanced gaseous N losses. In a seasonally dry Mexican forest, addition of NO₃⁻ also resulted in increases in N₂O and nitric oxide (NO) flux upon wetting

various studies of microbial biomass in monsoonal areas of India, the pulse of N mineralization associated with turnover of microbial biomass at the beginning of the rainy season was closely synchronized with maximum plant uptake and regrowth^{7,8,14}. Similarly, fine root proliferation in two Mexican dry forests also coincided with the first heavy rains after the dry season^{38,39}. Although the pulses of nutrients entering the soil were especially strong following these first rains, comparison with distilled water applications

of previously dry soil, which caused a large increase in nitrification⁴. In a Venezuelan savanna, NO emissions increased by 10–20 times with the addition of 3–15 mm of water⁴³. Additions of NO₃⁻ and burning (a natural feature of the savanna system) further stimulated losses of NO. In contrast, wetting of cloud forest soils in Venezuela resulted in no increased NO flux⁴³.

Although the nutrient pulse and disturbance associated with Hurricane Hugo induced short-term losses of N from the forest in Puerto Rico, pulsed additions of nutrients and organic matter associated with hurricanes may increase soil fertility and forest productivity in the long term⁴⁴. Simulation of repeated hurricane effects on the Puerto Rican forest using the Century model⁴⁴ (a model that links soil organic matter dynamics and nutrient cycling with primary productivity) resulted in increases in primary productivity over non-pulsed simulations through its effects on soil organic matter and associated P availability. Such predictions remain to be tested in long-term field studies. In many highly weathered tropical soils, P that is not associated with organic matter can become tightly bound or 'fixed' onto aluminum and iron oxides in clay, and is then much less available to plants. Sanyal *et al.*¹⁰ recently showed that the rate of P fixation in these tropical soils is accelerated by increasing the concentration of mineral P in soil solution, causing a greater proportion of the added P to become unavailable. They suggest that plants may therefore obtain proportionately more mineral P when it is added evenly at low rates than when it is added in pulses. However, plants that are in competition with decomposers for limiting nutrients may obtain an advantage when nutrients are released in pulses that coincide with crashes in the microbial biomass and the proliferation of fine roots (Box 1)^{7,8,14,38,39}. Thus, the fate of nutrients released in pulses can be very different from that of nutrients released steadily at lower concentrations.

Conclusions

The importance of pulse dynamics in determining the fate of nutrients has been discovered and forgotten several times in the literature on temperate ecosystems¹, so the future of pulse dynamics in tropical forest research is uncertain. The natural human tendency to simplify complexity¹ and (until the recent paper by Gaines and Denny⁴⁵) the familiarity of ecologists with statistics that deal only with means and central tendencies rather than frequencies and return times of extreme events, can lead researchers to think of fluctuations in microbial populations and nutrient pulses as nuisances. Therefore, the question posed by Anderson⁴⁶ regarding the significance of interactions between invertebrates and microorganisms (is it noise, or necessity for soil processes?) is highly relevant to the subject of nutrient pulses in ecosystems. Recent papers suggest that in some tropical forests where decomposers and plants are competing for limiting nutrients, environmental fluctuations and the resulting pulsation of nutrient release may be necessary to maintain high rates of nutrient mineralization, plant uptake and forest productivity, but that asynchrony between nutrient mineralization and plant uptake can sometimes lead to significant losses of nutrients from plant-available pools.

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