Removing Phosphorus from Ecosystems Through Nitrogen Fertilization and Cutting with Removal of Biomass

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ABSTRACT

High amounts of phosphorus (P) are in soil of former farmland due to previous fertilizer additions. Draining these residues would provide conditions for grassland plant species diversity restoration amongst other ecosystem benefits. Nitrogen (N) fertilization followed by cutting with subsequent removal of biomass has been suggested as a P residue removal method. We present a general model of N and P ecosystem cycling with nutrients coupled in plant biomass. We incorporate major P pools and biological and physico-chemical fluxes around the system together with transfers into and out of the system given several decades of management. We investigate conditions where N addition and cutting accelerate fertilizer P draining. Cutting does not generally accelerate soil P depletion under short-term management because the benefits of biomass removal through decreased P mineralization occur on too long a timescale compared to cutting's impact on the ability of plants to deplete nutrients. Short-term N fertilization lowers soil fertilizer P residues, provided plant growth remains N limited. In such situations, N fertilization without biomass removal increases soil organic P. Some scenarios show significant reductions in available P following N addition, but many situations record only marginal decreases in problematic soil P pools compared to the unfertilized state. We provide explicit conditions open to experimental testing. Cutting might have minimal adverse impacts, but will take time to be successful. N fertilization either alone or in combination with cutting is more likely to bring about desired reductions in P availability thus allowing grassland restoration, but might have undesired ecosystem consequences.

Key words: biodiversity; ecosystem modelling; grassland restoration; nutrient stoichiometry; cycling feedbacks; mineralization; input–output budget.

INTRODUCTION

Agricultural restructuring and conservation priorities have led to the abandonment of farmland in Europe and elsewhere (Smith and others 2005; McLauchlan and others 2006). At the time of abandonment, and due to intensive application of

inorganic and organic fertilizers over time, some nutrients have built up to high levels in soils (Bennett and others 1999; Sharpley and others 2004). Although much research has focussed on how excessive application of nitrogen (N) has influenced ecosystem processes and caused environmental problems (Boring and others 1988; Carpenter and others 1998), recent evidence suggests that phosphorus (P) can be equally important to the fate of ecosystems (Elser and others 2007), and may pose an intense environmental problem in certain areas (Carpenter and others 1998; Haygarth and Condron 2004).

P tends to build up in the soil whilst land is in agricultural use (Barrow 1980; Goh and Condron 1989). These high levels of P may remain in soil for some time (McCollum 1991; Carpenter 2005), and thus pose a number of persistent environmental problems (Sharpley and others 2004). High concentrations of available P are generally associated with low species diversity (Janssens and others 1998; Crawley and others 2005), particularly restricting rare species (Wassen and others 2005). Toxicity symptoms may be seen in some species where there is incapacity to down regulate the uptake of P (Shane and Lambers 2006) and/or micronutrients such as zinc become deficient (Loneragan and others 1979). In the absence of specific management to remove this long-term soil P problem (Carpenter 2005), it may therefore impose, in particular, a constraint to restoration of species-diverse grassland for decades. Condron and Goh (1990) showed that with successive cropping over the course of 2 years, and in the absence of further P fertilizer inputs, little change was observed in soil P fractions. At Rothamsted, similar management from 1902 to 1974, with some periods of fallow, still left an estimated 70 years' worth of fertilizer P residues to be depleted, even though P additions ceased in 1901 (Johnston and Poulton 1977). These findings contrast with N, which is typically lost from systems rapidly (Maron and Jefferies 2001).

The plant availability and chemical nature of fertilizer residue P are subject to debate (Frossard and others 2000; Johnson and others 2003), but include P molecules that are loosely bound on inorganic and organic soil particles through chemisorption processes, and material that is more tightly bound within the soil matrix and, consequently, less plant available. Loosely bound P together with immediately plant available P corresponds to the non-occluded P of the classical Walker and Syers model of pedogenic P forms; tightly bound material refers to occluded P (Walker

and Syers 1976). Occluded P is generally not plant available and, therefore, not a constraint to restoration (although note Richter and others 2006). The P that poses a constraint to restoration is the fraction that can be made available to plants in a relatively short timescale (several decades) and we call this ''reactive P'' (Perring and others 2008). Its relation to the different forms of P found by chemical fractionation is described in the ''Model Structure'' section.

A variety of strategies have been suggested to accelerate the removal of P from ecosystems (Walker and others 2004), such as topsoil stripping (Tallowin and Smith 2001) and burning (Marrs 1993). In this article, we critically investigate another strategy suggested to accelerate the decline in soil P pools: N fertilization and cutting (Marrs 1993).

The rationale behind the management strategy is that plant growth tends to be N limited in land that used to be farmed (Ruess and Innis 1977; Elser and others 2007). Following N addition, plant growth is increased, which leads to more available P uptake to support it (Marrs 1993). Reactive P declines as it buffers available P removal (Haynes and Williams 1992; Vadas and others 2006). The ensuing plant biomass is cut and removed from the ecosystem, thus taking away P from the system (Marrs 1993). This lowers the nutrient capital of the system, together with the problematic soil P pools. N addition with cutting thus accelerates the decline in reactive P and lowers available P given the reduction in supply from the reactive P pool.

Using a relatively simple general model, we aim to provide clear mechanistic predictions, open to experimental testing, as to when the strategy of N fertilization and cutting will accelerate the decline in reactive P. We describe N and P dynamics in ecosystems taking account of the fact that these nutrients are coupled in plant biomass in relatively constrained ratios (Elser and others 1996; Thompson and others 1997; McGroddy and others 2004). We investigate the general response of the system to N fertilization and cutting, deriving transient expectations from analytical equilibrium insights. Our approach complements that of more complicated simulation models such as versions of Century and EPIC (Sharpley and others 1984; Parton and others 1988; Vadas and others 2006). Although we show conditions under which short-term N addition successfully decreases soil P, pursuing such a strategy requires further investigation to quantify whether the costs of such short-term N addition outweigh its benefit in terms of restoration.
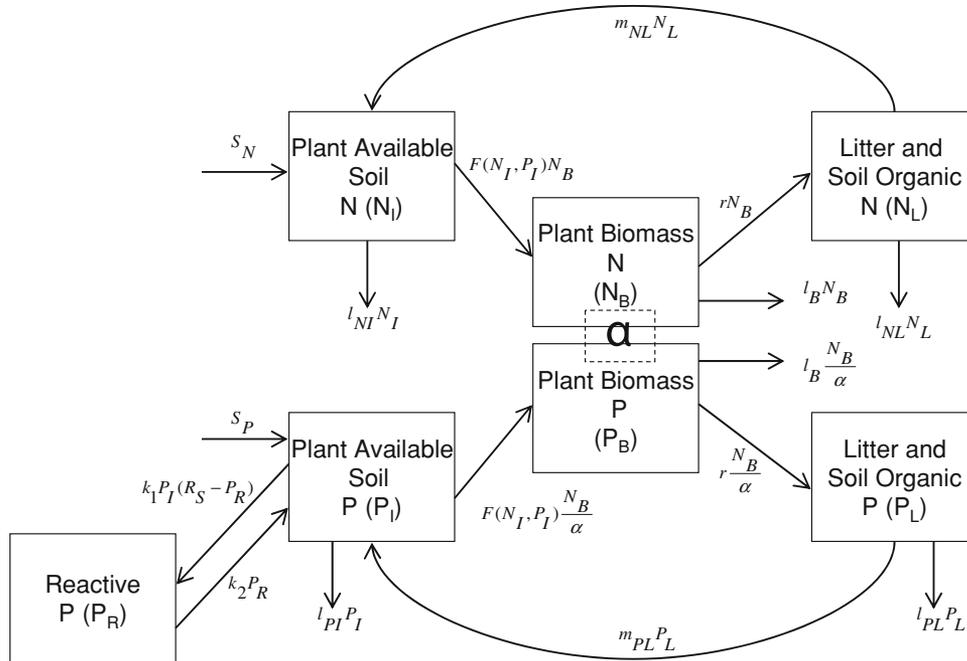
Figure 1. Model of N and P dynamics in an ecosystem. Plants take up available nutrients in a constrained ratio, and through tissue loss transfer material to an unavailable soil organic and litter pool. Through mineralization, unavailable nutrients in the soil are made plant available. These pools can lose nutrient from the system, whilst only available pools receive inputs from outside of the system. As explained in the text, occluded P is regarded as not being plant available and is therefore not included in the model. A reactive P pool buffers the supply of available P.

MODEL STRUCTURE

We introduce our model conceptually in Figure 1. N and P are explicitly coupled in plant biomass with a constrained ratio (α) such that plant P equals plant N divided by α. The model describes nutrient fluxes and compartments in a system that was formerly cropland, only including soil P pools that have the potential to become plant available in a few decades. This presents a realistic, albeit long-term in socio-economic contexts, management timescale. Both nutrients exist in three functionally distinct ecosystem pools: nutrients dissolved in solution that are available for plant uptake ("available nutrients") (N_I, P_I) which may be extracted with anion and cation exchange resins (Tiessen and Moir 1993); nutrients stored in live plant biomass above- and belowground (N_B, P_B); and nutrients that are locked in soil organic matter and plant litter, and are therefore unavailable to plants (N_L, P_L). Organic P in the soil may be estimated following digestion of soil extracts (Tiessen and Moir 1993). All pools represent an amount of nutrient measured as kg ha^{-1} or equivalent. Fluxes between pools generally define the biotic nutrient cycle: available nutrients are assimilated by the plants using an explicit increasing saturating function ($F(N_I, P_I)N_B$ and $F(N_I, P_I)N_B/\alpha$ for N and P, respectively); plant tissue loss (rN_B and $rN_B/$

α for N and P, respectively) transfers nutrients from the plant biomass to the litter and soil organic pool and mineralization ($m_{iL}i_L$, i = N, P) through biological and biochemical mechanisms (McGill and Cole 1981) transfers nutrients to the available pool from the previously plant-unavailable soil organic and litter pool. Mineralization of P may be influenced by the availability of N, for example, through the production of phosphatase enzymes (Olander and Vitousek 2000; Treseder and Vitousek 2001; Pilkington and others 2005), but as will be discussed later, taking this into account would not affect the results presented here.

We have explicitly included the reactive P pool (P_R): inflation of this pool following P fertilizer input (Barrow 1980; Goh and Condron 1989) poses the environmental problem management wants to solve. In our model, the pool represents inorganic P that is relatively loosely bound on mainly inorganic soil particles, given its former use as farmland, through chemisorption reactions (Goldberg and Sposito 1985). In the Hedley fractionation, reactive P can be considered equivalent to that P extracted with sodium bicarbonate and sodium hydroxide, in the absence of digestion and sonication. This differs from operationally defined reactive P as in the Murphy–Riley extraction (for example, McDowell

and others 2001). Reactive P is in flux with available P (Marrs 1985) such that its change through time is described by:

$$\frac{dP_R}{dt} = k_1 P_I (R_S - P_R) - k_2 P_R \qquad (1)$$

where R_S is the maximum density of sorption sites (in kg ha^{-1}), and k_1 and k_2 are constants that denote adsorption and desorption, that have units of ha kg^{-1} y^{-1} and y^{-1}, respectively. In simple terms, the rate of adsorption is more rapid with more available sorption sites; desorption is simply proportional to the size of the reactive pool.

Ecosystems are not closed, with nutrients being lost by both available and unavailable loss pathways. Available losses occur through leaching of N and P together with denitrification in the case of N. Organic matter can be lost from the system through a myriad of processes, including fire, grazers, particulate and dissolved nutrient loss. Losses are assumed to be proportional to the pool size from whence they originate, these proportions being denoted by l_{iI}, l_B, l_{iL}, i = N, P and measured in units of y^{-1}. Our model does not take into account particulate loss of reactive P. We shall discuss later how the qualitative results remain unchanged when including this loss. We assume nutrients enter the ecosystem in available form from atmospheric and weathering sources, together with fertilization for N; unavailable organic inputs are negligible (Newman 1995; Schlesinger 1997). Available input is denoted by S_i, i = N, P, and is in units of kg ha^{-1} y^{-1}.

Changes in pool sizes through time are therefore:

Change in available N:

$$\frac{dN_I}{dt} = S_N + m_{NL}N_L - l_{NI}N_I - F(N_I, P_I)N_B \qquad (2)$$

Change in available P:

$$\frac{dP_I}{dt} = S_P + k_2 P_R + m_{PL}P_L - F(N_I, P_I)\frac{N_B}{\alpha} \\ - l_{PI}P_I - k_1 P_I(R_S - P_R) \qquad (3)$$

Change in plant biomass N:

$$\frac{dN_B}{dt} = F(N_I, P_I)N_B - l_B N_B - rN_B \qquad (4)$$

Change in plant biomass P:

$$\frac{dP_B}{dt} = \frac{N_B}{\alpha}(F(N_I, P_I) - l_B - r) \qquad (5)$$

Change in soil organic and litter N:

$$\frac{dN_L}{dt} = rN_B - m_{NL}N_L - l_{NL}N_L \qquad (6)$$

Change in soil organic and litter P:

$$\frac{dP_L}{dt} = \frac{rN_B}{\alpha} - m_{PL}P_L - l_{PL}P_L \qquad (7)$$

$F(N_I, P_I)$ denotes plant uptake. We consider the general case of N and P co-limitation and also assess N and P limitation alone. With single nutrient limitation, the function is simply any monotonic increasing function that saturates as the concentration of available limiting nutrient increases. In the case of co-limitation, we use the additive model of O'Neill and others (1989), which best described the observed plant biomass responses in co-limited conditions amongst a number of candidate models:

$$F(N_I, P_I) = \left(\frac{U_{max}N_I P_I}{K_P N_I + N_I P_I + K_N P_I}\right) \qquad (8)$$

where U_{max} (y^{-1}) is the maximum potential uptake rate in the absence of limitation by either nutrient, and K_N and K_P are equivalent to Michaelis–Menten half saturation constants. This model necessarily lies between cases of single nutrient limitation (Appendix A in the Digital Appendices). Uptake is assumed to be proportional to the amount of plant biomass in the system. Our model assumes that available nutrients are able to be accessed by plants at all times, and P uptake is dependent on P concentration. P may be diffusion limited (Tinker and Nye 2000) in its availability to plants, but such an assumption is unlikely to change the conclusions presented (Digital Appendix C).

Our model is a more simplified schematic of biogeochemical P pools and fluxes than that which is usually presented in conceptual and simulation models (for example, Walker and Syers 1976; Tiessen and others 1984; Parton and others 1988). Conceptual models tend to include a primary mineral P pool of apatite P, and a pool of recalcitrant occluded P. In the ecosystem considered by our model, and given the management timescale of a few decades, apatite P can be considered a constant input or can be assumed to have been weathered out. Occluded P is assumed to be unavailable to plants, although this is not always the case (Richter and others 2006). We argue that our model provides a suitable baseline for investigating the effects of N fertilization and cutting on soil P.

INVESTIGATIVE RATIONALE

Equations (1)–(7) could not be solved explicitly through time. Attempting to find generalities in transient dynamics is notoriously difficult (Neubert

and Caswell [1997](#); Baisden and Amundson [2003](#)). To understand the response of the system to N fertilization and cutting, we solved the system at equilibrium, and then asked what happens to equilibrium pool sizes following sustained application of management. Solutions provided expectations, as to when management may be successful over the short-term, which we tested using simulations.

EQUILIBRIUM RESULTS: EXPECTATIONS FOR TRANSIENT DYNAMICS

To solve the system at equilibrium, we set equations (1)–(7) equal to 0. We then differentiated equilibrium solutions with respect to N addition (S_N) and cutting (l_B) (see Digital Appendix A). To deplete reactive P at equilibrium, it is necessary to deplete available P (Perring and others [2008](#) and equation A35). Available P can decline at equilibrium with N fertilization providing plant growth is N limited, either singly or in combination with P. This is because, under such conditions, N addition stimulates plant growth which necessitates uptake of available P (Perring and others [2008](#)).

Cutting may deplete available P at equilibrium but only under a stringent set of conditions. The system must be N limited, and the recycling of N must be sufficiently poor compared to that of P. With only N limiting plant growth, the recycling condition is:

$$\sigma_N \sigma_P + (l_B + \sigma_P)\left(\frac{l_{NI}}{F'(N_I^*)N_B^*}\right) \qquad (9)$$

where $\sigma_i = \frac{rl_{iL}}{l_{iL} + m_{iL'}}$, i = N or P, refers to the rate constant of nutrient lost from the plant pool that is not recycled in the system. Where the condition in equation (9) is met, the differential of available P is negative with respect to increasing cutting rate. However, when cutting rate (l_B) increases, there comes a point at which the inequality in equation (9) becomes equal. This is because as cutting increases, the right-hand side gets larger: N_B^* get smaller, and l_B increases. The left-hand side of the inequality remains constant. The point at which both sides are equal is the optimal cutting level (l_{Bopt}), as shown in Figure A1 (Digital Appendix). Beyond this value, equilibrium available P will start increasing with cutting, given that the differential is now positive, thus slowing down the depletion of the reactive P pool. Eventually, too large a loss rate from the plant pool will lead to plant extinction (Condition [A9]). Under conditions of co-limita-

tion, the condition in equation (9) was approximated by the expression (see Digital Appendix A):

$$\sigma_N \sigma_P + (l_B + \sigma_P)\left(\frac{l_{NI}}{(\partial F(N_I^*, P_I^*)/\partial N_I^*)N_B^*}\right) \qquad (10)$$

The decline in available P with cutting occurs because of a greater decrease in mineralization from a smaller litter pool as compared to the decreased uptake that results from reduced plant biomass (see equations A31–A34). Under sole P limitation in our model, available P is controlled by the plant, and independent from nutrient supply through mineralization. Under sole P limitation, cutting results in increased available P (equation A27).

Management is not applied permanently, nor will the ecosystem initially be at equilibrium. Equilibrium predictions (Table A1, Digital Appendix A) were therefore investigated through transient simulations over the management timescale (50 years).

A combined N addition and cutting strategy is interesting only if both aspects of the strategy reduce problematic soil P pools compared to when they are not applied: that is, when cutting is successful under N addition, and N addition is successful under cutting. Therefore, we investigated the conditions for success of the two strategies independently. We present the results for cutting first given that this is likely to have fewer detrimental side effects. When we show that cutting is unlikely to be successful over short timescales, we present results of fertilizing the ecosystem with N. We discuss why the management strategy, with N fertilization and cutting together, may be more successful in practice than our results suggest.

TRANSIENT METHODOLOGY

Preliminary analyses showed the system to be variable in its response depending on parameters and initial conditions. We made reasonable assumptions as to the initial conditions of the system (Digital Appendix B, Table B1) concurrent with time of abandonment: low biomass, given its former use for crop cultivation; very low litter and soil organic pools, given the declines in soil organic matter content observed with agricultural use (Tiessen and others [1982](#); McLauchlan and others [2006](#)); saturated reactive pool due to repeated applications of fertilizer (Barrow [1980](#); Goh and Condron [1989](#)); and variable available pools (Marrs and others [1998](#)). We scaled initial conditions to be proportional to the equilibrium pool sizes of the

system. Parameters were randomly drawn from biologically reasonable ranges given that we aim to assess generalities. Values were assigned from uniform distributions taking an order of magnitude different from available estimates (ranges shown in Table B2, Digital Appendix B). Where estimates were not available, we used wide, biologically reasonable ranges. Inspection of Digital Appendix B shows that many of the parameters did not come from former farmland or grassland systems due to the lack of data availability. Because we aimed to assess generalities as to when the management would decrease problematic soil P pools rather than generate quantitative predictions, our approach is reasonable. Our search for parameters highlights the requirement for more practical estimation of ecosystem nutrient flux parameters. We retained parameter sets where pools maintained positive, non-zero values throughout the simulation.

Management success was expected to depend on plant limitation status (Tables 1 and 2). Indices of N and P limitation through time are given by $K_N/N_I(t)$ and $K_P/P_I(t)$, respectively; whichever is greater indicates the nutrient predominantly limiting growth. We built up a range of possible limitation scenarios (details in Digital Appendix B, Table B3, summarized in Tables 1 and 2) for the managed and unmanaged systems with associated predictions as to management impact on available and reactive P pools. We ran our model, using the NDSolve function in Mathematica v5.2, comparing results from 10,000 scenarios with our predictions derived from our equilibrium expectations. Cutting was applied at the optimum level to decrease available P as first calculated from initial conditions, and applied at this level throughout the simulation, providing that it was positive, and allowed plant persistence at equilibrium. However, the optimum value would change through time, given alteration in state variables; we therefore compared cases where the optimum level applied throughout the scenario was lower or higher than that calculated through time in both the managed and unmanaged scenarios, with the expectation that where it was lower in both cases, reactive and available P should have declined in the cut system relative to the uncut system, provided the ecosystem remained N limited throughout. Further details of the range of limitation scenarios, and how the optimum level of cutting could vary, are described in Digital Appendix B.

We present the overall results in Tables 1 and 2, highlighting typical cases in Figures 2 and 3. Large changes could be seen in control situations because the system starts right after agricultural abandon-

ment, far from equilibrium, thus highlighting the variability inherent in transient dynamics. For systems where parameters were estimated (that is, Figures 2 and 3), we carried out a sensitivity analysis by altering all the parameters by ±10% and re-running the simulations for each altered parameter whilst maintaining others at the values stated in Digital Appendix B.

TRANSIENT RESULTS

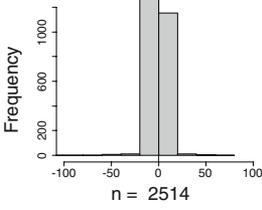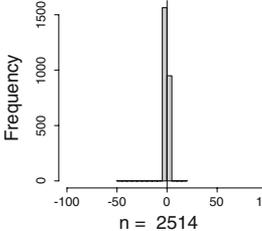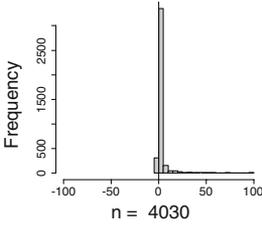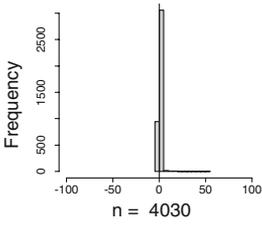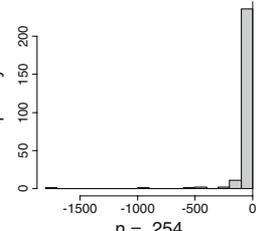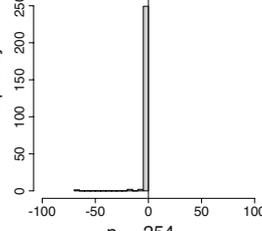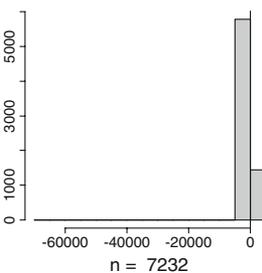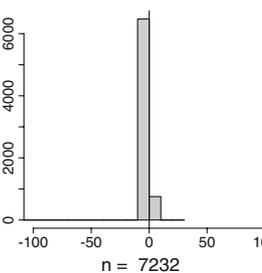### Cutting

Cutting had two contrasting effects in our model at equilibrium: by decreasing plant biomass, it disrupted nutrient uptake, thus preventing depletion of available and reactive P. On the other hand, cutting disrupted available P supply through mineralization of soil organic P, which affects the available P pool when growth is not solely P limited. As the net result, cutting could decrease available P at equilibrium in some N limited systems, with appropriate nutrient recycling propensities, with an optimal cutting level (l_{Bopt}) minimizing the pool (Digital Appendices A and B, Figure A1). We predicted that applying cutting below l_{Bopt} should decrease available and reactive P in systems that satisfied the recycling and limitation conditions. In P limited cases, we expected available P to increase with cutting.

P decline was indeed observed in certain situations (Figure 2A). However, as the top results row in Table 1 shows, in many cases the expected decline was not observed. We hypothesized that the reduction in mineralization due to cutting was too low because of the non-equilibrium state of the system. We tested this hypothesis by making soil organic matter decomposition instantaneous. In essence, this means that the plant pool re-supplies available P directly, with a certain fraction ($l_{PL}/(l_{PL} + m_{PL})$) being lost during the transfer. In the majority of cases available P did now decline with cutting as expected. However, even though this should lead to the maximum possible success in terms of lowering available P, most cases still only had small magnitude decreases (Table 1, second row), with very small impacts on the reactive pool.

Cutting should not be used in P limited cases. Here, large increases in available and reactive P were observed (Table 1). Increased pool sizes could also be observed where systems move into P limitation as shown in Figure 2B. Once the system moves into P limitation, there is no level of cutting at which management will lower available P.

Cutting was therefore generally not successful at reducing available and reactive P pool sizes, with

Table 1.   Impacts of Cutting on Available and Reactive P Pools

CONDITION	PREDICTION	RESULTS		SUCCESSFUL MANAGEMENT
		ΔP_I	ΔP_R	
N limited throughout; Calculated optimum cutting level above what is applied throughout simulation. Full model.	**Lower available and reactive P**	n = 2514	n = 2514	NO
N limited throughout; Calculated optimum cutting level above what is applied throughout simulation. Instantaneous decomposition	**Lower available and reactive P**	n = 4030	n = 4030	NO
P limited throughout; No optimum cutting level	**Increased available and reactive P**	n = 254	n = 254	NO
Other limitation cases	**No prediction**	n = 7232	n = 7232	NO

Predicted and actual impacts of cutting given limitation and optimum cutting level constraints. Histograms denote counts of ΔP_i, $i = I, R$, defined as ((unmanaged pool size − managed pool size)/unmanaged pool size)*100. This measure refers to the scaled difference between unmanaged and managed scenarios, estimated at the end of the simulation. Positive values show where management has been successful; negative values indicate an increase in available and reactive P pools following cutting.
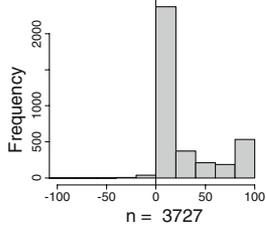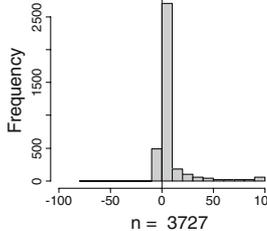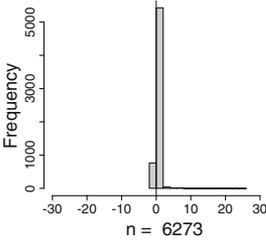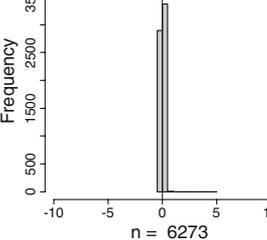
small magnitude decreases in the best scenarios (Table 1). In some instances, large increases in the available pool were recorded.

Nitrogen Fertilization

In N limited systems, we expected N fertilization to accelerate any reductions in reactive P and lower the available P pool (Perring and others 2008). We did not expect there to be large changes in pool sizes

where the system was predominantly P limited. Expectations were confirmed by simulations: N fertilization always led to a decline in available and reactive P whilst systems were N limited (Table 2; Figure 3A). N fertilization could lead to a system becoming P limited. The switch in limitation may also occur in the unmanaged system. In these cases, the time of the switch in limitation was earlier with N addition. N addition, therefore, accelerated the decline in available P. In general, fertilization led to a

Table 2. Impacts of N Fertilization on Available and Reactive P Pools

CONDITION	PREDICTION	RESULTS ΔP_I	ΔP_R	SUCCESSFUL MANAGEMENT
N limited at least some of the time	**Lower available and reactive P**	n = 3727	n = 3727	YES
P limited throughout	**No or small magnitude effects**	n = 6273	n = 6273	NO

Predicted and actual impacts of N fertilization following 50 years of management given limitation constraints. ΔP_i, $i =$ I, R is as defined in Table 1. Note the difference in the x-axis limits between the two limitation scenarios. Management is generally successful in N limited scenarios, with a mean reduction of 25% (±0.6%, 1SE) and 6.4% (±0.3%) in the size of the available and reactive P pools, respectively.

reduction in available and reactive P as estimated at the end of the scenarios. However, in some cases, and subsequent to the switch in limitation, available and reactive P pools may increase in size, albeit with small magnitude (Figure 3B). This appears counter to the aim of the management strategy, given that we defined success as lowered available and reactive P. However, plant biomass in this system is lower than in the unmanaged system, a somewhat counterintuitive response to N fertilization. In addition N leads to a rapid use of available P leaving the system extremely P poor, and therefore only able to sustain low plant biomass. The decreased biomass then allows the reactive and available P pools to increase in size, even though growth remains P limited. Such an example where N addition results in extreme P limitation demonstrates that the available pool size is not a perfect index of limitation, that is, the available P pool size following N addition is greater than in the unmanaged scenario and the index of limitation would decline by definition. Even though this is the case, the amount of biomass in the system is lower, suggestive of greater P limitation. In such cases, short-term N fertilization is a highly successful management strategy given the P limited state of the system, though N fertilization should be stopped as soon as such a biomass decline is observed.

In cases where systems remain P limited throughout, N fertilization has little impact on available and reactive P (Table 2). Available P declines on average as our model assumes some degree of N limitation, but plants are unable to efficiently use additional N and thus P uptake is only marginally increased. With little alteration in the available P pool, the reactive P pool essentially remains static. The largest impact of N addition, in terms of reduced available and reactive P, occurs when N fertilization maintains an ecosystem in a P limited state in comparison to where it would become N limited in the absence of management. In these cases, N addition maintains low available and reactive P whereas in the unmanaged scenario, the onset of N limitation prevents the efficient use of available P and therefore available P builds up in size and the reactive P pool is maintained at a high level. We could not find any significant relationships between the average strength of N limitation in the unmanaged scenarios and the amount of reduction in available or reactive P. Further analyses also did not indicate any significant correlations between parameter values and the magnitude of the reduction in available and reactive P. This may be because of interactions between parameters and also a dependence on initial conditions.

Experimental work could clarify which fluxes are important in determining the response in real ecosystems.

In essence, if the system is N limited, N fertilization is a highly successful management strategy at removing available P and leads to declines in reactive P. Where a switch to P limitation occurs, N fertilization leads to quicker attainment of this switch and, in some cases, lower plant biomass. Ideally, N fertilization should be stopped as soon as the system stops being N limited, but this might be difficult to assess. N addition should be stopped if the N fertilized system presents a lower plant biomass.

Sensitivity Analysis

We carried out a sensitivity analysis by changing each parameter by $\pm 10\%$ for those systems described by Figures 2 and 3, and then running our simulations again. In all the cases, plant P, available P, and reactive P pool dynamics mirrored those shown in the figures, and the management outcomes did not change at $t = 50$. The management target, that is, the reduction in reactive P pool size, was in general little affected: across all the simulations and on average, it changed by about 9% for the plant N:P ratio (α), around 5% for available nitrogen input (S_N) and by less than 1% for all other parameters. Changes to available and unavailable loss rates for both N and P had the smallest effect on the impact of management (Table B4 in Digital Appendix B). Slightly bigger changes were observed in the N fertilized scenarios for parameters influencing plant uptake (U_{max}, K_N, K_P), but even here, the maximum difference in the plant pool was 2.1% following a 10% increase in U_{max} (results not shown).

DISCUSSION

When and Why Does Management Successfully Reduce Reactive P?

As first hypothesized, N fertilization and cutting as a strategy to reduce soil P (Marrs 1993) should have been applied together. However, equilibrium results showed that N fertilization and cutting only work together where they work independently. Conditions under which cutting will lower available P were more stringent than the conditions under which N fertilization will lower available P but both require N limited systems. We, therefore, investigated each aspect of the management separately. We thus discuss each aspect of the management separately before considering why it may

Figure 2. Two examples of typical transient dynamics given cutting where (**A**) the system is N limited throughout and (**B**) where the system tends to P limitation before the end of the simulation. (i) available P; (ii) reactive P; (iii) above- and belowground plant biomass P and (iv) indices of N and P limitation ($K_N/N_I(t)$ and $K_P/P_I(t)$, respectively). *Solid lines* are the background scenario with no management. *Dashed lines* are the state of the system following cutting at the calculated initial optimal level to reduce available P (see Digital Appendices A and B). In sub-figure (iv), black lines refer to the index of N limitation and grey lines refer to the index of P limitation. Sub-figure (v) denotes how the optimal level (l_{Bopt}) of cutting changes as a function of the state variables of the system. The *solid line* denotes the situation where the uncut system is used to calculate the optimal level. The *dashed line* shows the calculated optimum cutting level as a function of the system when it has been cut. The dotted line gives l_{Bopt} calculated with initial conditions. In (**B**), the system goes into P limitation and cutting becomes unviable as a management strategy, whereas in (**A**) N limitation persists throughout the simulation, and l_{Bopt} tracks the change in plant biomass. Parameter values in Digital Appendix B. A sensitivity analysis for this figure and Figure 3 indicated that dynamics were unchanged by parameter perturbations of $\pm 10\%$, with no qualitative difference in the impact of management at $t = 50$ (see main text for further details).

be more successful in practice than what our results suggest. Our discussion emphasizes the need to carry out practical tests to interrogate our model results.

Cutting

Cutting was only successful at depleting available and reactive P under very restricted conditions. This was because in our model, cutting of live plant tissue reduces total plant nutrient uptake. Cutting around l_{Bopt} may decrease available and reactive P pools where the recycling of P is sufficiently greater than the propensity to recycle N. In the N limited systems, with these recycling characteristics, it was possible for management to reduce reactive and available P, albeit marginally, providing the turnover of the litter pool was sufficiently fast. In such situations, the reduction in plant uptake of available P is sufficiently lower than the disruption of its supply from the soil organic and litter P pool and thus available P is lowered overall.

In our model, decreased biomass brought about through cutting reduces the total amount of nutrient uptake. Note that were recycling rates sufficiently enhanced, net uptake could still increase even with lowered plant biomass (de Mazancourt and others 1998). However, in our model, cutting removes biomass from the system and recycling is
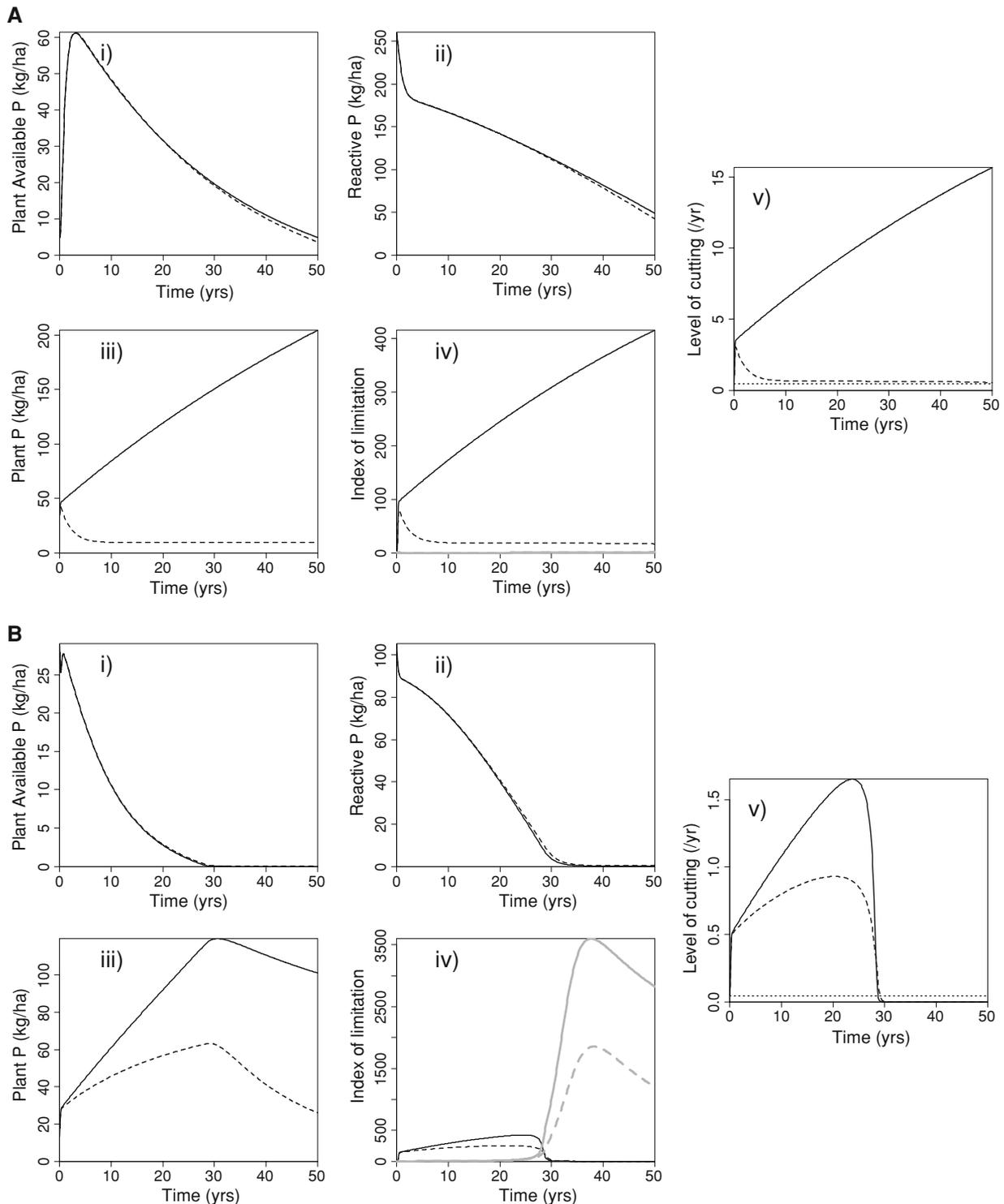
disrupted rather than increased, whilst the ability of the plants to deplete nutrients is compromised. Such decreased ability to take up nutrients under cutting has been shown in some studies (MacDuff and Jackson 1992; Jiang and Sullivan 2004), whereas others argue that cutting could stimulate nutrient uptake (McNaughton and Chapin 1985; Wallace

and Macko 1993; Hiernaux and Turner 1996). If that was the case, available P would then be lowered both through increased uptake and decreased supply from the litter pool, that is, increasing the likelihood of cutting being successful.

Cutting timing may play a key role in its success. Our model does not incorporate a dormant phase of

plant growth. However, if cutting was carried out at the end of the growing season, then it would remove nutrients from the system whilst having no effect on P uptake. Plant growth in the following year may be stimulated by removing the inhibitory effects of a litter layer (Xiong and Nilsson 1999) and relieving space and light competition (Collins and others 1998). Thus, although cutting was rarely, and only marginally, successful in our model, there are a number of reasons why it may be a viable strategy to remove available P, and consequently reactive P, in real systems.

Nitrogen Fertilization

N fertilization led to available and reactive P decline, provided plant growth in the system was N limited. Under such conditions, N addition promoted available P uptake pumping fertilizer P residues out of the reactive pool. Provided N addition does not push the system into sustained P limitation, N applications should continue and the goal of draining the reactive P pool should be realized. The P taken up by the plants will end up in the organic pools of the system, thus re-building the soil organic levels depleted by agricultural practices (McLauchlan 2006). Although high soil organic levels might lead to increased mineralization, and potentially an increased overall supply to the available P pool, this is unlikely to be a management problem given the long residence time of soil organic matter, and may well aid soil structure and ecosystem function, given the importance of organic matter for the P cycle in natural grasslands (Halm and others 1972).

Occasionally, increased P uptake following N addition caused systems to go into a highly P poor state with lower biomass than unamended plots. The mechanism of a highly P deficient system contributing to reduced biomass contrasts with other explanations of this phenomenon. Usually, decreased biomass due to additional N is attributed to toxicity or pH effects (Krupa 2003). Whatever the cause, a decreased biomass in comparison to a control would definitely indicate the need to halt N additions immediately.

Wider implications of N fertilization should not be ignored. Transient application of N could lead to increased nutrient losses (McDowell and Monaghan 2002) especially given high mobility of nitrate ions (Tinker and Nye 2000; Raynaud and Leadley 2004), potentially contributing to eutrophication (Carpenter and others 1998). We hope that reasonable N addition can be used relatively safely in abandoned agricultural systems: they have received a lot of fertilizers and adverse effects of further N are likely to be of limited scope. Given potential adverse effects, N addition should not be used elsewhere. Experiments are required to compare the overall costs and benefits of such a management strategy for restoration.

Nitrogen Fertilization and Cutting in Combination

As originally conceived (Marrs 1993), N fertilization and cutting would have been applied in combination. For reasons already discussed, we investigated each aspect of the management strategy separately, but N fertilization together with cutting may be more successful in practice than our model suggests, particularly if cutting does not disrupt nutrient uptake. The strategy has been applied in a number of systems, with mixed success. At Rothamsted, N addition and cropping led to the depletion of fertilizer P residues, whereas lack of N fertilizer input led to little removal—even with cropping (Johnston and Poulton 1977). Increased growth leading to P depletion was also observed in a fertile grassland system (Tallowin and others 2002), but not elsewhere (Condron and Goh 1990; Marrs and others 1998). Our model provides mechanistic explanations as to how experimental results could have occurred—systems may have had properties that prevented management from lowering problematic soil P. These results emphasize the need to maintain vegetation in a state that can deplete nutrients.

Robustness of the Model

We have considered the robustness of our model with respect to the cutting conditions above. In terms of N fertilization, qualitative results will not depend on the level of N added: however, the timing and magnitude of application will influence the speed at which reactive P depletion is achieved. In Digital Appendix C, we discuss changes to the model assumptions and show that our qualitative conclusions remain unchanged with respect to including: (1) a particulate loss pathway for reactive P, (2) the impact of N addition on P mineralization, (3) the impact of N addition on the exchange reaction between available and reactive P given pH changes, (4) variable plant nutrient ratios given community change and/or plastic response of species to management and (5) diffusion rather than the absolute concentration of available P determining plant P uptake. However, only experiments can corroborate these arguments.
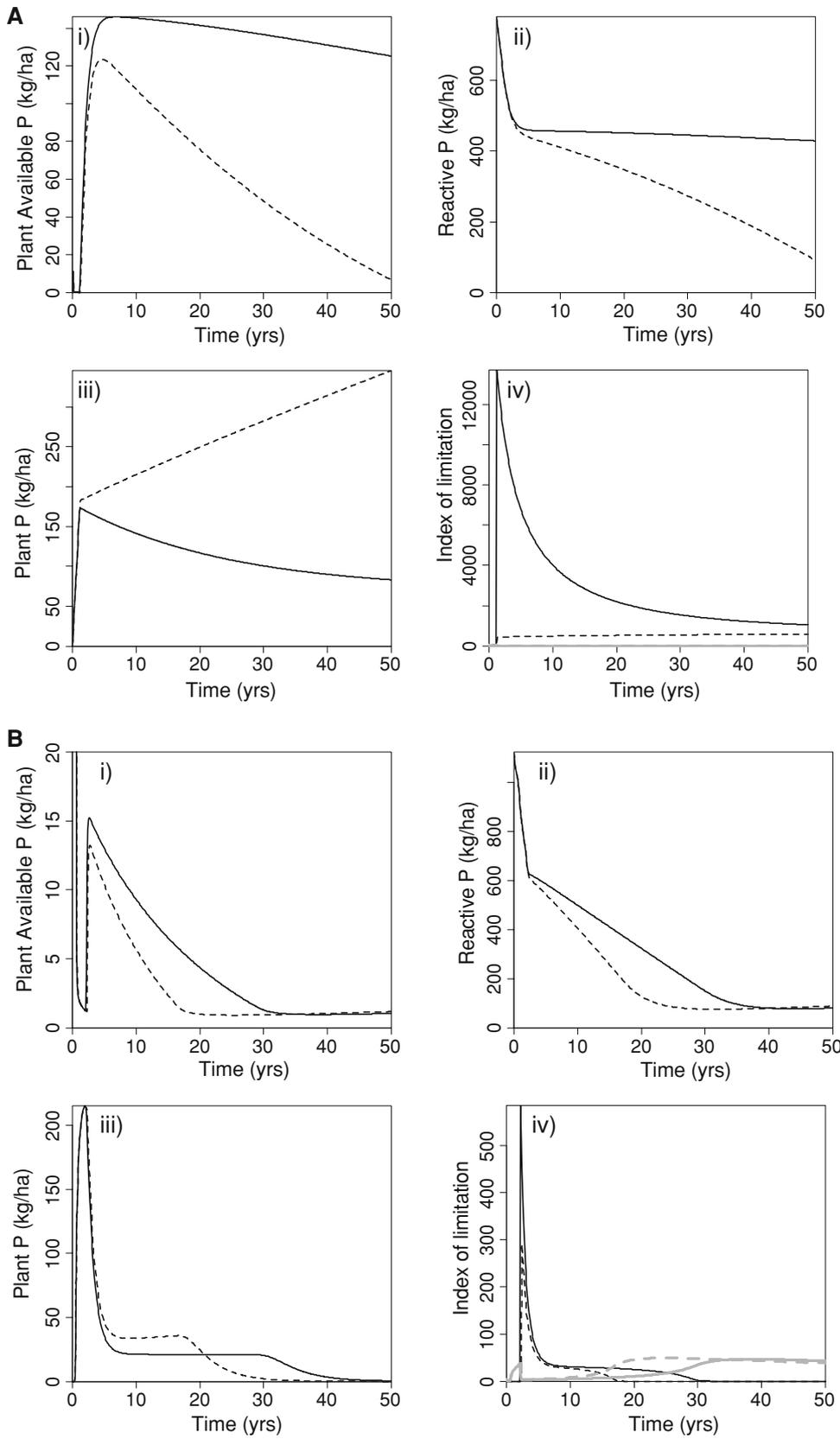
Figure 3. Typical transient dynamics given N fertilization where the system is N limited throughout (**A**) and where the system tends to P limitation before the end of the simulation (**B**). (i) Available P; (ii) reactive P; (iii) above- and belowground plant biomass P and (iv) indices of N and P limitation ($K_N/N_I(t)$ and $K_P/P_I(t)$, respectively). *Solid lines* are the background scenario with no management. *Dashed lines* are the state of the system following N fertilization of background plus 50 kgN ha^{-1} y^{-1}. Indices of limitation as in Figure 2, with parameter values in Digital Appendix B.

Environmental Benefits of Management: Restoration of Species Diversity

Given the multiple constraints to the restoration of diversity (Walker and others 2004; Pywell and others 2007), it will likely not be enough to decrease P availability in former cropland; active management is probably required to promote seed dispersal and germination (Firbank and others 2003).

Although management is targeted at removing fertilizer P residue thus creating conditions suitable for restoration of species diversity in grasslands, there may be direct impacts on species following the application of management. N addition generally leads to declines in species diversity (Bobbink 1991; Stevens and others 2004), through high productivity and/or pH changes (Rajaniemi 2003; Crawley and others 2005). Moderate N fertilization with non-acidifying fertilizers should therefore be a temporary management strategy in areas that have already received high levels of nutrients thus limiting the impact of further N addition on species diversity. As discussed above, cutting may further increase diversity by reducing the dominance of presumed good light competitive species, removing a litter layer and providing recruitment microsites. Experiments are required to test our predictions on the conditions for N addition and cutting to successfully lower soil P, and to explore other potential effects of such management strategies.

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