CLIMATE-CHANGE-INDUCED TEMPORAL VARIATION IN PRECIPITATION INCREASES NITROGEN LOSSES FROM INTENSIVE CROPPING SYSTEMS: ANALYSIS WITH A TOY MODEL

Peter M. VITOUSEK (▷)¹, Xinping CHEN², Zhenling CUI³, Xuejun LIU³, Pamela A. MATSON⁴, Ivan ORTIZ-MONASTERIO⁵, G. Philip ROBERTSON⁶, Fusuo ZHANG³

- 1 Department of Biology, Stanford University, Stanford, CA 94305, USA.
- 2 College of Resources and Environment, and Academy of Agricultural Sciences, Southwest University, Chongqing 400716, China.
- 3 College of Resources & Environmental Sciences, China Agricultural University, Beijing 100193, China.
- 4 Department of Earth System Science, Stanford University, Stanford, CA 94305, USA.
- 5 International Maize and Wheat Improvement Center (CIMMYT), El Batan, Texcoco 56237, Mexico.
- 6 W.K. Kellogg Biological Station, and Department of Plant, Soil and Microbial Sciences, Michigan State University, Hickory Corners, MI 49060, USA.

KEYWORDS

crop yield, fertilizer timing, nitrogen loss, precipitation variability, toy model

HIGHLIGHTS

- A simple model was used to evaluate how increasing temporal variability in precipitation influences crop yields and nitrogen losses.
- Crop yields are reduced and nitrogen losses are increased at current levels of precipitation variability.
- Increasing temporal variability in precipitation, as is expected (and observed) to occur with anthropogenic climate change will reduce yields and increase nitrogen losses further.

Received April 13, 2022; Accepted May 23, 2022.

Correspondence: vitousek@stanford.edu

GRAPHICAL ABSTRACT



ABSTRACT

A simple 'toy' model of productivity and nitrogen and phosphorus cycling was used to evaluate how the increasing temporal variation in precipitation that is predicted (and observed) to occur as a consequence of greenhouse-gasinduced climate change will affect crop yields and losses of reactive N that can cause environmental damage and affect human health. The model predicted that as temporal variability in precipitation increased it progressively reduced yields and increased losses of reactive N by disrupting the synchrony between N supply and plant N uptake. Also, increases in the temporal variation of precipitation increased the frequency of floods and droughts. Predictions of this model indicate that climate-change-driven increases in temporal variation in precipitation in rainfed agricultural ecosystems will make it difficult to sustain cropping systems that are both high-yielding and have small environmental and human-health footprints.

© The Author(s) 2022. Published by Higher Education Press. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0)

1 INTRODUCTION

Nitrogen is both an essential resource for intensive agriculture^[1,2], and a cause of damage to the environment and to human health^[3-5]. Substantial quantities of N are removed from intensive agricultural systems in harvested crops, and also, due to the mobility of N in flowing water and through multiple pathways to the atmosphere, losses of N occur readily during times when N is available in excess of crop demand, particularly during times when crops are absent. Replacement of the N (and other nutrients) removed via harvest and of the N (in particular) lost to stream flow, surface flow, and/or groundwater and/or to the atmosphere is essential to the maintenance of sustained agricultural production. Losses of fertilizer-derived N by most pathways are greater when N is applied in excess of crop requirements^[6]. Even where just the appropriate amount of fertilizer is applied, if is applied at an inappropriate time it may temporarily be present in excess of crop demand and hence drive losses of N.

Substantial research has been directed toward matching N fertilizer applications to crop demand^[7]. Other pathways for synchronizing supply and demand for fertilizer exist (e.g., slow-release fertilizer, deep placement of fertilizer); however, the timing of fertilizer application has been the subject of much research. One major challenge to the ability to synchronize the supply of N with crop demand through the timing of fertilizer applications is variability in precipitation. Precipitation variability can induce asynchrony between N supply and N demand, thereby causing N losses that are difficult to avoid^[8]. One of the most robust predictions about precipitation and anthropogenic greenhouse-gas-driven climate change is that precipitation variability will increase as Earth warms^[9,10], as has already been observed in many regions (e.g., Pryor et al.^[11]). This increase in the variability of precipitation means more frequent floods (and droughts), and therefore an increase in losses of fertilizer-derived nutrients^[12,13], especially N^[14]. Here we ask to what extent could an increase in the temporal variability of precipitation lead to losses of N that would make it more difficult to synchronize the supply of N to crops with their demand for that N.

2 METHODS

To address this question, we made use of a toy model of production and N cycling in row-crop agricultural systems (models known as toy models have a simplified set of objects and equations that can be used to understand a mechanism). We found developing such a model was particularly useful for testing our understanding of the implications of biogeochemical processes by requiring the expression of mechanisms as simplified equations that can be tested against field observations.

Our model was developed for a climate gradient on the Island of Hawai'i; it reasonably simulates the pattern of ¹⁵N natural abundance across the gradient and reproduces the location and magnitude of a peak in soil phosphorus that is caused by biological uplift in the mesic portion of that gradient^[15]. We wrote the program that runs the toy model in Matlab version 2018a (Mathworks Inc., Natick, MA, USA); the code is available as online supplementary information associated with this article. This program is built upon earlier versions that evaluated controls of symbiotic biological N fixation in Vitousek & Field^[16,17], were modified to evaluate the weathering of soil minerals in Vitousek et al.^[18], and modified again to apply to the climate gradient on the Island of Hawai'i in Vitousek et al.^[15]. Most recently, the model was modified to evaluate conditions under which N supply can constrain net primary production in little-managed perennial vegetation.

The question of how there can be N limitation to net primary production is one of the great mysteries in biogeochemistry,

because symbiotic biological N fixers are ubiquitous, and they should have a substantial competitive advantage where N is in short supply. Also, through their activity they should rapidly bring N supply close to equilibrium with other resources. This model-based analysis supported other approaches (e.g., Menge^[19]) in showing that N limitation that is more than marginal and/or ephemeral requires the co-occurrence of constraints to symbiotic N fixation and losses of N that cannot be prevented by N-limited organisms within the ecosystem. These unavoidable losses are important in that in their absence, even low inputs of N would accumulate to the point that a slow turnover of a large pool of N would supply sufficient N to offset N limitation. Additionally, analyses using the model demonstrated that precipitation variability and the associated asynchrony between N supply and N demand could drive losses of N that organisms cannot prevent.

The importance of N limitation to productive agricultural systems is not the mystery it is in little-managed perennialdominated ecosystems. Farmers control the composition of vegetation and often actively exclude symbiotic biological N fixers (except where they are planted intentionally), and the mobility of N causes its loss during seasons when crops are absent or inactive. Here, rather than evaluating causes of N limitation, we used the model to evaluate: (1) how the timing of applications of N fertilizer and the number of split applications influences the recovery of N in the harvested portion of crops (as a proxy for yields) and the losses of reactive N to the environment, at a low level of temporal variability in precipitation; (2) how increasing the simulated temporal variability in precipitation will influence the recovery of N in harvests and losses of reactive N to the environment; and (3) whether model-derived insights might provide potentials pathways for mitigation in the face of increasing temporal variability in precipitation.

The program we used to run the model is described in detail in Vitousek et al.^[15] and the structure of the version of the model that we used here is summarized in Fig. 1. Briefly, the program calculates the productivity of a non-N-fixing crop from simulated soil moisture and temperature, and biologically available N and P from all sources (fertilizer, atmospheric deposition, and mineralization of N and P from soil organic N and P). We focus on the productivity (net primary productivity or NPP) of a generic non-leguminous crop, although we recognize that yields of harvested products and NPP are not perfectly correlated for many crops. Mineralization of N (and P) from soil organic matter (adjusted by temperature and soil moisture; details not shown) was calculated for N (N_{min}) as Eq. (1):

$$N_{min} = SoilorgN - \frac{SoilorgC}{CN_{crit}}$$
(1)

where, SoilorgN and SoilorgC are soil organic N and C,



Fig. 1 The structure of the toy model. The soil pool is divided into organic forms of C, N and P; biologically available forms of water, N, P and a cation (modeled on calcium and described as M⁺); primary (unweathered) minerals of P and a cation, and secondary (formed in the soil) minerals of P. It includes atmospheric deposition of water, N, P and a cation; losses of inorganic forms of N, P and a cation by leaching, losses of dissolved organic forms of C, N and P by leaching, and gaseous losses of C and N. For the crop, we include uptake of water, N and P from the soil, removals of C, N and P in harvested material, and a flux of C, N and P back to the soil in crop residue.

respectively, and CN_{crit} is the critical C:N ratio above which N is immobilized and below which it is mineralized. We assumed a critical C:N ratio of 20:1 (the critical C:P ratio for net mineralization, which was calculated identically, was 200:1). Both plant production and decomposition are treated as linear functions of soil water content (as a fraction of soil water holding capacity, which we assumed to be 20 cm of water) (with no uptake of water and so no productivity below a permanent wilting point of 5 cm of water). Production and rates of primary mineral weathering were also treated as linear functions of temperature, with a maximum rate at 30 °C, but the dependence of decomposition on temperature was assumed to follow an exponential relationship with a Q₁₀ of 2.5. The crop plant was assumed to have a constant C:N:P stoichiometry of 500:10:1 and a maximum productivity per month of 1000 units of C; accordingly, the crop could not use more than 20 units of N or 2 units of P in any month.

At the end of the growing season we simulated a harvest of half the biomass C and three quarters of the biomass N and P (with the remainder going into soil organic C, N, and P pools at that time). Given the constant stoichiometry of the crop, harvested C was always set to $33.3 \times$ harvested N (not 50, as the whole plant is, because 75% of plant N and P but only 50% if plant C was harvested), and harvested P was always set to 0.1 \times harvested N. We calculated losses of N by various pathways, including nitrate loss (without concern for whether that loss occurred by leaching or denitrification), leaching of dissolved organic N^[20], losses of N-containing trace gases during nitrification^[21] and ammonia volatilization. Ammonia fluxes depend on soil pH, which was not calculated by the model, so we used the abundance of weathering-derived cation as a surrogate for pH. For P, we assumed lower losses than for N due to the much lower mobility of P in soils, and we assumed half of the residual phosphate (the biologically available P that remained in the soil after plant uptake) formed relatively recalcitrant secondary minerals that weather slowly.

The version of the program that we used for this paper differed from that in Vitousek et al.^[15] in that here we included an explicit treatment of months within years, and an explicit calculation of seasonality in temperature. We also included a 5month crop growing season rather than the continuous plant productivity in Vitousek et al.^[15]. This version of the model (Fig. 1) had no transpiration (but continued evaporation from the soil surface) during the non-growing season, no symbiotic biological N fixer, and we did not simulate a deep soil layer.

In the absence of temporal variability in precipitation, the program rapidly converges to an equilibrium, with a stable threshold in simulated soil and ecosystem properties where precipitation equals evapotranspiration. However, when temporal variability in precipitation is included, this threshold migrates slowly to progressively drier positions along a precipitation gradient over time, in a reasonable pattern^[15,18]. Precipitation variability is particularly important in that increasing precipitation variability (together with the related occurrence of extreme precipitation events such as floods and droughts) is one of the most robust predictions (and observations) for consequences of greenhouse-gas-driven anthropogenic climate change^[9,10]. We simulated the temporal variability of precipitation with a random component to monthly variation. We simulated precipitation with different levels of temporal variability, but the same mean precipitation, as Eq. (2):

Simulated precipitation (for that time interval, assumed and adjusted to be a month) = mean monthly precipitation + [mean monthly precipitation × a constant (≥ 1) × a random number (uniformly distributed from 0 to 1) a constant (0.5 to < 1)] (2)

We set precipitation to 0 when this calculation yielded a negative value. The constants were chosen to provide five levels of temporal variability (including zero variability) with the same mean precipitation.

We performed all of our analyses at a mean precipitation of 12 cm per month, initially with no seasonal variation. We ran the program for the first 1000 simulated years (12,000 months) to allow it to equilibrate, then introduced the level of temporal variation we were testing and ran the program for another 4000 simulated years. Fertilizer additions took place beginning in simulated year 3500 (after 2500 years of the level of temporal variation in precipitation being tested), and we averaged results (by month) for the last 1000 simulated years. The output of interest was yields of N in harvested crops after the 5-month growing season (from which yields of C and P could be calculated directly as described above), losses of N as reactive N, and the total number of floods and droughts in the last 1000 years of simulation (floods were defined as leaching losses in excess of the water holding capacity of the upper 50 cm of soil, droughts were defined as any two consecutive months with no precipitation).

3 RESULTS AND DISCUSSION

We first ran the program with a low level of variation in precipitation among months, and evaluated the consequences

of the timing of fertilization and number of split applications of fertilizer during the crop growing season for yields of N in harvested material and for losses of N. The level of temporal variation we used here was that used for 12 cm of precipitation/month) in Vitousek et al.^[15]; it had a coefficient of variation (standard deviation/mean) of 0.29. Subsequent analyses showed that this level of variability is less than the 0.74 coefficient of variation observed for 12 cm per month of precipitation at Ponoholo Ranch near the climate gradient (P. von Holt, personal communication). The results of this analysis of the timing of fertilization and of the number of split applications of fertilizer are shown in Fig. 2. A single addition of fertilizer (100 and 20 units of N and P, respectively) was more effective in supporting yields and in reducing losses of reactive N the closer to the start of the crop growing season it was applied; a quantity of N equivalent to nearly half of the applied N (48.8%) was recovered in the harvest when fertilizer was added as a single application at the time the crop was planted and began to grow (Fig. 2). Similarly, losses of reactive N declined sharply as the simulated application of fertilizer occurred closer to the start of the crop growing season. Splitting the simulated application of fertilizer so that 40% was



Fig. 2 Effects of the timing of simulated applications of fertilizer (left of x-axis) and of the number of simulated split applications of fertilizer (right of x-axis) on the simulated recovery of N in harvested material (solid line, a proxy for yield) and on losses of reactive N to the environment via leaching and gas fluxes (dashed line). In all cases a consistent 100 and 20 units of N and P were applied, respectively, per growing season, and both recovery and losses of N were averaged over the last 1000 years of simulation. Multiple runs of the model were performed for the November application of fertilizer and for the five-increment application; means and standard deviations are reported for these treatments but standard deviations were small and error bars largely are hidden behind the symbols. For two split applications of fertilizer, application of 40 units of N upon planting in May and 60 units of N in June was used.

added in the first month of the crop growing season, with the other 60% applied two months later in July, caused a further increment in the simulated recovery of N in harvested material (to 53.6% of applied N), and a further decrease in simulated losses of reactive N (Fig. 2). This result differed slightly from applying the same two splits of fertilizer in May and June (an amount of N equivalent to 52.5% of applied N was recovered in harvest), a more common agricultural practice because it maximizes yields rather than crop NPP, in that fertilization later in the growing season can increase NPP without increasing yields.

Additional splits in simulated fertilizer application were unrewarding; in particular adding 20% of the fertilizer each month (which matched maximum demand for N by the crop) did not improve simulated recovery of N in the harvested crop, or simulated loss of reactive N, meaningfully (Fig. 2). While monthly precipitation and so yields and N losses have a stochastic component, the fact that we averaged results (by month of the year) for the last 1,000 years of simulation meant that the variance of results was low, with a standard deviation of < 0.2 compared with 53.6 for N in harvested material and 60.8 for N losses. At this low level of temporal variation in precipitation, there were no floods or droughts in any treatment, and so there would be no substantial losses of fertilizer P via erosion (P is nearly immobile in soils and so it accumulates in surface soil). Our results would be less extreme than those in Fig. 2, if the non-growing season was relatively dry or if precipitation occurred as snow that melted at the beginning of the growing season and did not contribute substantially to soil water during the non-growing season.

We then explored the consequences of five intensities of temporal variation in precipitation, with coefficients of variation ranging from 0 (no temporal variation) to 1.69. In each case, we simulated the application of fertilizer (100 and 20 units of N and P, respectively) in two increments which is a recommended best practice for many field crops including maize. The results were remarkable; increases in temporal variation caused declining yields, progressively larger losses of reactive N, and (consequently) floods and droughts (the latter summed during the growing season only) were more frequent (Fig. 3). We ran the program multiple times and calculated standard deviations at the highest level of variability in precipitation; standard deviations were < 1% of the mean for all outputs from the model except floods, for which they were < 2%. Floods were defined as occurring whenever water losses in a month exceeded the water holding capacity of the soil; at some point (perhaps not right at this point, but not far from it) intense precipitation will lead to surface runoff and erosive



Fig. 3 Effects of simulated temporal variability in precipitation on the simulated number of floods (solid line) and droughts (dashed line). Both were summed over the last 1000 years of simulation. Simulated temporal variability in precipitation is given as the coefficients of variation of precipitation per month, and (as in Fig. 5) multiple model runs were performed with means and standard deviations calculated and reported at the highest level of variability in precipitation. Floods were defined as occurring when simulated water loss exceeded the water-holding capacity of the upper soil (20 cm of water). Droughts were defined as occurring when two consecutive months received simulated zero precipitation; only droughts that occurred during the crop growing season were included.

losses of soil and nutrients. Such losses are likely to be particularly important for P, since in our simulation (as well as in practice) the relative immobility of P causes large pools of fertilizer-derived P to accumulate in surface soils, where they are vulnerable to losses via erosion.

Finally, we explored whether insights from our toy model could help to mitigate the consequences of increasing temporal variation in precipitation. Earlier field studies showed that notill cropping systems could buffer the effects of increased temporal variation in precipitation^[12,13] more effectively than could tilled cropping systems, but we could not represent either tilled or no-till cropping systems with this toy model. We tested alternative scenarios at the second highest level of temporal variability in precipitation (a coefficient of variation of 1.28, for monthly variation in precipitation), and we compared the consequences of two splits of simulated fertilizer application (as above) versus the same total quantity of fertilizer divided into five splits (with a fifth of the fertilizer applied each month) versus a situation in which we made two or five splits of simulated fertilizer application, and adjusted each one by the water content of the soil (so that no more fertilizer was added than could be used by the crop). We made this adjustment by multiplying the target fertilizer application by the water content of the soil divided by the water-holding capacity of the soil. This approach resulted in lower total applications of fertilizer; it involves the use of information on soil water content that could be predicted with crop models used for irrigation scheduling and daily weather data.

Results of these analyses are summarized in Fig. 4. Adjusting the simulated amount of fertilizer applied depending on soil water content had a relatively small effect on yields and (consequently) the recovery of N in harvested material, but it did greatly decrease simulated losses of reactive N (Fig. 4). The model-based analysis did not indicate a way to enhance yields and thus to maintain food security in the face of increasing demand for food and increasing temporal variation in precipitation, but it did indicate a way to sustain yields while substantially reducing losses of reactive N to the environment. Based on these results, it seems likely that we will face



Fig. 4 Consequences of a management practice designed to offset the effects of greater simulated variability in precipitation. This simulation was performed at the secondhighest level of temporal variation in simulated precipitation; it compared the effects of two with five splits in standard fertilizer application both with a total of 100 units of N and 20 units of P. The two applications were simulated to occur in May and July. The height of the bars in each group represent the simulated recovery of N in harvested material, simulated losses of reactive N and the total quantity of N fertilizer applied. Results of these standard treatments were compared with treatments in which we simulated two and five splits of adjusted fertilizer application with lesser and variable amounts of fertilizer applied. Multiple model runs were performed with means and standard deviations calculated and reported for the outputs summarized; standard deviations were small (always < 2% of means) so the error bars are not readily visible.

463

increasing challenges to food security with the ongoing enhancement in precipitation variability (Fig. 5).

4 CONCLUSIONS

A simple model of the consequences of the increase in temporal variability of precipitation that is expected^[9,10]—and already has been observed^[11]—to occur as a consequence of anthropogenic climate change shows that increasing temporal variability in precipitation drives asynchrony in the supply of nutrients by fertilizer or other sources and the demand for those nutrients by crops. Increasing temporal variability in precipitation also increases the frequency of floods and droughts straightforwardly, and so causes loss of soil and associated immobile elements. Results of the model support and extend empirical studies showing the temporal variation in precipitation causes losses of nutrients from intensive agricultural systems^[12,13]. Use of this model to evaluate pathways by which yields could be increased and the environmental damage caused by fertilizer losses mitigated showed that while fertilizer use and associated N losses could be reduced, climate-change-driven increases in temporal variation in precipitation in rainfed agricultural ecosystems will make it difficult to sustain cropping systems that are both highyielding and have small environmental and human-health footprints.



Fig. 5 Effects of simulated temporal variability in precipitation on the simulated recovery of N in harvested material (solid line) and on losses of reactive N to the environment via leaching and gas fluxes (dashed line). Both recovery and losses of N were averaged over the last 1000 years of simulation. In all cases we simulated the consequences of two split applications with 40 units of N applied, with 8 units of P, at planting, and the second application with 60 units of N and 8 units of P in July. Simulated temporal variability in precipitation is given as the coefficients of variation of monthly precipitation, and multiple model runs were performed with means and standard deviations calculated and reported at the highest level of variability in precipitation.

Acknowledgements

We thank Pono von Holt and Ponoholo Ranch for providing information on precipitation and its variability along a rainfall gradient. Model development and manuscript preparation were supported by a US National Science Foundation grant (2027290) awarded to Stanford University.

Compliance with ethics guidelines

Peter M. Vitousek, Xinping Chen, Zhenling Cui, Xuejun Liu, Pamela A. Matson, Ivan Ortiz-Monasterio, G. Philip Robertson, and Fusuo ZHANG declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

REFERENCES

- Galloway J N, Townsend A R, Erisman J W, Bekunda M, Cai Z, Freney J R, Martinelli L A, Seitzinger S P, Sutton M A. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science*, 2008, **320**(5878): 889–892
- 2. Liu X J, Xu W, Du E Z, Tang A H, Zhang Y, Zhang Y Y, Wen Z, Hao T X, Pan Y P, Zhang L, Gu B J, Zhao Y, Shen J L, Zhou F, Gao Z L, Feng Z Z, Chang Y H, Goulding K, Collett Jr J L, Vitousek P M, Zhang F S. Environmental impacts of nitrogen emissions in China and the roles of policies in emission

reduction. *Philosophical Transactions. Series A: Mathematical, Physical, and Engineering Sciences,* **378**(2183): 20190324

- Sutton M A, Howard C M, Erisman J W, Billen G, Bleeker A, Greenfelt P, van Grinsven H, Brizzetti B. The European Nitrogen Assessment: Sources, Effects, and Policy Perspectives. Cambridge: *Cambridge University Press*, 2011
- 4. Liu X, Zhang Y, Han W, Tang A, Shen J, Cui Z, Vitousek P, Erisman J W, Goulding K, Christie P, Fangmeier A, Zhang F. Enhanced nitrogen deposition over China. *Nature*, 2013,

464

494(7438): 459–462

- Gu B, Ju X, Chang J, Ge Y, Vitousek P M. Integrated reactive nitrogen budgets and future trends in China. *Proceedings of the National Academy of Sciences of the United States of America*, 2015, 112(28): 8792–8797
- 6. Chen X, Cui Z, Fan M, Vitousek P, Zhao M, Ma W, Wang Z, Zhang W, Yan X, Yang J, Deng X, Gao Q, Zhang Q, Guo S, Ren J, Li S, Ye Y, Wang Z, Huang J, Tang Q, Sun Y, Peng X, Zhang J, He M, Zhu Y, Xue J, Wang G, Wu L, An N, Wu L, Ma L, Zhang W, Zhang F. Producing more grain with lower environmental costs. *Nature*, 2014, **514**(7523): 486–489
- 7. Zhang F, Chen X, Vitousek P. Chinese agriculture: an experiment for the world. *Nature*, 2013, **497**(7447): 33–35
- Robertson G P. Nitrogen use efficiency in row-crop agriculture: crop nitrogen and soil nitrogen loss. In: Jackson L, ed. Ecology in Agriculture. New York: *Academic Press*, 1997, 347–365
- Kharin V V, Zwiers F W, Zhang X B, Hegerl G C. Changes in temperature and precipitation extremes in the IPCC ensemble of global coupled model simulations. *Journal of Climate*, 2007, 20(8): 1419–1444
- Pendergrass A G, Knutti R, Lehner F, Deser C, Sanderson B M. Precipitation variability increases in a warmer climate. *Scientific Reports*, 2017, 7(1): 17966
- 11. Pryor S C, Scavia D, Downer C, Gaden M, Iverson L, Nordstrom R, Patz J, Robertson G P. Midwest. In: Melillo J M, Richmond T C, Yohe G W, eds. Climate Change Impacts in the United States: the Third National Climate Assessment. Washington, D.C.: US Global Change Research Program, 2014, 418–440
- 12. Michalak A M, Anderson E J, Beletsky D, Boland S, Bosch N S, Bridgeman T B, Chaffin J D, Cho K, Confesor R, Daloglu I, Depinto J V, Evans M A, Fahnenstiel G L, He L, Ho J C, Jenkins L, Johengen T H, Kuo K C, Laporte E, Liu X, McWilliams M R, Moore M R, Posselt D J, Richards R P, Scavia D, Steiner A L, Verhamme E, Wright D M, Zagorski M A. Record-setting algal bloom in Lake Erie caused by

agricultural and meteorological trends consistent with expected future conditions. *Proceedings of the National Academy of Sciences of the United States of America*, 2013, **110**(16): 6448–6452

- Hess L J T, Hinckley E L S, Robertson G P, Matson P A. Rainfall intensification increases nitrate leaching from tilled but not no-till cropping systems in the U.S. Midwest. *Agriculture, Ecosystems & Environment*, 2020, **290**: 106747
- Robertson G P, Bruulsema T W, Gehl R J, Kanter D, Mauzerall D L, Rotz C A, Williams C O. Nitrogen-climate interactions in US agriculture. *Biogeochemistry*, 2013, 114(1-3): 41–70
- Vitousek P M, Bateman J B, Chadwick O A A. "toy" model of biogeochemical dynamics on climate gradients. *Biogeochemistry*, 2021, 154(2): 183–210
- Vitousek P M, Field C B. Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications. *Biogeochemistry*, 1999, 46(1-3): 179–202
- Vitousek P M, Field C B. Input-output balances and nitrogen limitation in terrestrial ecosystems. In: Schulze E D, Harrison S P, Heimann M, Holland E A, Lloyd J, Prentice I C, Schimel D, eds, *Global Biogeochemical Cycles in the Climate System*. San Diego: Academic Press, 2001, 217–225
- Vitousek P M, Dixon J L, Chadwick O A. Parent material and pedogenic thresholds: observations and a simple model. *Biogeochemistry*, 2016, 130(1-2): 147–157
- Menge D N L. Conditions under which nitrogen can limit steady state net primary production in a general class of ecosystem models. *Ecosystems*, 2011, 14(4): 519–532
- Hedin L O, Armesto J J, Johnson A H. Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory. *Ecology*, 1995, **76**(2): 493–509
- 21. Firestone M K, Davidson E A. Microbiological basis of NO and N₂O production and consumption in soil. In: Andreae, M O, Schimel D S, eds. Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere. Chichester: *John Wiley and Sons*, 1989, 7–21