Temperature effects on rates of nitrogen mineralization across ecosystem types: Consequences for global warming

Temperature increases due to global warming have the potential to seriously impact the function, productivity, and composition of ecosystems. In order to gain a better understanding of the potential changes caused by warming, it is necessary to understand the impacts on essential processes, especially soil processes. Here we analyzed the impact of warming on the rate of nitrogen mineralization across biomes to help provide a framework to predict changes in NPP and NEP. Regardless of ecosystem type, increasing temperatures result in increases in N-mineralization rates provided that water is not limiting. Nitrogen will then become more available to plants, and is predicted to lead to increases in NPP, especially in currently N-limited ecosystems. Ultimately, to predict with certainty the ecosystem impact on a global scale, more research is needed on a greater number of biome types, and also on interactions between soil and plant processes.

While the phenomenon of global warming is gaining increasing support in both the scientific realm and in the media, uncertainty exists about the possible effects of temperature shifts on a global scale. Theory and models have proposed changes on the scale of nominal to catastrophic in many areas of biology, including major effects on climate and weather patterns, losses of biodiversity, drastic changes in community structure and ecosystem composition, and changes in ecosystem function. It may even act to alter speciation and extinction rates, and alter evolutionary trajectories of plants and animals due to the expected changes in environment. Global warming has been predicted to increase average temperatures from 1 to 3.5 degrees Celsius over the next 50 to 100 years [1]; although some predictions are much higher. Temperature is a key factor for soil processes such as decomposition and nitrogen mineralization, as well as plant processes such as photosynthetic rate, plant productivity, and nutrient uptake. Temperature effects from global warming are predicted to be more variable in space and time than the effects of elevated atmospheric CO_2, as temperature will be more heterogeneous on the landscape level. Factors such as local geography, latitude, and elevation will impact temperatures, whereas the atmospheric CO_2 concentration is

2

roughly uniform. Additionally, a stronger response to warming is predicted to occur in higher latitudes, or ecosystems that are currently colder [1, 2]. Temperatures also fluctuate on daily and seasonal scales, further adding to the variability in temperature-related impacts on processes such as N-mineralization.

Variability in temperatures (and the resulting impact on ecosystem processes) highlights the need for a large amount of site-specific research. Because so many variables will be altered, a holistic approach to understanding and predicting these consequences is impractical. In order to begin to appreciate how an increase in temperature may affect ecosystem structure and function, it is necessary to start at the ground level by examining soil processes that control net primary productivity (NPP), which in turn controls net ecosystem productivity (NEP). Specifically, it is imperative to understand the direct effect of temperature and the indirect effects of related changes in soil moisture and CO_2 concentration on rates of nitrogen mineralization.

In most ecosystems, nitrogen (N) is the key limiting resource, thereby exerting direct control over NPP and influencing NEP. Human activity, through fertilization and the burning of fossil fuels, has both contributed to increased additions of N into terrestrial nutrient cycles, and spurred global warming. Because ecosystems vary in so many biological and geochemical aspects, and results from warming experiments are so varied, to fully understand the effects on NPP and NEP due to elevated temperatures and N-mineralization, it is useful to categorize the data into biome-groups. Here, we examine temperature effects on N-mineralization in high-N (tropical forests), medium-N (temperate forest and grasslands), and low-N (arctic tundra and boreal) ecosystems [3] in order to gain insight into the possible effects of increased temperature from global warming on NPP, which will ultimately contribute to changes in NEP and ecosystem biodiversity. We predict that while there will be a large amount of variation in ecosystem response, overall NPP will increase under elevated temperatures due to increases in N-mineralization rates. Overall nitrogen availability may increase (possibly to excess), which has the potential to lead to very negative impacts, such as nitrogen saturation, shifts in dominant species and reduction of species diversity, and also shifts in ecosystem type (for example, from species-rich heathlands to species-poor forest or grasslands);

3

species losses have the potential to make the system less stable or resistant to disturbance, such as drought or fire [4].

General model and experiment results

Both experiments and models have been used to understand the effects of elevated temperature on N-mineralization, but predictions for ecosystem response are difficult due to the long-term scale of the change, and the complexities of the underlying interactions. The nitrogen cycle is inherently complex due in part to the highly specific microorganisms involved in N-mineralization; this has given rise to variation and discrepancies in reported results of simulations [2, 5]. Additionally, models differ in their underlying assumptions of the relative importance of plant physiological processes versus soil nutritional processes. Those emphasizing the former predict a decrease in plant productivity under warming due to a decreased stomatal conductance, whereas those emphasizing the latter predict an increase in productivity due to greater N-mineralization [2]. Here we will focus on experiments and models emphasizing soil processes, as we propose that N-mineralization is the most important process determining changes in NPP in response to global warming.

The general consensus of experimental results and models shows that with increasing temperature, rates of N-mineralization will increase. There is however, a large amount of variation in the magnitude of the effect, and some studies do not support this trend [1, 2, 5-7]. Of great importance for predicting response are the initial conditions of the ecosystem: primarily, soil moisture content, and the dominant form and relative availability of nitrogen in the soil. For example, in the results of their model, Medlyn et al [2] showed an initially large increase in NPP, then a smaller but long term increase in NPP. Plant physiological responses were shown to be important for the short-term increase in NPP, but the medium and long-term increases were due to stimulated N-mineralization rates from increases in both soil and air temperatures. However, the study made the assumption that water availability was not limiting NPP.

In a meta-analysis of 32 warming experiments from a variety of latitudes, Rustad *et al* [1] found that overall, warming contributes to increases rates of N-mineralization. Warming significantly increased rates of N-mineralization across ecosystem types, which

4

led to significant increases in above-ground biomass. Different types of ecosystems responded quite differently, with increases in productivity highest in tundra and lowest in grassland. Rustad *et al* [1] also found that there were significant positive relationships between mean net N-mineralization, mean annual precipitation, and mean temperature, highlighting the importance of soil moisture for sustaining increases in mineralization rates.

Additional studies also demonstrate the importance of soil moisture on rates of N-mineralization. Niklinska *et al* [6] found that the rate of organic matter decomposition of forest ecosystems depends primarily on temperature and humidity, and N-mineralization rates were positively correlated to temperature. Leiros *et al* [5] also found that increased temperature and moisture levels increased N-mineralization rates and that the temperature-moisture interaction significantly influenced mineralization rates. It was also noted that the effect of a 2-degree increase in temperature was roughly countered by a concurrent 10% decrease in soil moisture content. Clearly, in ecosystems with water limitations, this coupling between increased temperature and decreased moisture will have strong impacts on mineralization rates, and therefore on NPP. Pendall *et al* [7] also found N-mineralization rates to be stimulated by increases in temperature, and proposed that this may act as a positive feedback on plant productivity. However, the extent of the increase of mineralization was dependent on the type of soil: upland soils were likely to experience drying, which could result in mineral immobilization and reduction of decomposition. In contrast, in wetlands, drying could result in increased aerobic respiration and decomposition as water tables were lowered. But, in any type of system, drying could be alleviated if elevated CO_2 reduces transpiration rates. Most models agree that elevated temperatures will decrease soil moisture, whereas elevated CO_2 will increase moisture. It is unclear how their interaction will affect actual moisture availability, but it is likely to depend on both ecosystem type and species composition.

While temperature has been shown to increase N-mineralization rates, there is a maximum to the effect. Twenty-five degrees Celsius has been shown to be the optimal temperature for maximizing N-mineralization [5]. So, while there are many areas and ecosystems where there would be a net increase in NPP due to increased N-mineralization rates, areas where the temperature was pushed beyond 25 degrees Celsius

5

may experience a net decrease in mineralization rates. Additionally, some ecosystems could experience a shift from net immobilization (i.e. negative net mineralization) to zero or positive net mineralization due to global warming. Niklinska *et al* [6] found that experimentally warming soils from northern European Scots pine forests caused a switch in one site from net immobilization to net mineralization. The ramifications of this type of biochemical shift are potentially very strong—in this forest system, there could be more than double the current rate of nitrogen turnover during the growing season.

High N/Tropical systems

Nitrogen-rich ecosystems are typically tropical forests or agricultural systems. It is crucial to understand the impacts of temperature increases due to global warming on tropical forests as they account for approximately 43% of global NPP, and 27% of the carbon stored in forest soils [8]. However, relatively little research has been conducted to determine temperature effects on N-mineralization rates in tropical soils, perhaps due to the general belief that the larger effects of global warming will be seen in higher latitudes and colder ecosystems.   However, the high rates of soil respiration in tropical systems are very sensitive to small changes in temperature, so large effects could be seen even if the temperature increases are relatively small [9]. In humid or wet tropical systems, the climate is nearly constant throughout the year, so even minor temperature changes could have drastic impacts, and in the dry tropics, temperature changes could alter the frequency of disturbance (drought, fire), which would have large impacts on both NPP and N-mineralization rates [8]. In tropical forests, N-mineralization rates have been shown to increase with increasing temperature [10]. However, in these systems, phosphorous tends to be the limiting resource for plant growth, not nitrogen [8]. Therefore, when phosphorous is limiting, increases in N-mineralization rates will not lead to increases in NPP. Townsend *et al* [9] found increases in the turnover times of soil organic carbon in tropical forest systems, and models for the Amazon basin predict increases in carbon storage [11]. However, trees grown under elevated CO_2 showed no increase in concentrations of lignin, nitrogen or carbon, and there was no effect on decomposition (temperature itself was not tested; [12]. It has been predicted that for tropical systems, if NPP does initially increase under global warming conditions, those

6

increases could lead to changes in litter quality, reducing the nutrient content and ultimately leading to a reduction of NPP [8]. Currently, there are tropical forest systems that are both water and non-water limited. Projections on the effects of global warming on climate and weather patterns are varied so it is not clear if increased temperatures will cause lower water availability. Increased temperatures themselves are predicted to decrease soil moisture availability and rainfall, which would therefore lower N-mineralization rates; however, CO_2 fertilization can increase water use efficiency in plants, and may therefore increase soil moisture [8]. Dry tropical forests could experience prolonged drought, which would also reduce N-mineralization rates; both factors would therefore lower NPP. However, there could be an increase in precipitation, which would then increase N-mineralization and NPP [8]. Another problem with predicting rates of N-mineralization under higher temperatures for tropical systems stems from the problem of weather pattern shifts. Hurricane frequency, for example, may increase or decrease, but both possibilities will impact successional states of the forests, which will in turn impact nutrient cycling: N-mineralization tends to increase through secondary rainforest succession [13]. Lastly, human use of tropical forests, specifically slash-and-burn agriculture, will change nutrient availability in the system, which will then impact the rates of N-mineralization. These practices ultimately remove nitrogen from the system, which would have the obvious impact of slowing mineralization rates.

In summary, it is very difficult to predict the impact of global warming on NPP for tropical forests. N-mineralization will increase with temperature, but due to phosphorous limitations, and potentially large changes in water availability and climate patterns (we will ignore human use at this point), it is difficult to know the magnitude and direction of change for NPP.

Medium N/Temperate Systems

In many cases temperature, moisture availability and substrate properties may play a more important role in controlling soil respiration rates than area vegetation type [14]. This is not to say that vegetation type is unimportant. Respiration rates do vary with vegetation, and it has been shown that vegetation affects soil respiration through influences on soil microclimate and structure, the quantity and quality of detritus supplied

7

to soil, and by the overall rate of root respiration [14]. The studies reviewed by Raich and Tufekcioglu [14] indicate that soil respiration rates vary among different temperate forest types. In the studies reviewed, soil respiration rates in coniferous forests were found to be lower than those in broad-leaved forests existing on the same soil types. Rather than a direct effect of temperature though, this study suggests that the difference is likely due to the variation in plant litter quality (N and lignin content). Both mechanisms could operate within a single system, but over different time scales. One example of this scenario is the temperate forest warming study in Harvard Forest, MA. Initially, with a $5°$ C increase in soil temperature, soils experienced faster decomposition and overall C loss [28]. Over the long-term, however, N is taken up by biomass with a higher C:N ratio than soil, resulting in C storage but no change in ecosystem N. This is due to the ammonium economy of the system; mineralized N that becomes nitrified has the potential to be leached from the soil. Finally, without extraneous inputs of N, the system reaches equilibrium such that biomass no longer accumulates, and increases in respiration may result in overall C loss. Existing scientific literature also strongly points to the influence of soil temperature and moisture content on respiration rates, such that changes in precipitation induced by global warming can alter C and N cycles. Ultimately, primary productivity and decomposition rates are strongly linked processes that are controlled by primarily by temperature, moisture availability and substrate quality [14].

There is strong evidence suggesting that forest disturbances influence nutrient availability (C and N most significantly) in the ecosystem. Climate change will likely have an impact on forest disturbances in various and unpredictable ways. Alterations in temperature may mean greater variability in annual climatic events. Some models predict more and prolonged periods of drought. Other models suggest that we may expect heavier rainy seasons with increased flooding and landslides. This range of possible increased numbers and severity of disturbance events may lead to unpredictable results [15]. For example, when an ecosystem experiences combinations or series of disturbances, it may not have sufficient recovery time from an initial disturbance before the next disturbance occurs. This phenomenon of reduced recovery time may lead to new and unforeseen long-term conditions. Increased variability in wet/dry season fluctuations may lead to a big increase in biomass in some years that experience higher

8

than normal precipitation. Then, if several drought years follow, there is an unusually large amount of dead organic matter as a consequence of decreased NPP, decreased decomposition resulting in the potential for massive forest fires which may lead to a net loss of nutrients in the ecosystem. Increased temperatures may lead to increased rates of evapotranspiration, causing moisture stress in the forest ecosystem. Some models suggest that this mechanism may cause future increases in drought in the Southeast, Southern Rockies and parts of the Northwest in the United States. Some fire history studies though suggest that there may be a decrease in fire disturbances if precipitation rates increase but high precipitation rates can lead to increased landslides and flooding as well.

Low N/Tundra and Boreal Systems

High latitude tundra and boreal ecosystems are considered nitrogen poor environments. In these regions low temperatures and wet soil conditions inhibit decomposition, and it is the slow release of N and P from organic matter that limits NPP [16-20]. Despite low NPP, high latitude soils account for a third of the world's terrestrial organic carbon [21].   The size of this carbon sink is directly proportional to rates of change in NPP and carbon residence time as controlled by decomposition [21]. With warmer conditions decomposition rates should increase, thus these stores represent a potential positive feedback for global warming if they are decomposed and respired into CO_2 and CH_4 . Rates of N mineralization have been shown to increase with temperature as well [22]; since both decomposition and plant productivity are nutrient limited, warming has the potential to further stimulate decomposition and increase NPP [23]. However, this simple framework does not account for the long-term effects of plant community composition on rates of decomposition and N-mineralization.

Several long-term studies at Abisko, Sweden and Toolik Lake, Alaska have demonstrated that fertilization, which increases nutrient availability to plants, elicits significant changes in tundra plant communities in either NPP or in structure and function [24-27]. For example, Alaskan tussock tundra systems are typically dominated by roughly equal biomass of graminoids, deciduous shrubs, evergreens, and with intertussock areas covered by mosses [28]. However, fertilization of tussock tundra for

9

several decades has led to an increased abundance of deciduous shrubs, and a decrease in mosses and evergreen shrubs [24, 25]. Similar long-term experiments at Toolik Lake have directly manipulated temperature; the effects on plant communities are less extreme, but generally follow the same trends as the fertilizer experiments, with species shifts presumably driven by increased nutrient availability [24, 29]. Plant community composition is an important determinant of decomposition and nutrient cycling rates: In Alaskan taiga systems, faster decomposition rates in birch versus spruce forests were observed despite warmer temperatures in the birch forest, and differences in decomposition rate among tundra species can be greater than the effect of a 6° C increase [18, 21]. Therefore, replacement of relatively high quality litter, such as that from graminoids, by more lignified low quality litter, like shrub stems, may negatively affect decomposition rates and nutrient cycling in contrast to the positive effects of temperature, rendering the effects of warming on NEP and carbon storage uncertain [18, 24]. Furthermore, even if soil organic matter turnover and N mineralization increases with warming over the short term, there is potential for redistribution of nitrogen from soils (low C:N) to shrub biomass (high C:N) over the long term, resulting in net C storage [30]. It must be noted that warming-induced plant community composition shifts across the Arctic are not ubiquitous; in contrast to the tussock dominated tundra systems, plant response to warming in the low biomass Arctic heath system at Abisko was an increase in NPP without any significant changes in species composition [27].

There are numerous other factors besides shifts in plant community composition that further confound our ability to predict the long-term effects of global warming on NEP in high latitude regions. Warming is anticipated to increase permafrost depth, allowing microbes access to deeper stocks of organic material, but the degree and distribution of permafrost thawing remains uncertain. Climate models universally predict an increase in temperatures across the Arctic, but there is no consensus on whether summer precipitation will increase or decrease. Precipitation is important because soil moisture influences the responsiveness of decomposition to temperature [31]. Decreasing soil moisture, particularly in saturated wet meadow tundra habitats, would increase decomposition rates and N-mineralization as soils become oxygenated [32]. Another consideration is the effect of warming on seasonal nutrient and carbon

10

dynamics.   One effect of temperature on seasonal dynamics occurs through increased winter snow cover brought about directly through changes in precipitation or indirectly through shrub growth, which trap snow beneath them [33]. Snow insulates the ground and elevates soil temperatures, resulting in unfrozen water pockets that in turn stimulate microbial activity and enhance N-mineralization [34]. This phenomenon may provide a positive feedback for shrub growth as well, since higher nutrient availability following the spring thaw favors shrub growth [24, 35].

Summary and Conclusions

Ultimately, to predict the effects of warming on NEP we must better synthesize our knowledge of plant physiology, soil processes, temporal and spatial dynamics, and changes in climate patterns.   Across ecosystem types and biomes, research has shown that increases in temperature (and CO_2 concentration) cause increases in rates of N-mineralization (although there is variation and contradictory results). However, these rates are limited by other factors such as moisture availability and quality of the substrate. Clearly, such increases can potentially lead to increases in NPP and therefore NEP. There is, however, a maximum to these increases; ecosystems with temperatures pushed past the optimum temperature for mineralization will likely show decreases in NPP and NEP. With these changing conditions and changes in NPP, community structure is likely to change due to the relative competitive abilities of plants under different light, temperature, and nutrient conditions. Currently our predictive powers are limited: interactions among different soil and plant physiological processes are quite complex, and little is known about the outcomes of these interactions. N-mineralization is one process, which in nature does not act alone; mineralization rates will be impacted by other processes, and these effects may not be linear (and therefore difficult to predict). Weather patterns are predicted to become more variable and severe; drastic changes in amounts of available precipitation and disturbances will greatly impact ecosystem function and productivity, which will obviously change NPP and NEP. As always, there is a need for more research, both on the effects of interactions between processes, and on processes in more ecosystem types (for example, little work has currently been conducted in desert systems).

11

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12

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