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Biological Nitrification Inhibition Has Clear Impacts on Nitrification and Nitrogen Use Efficiency but Impacts on Nitrate Leaching in Real World Settings Remain Uncertain

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ABSTRACT

Nitrogen pollution is one of the major problems faced by modern agriculture. It accelerates global warming and contaminates water. Nitrate leaching is one of the main pathways by which nitrogen becomes pollution. Biological nitrification inhibition (BNI) is a process where certain plants release chemical compounds from their roots that help with suppressing nitrification. BNI has been widely studied and seen as an effective and sustainable way to reduce nitrification. However, the effects of BNI on nitrate leaching in realistic field conditions remain uncertain. This paper examined studies on the effects of BNI-producing plants on nitrification, nitrogen use efficiency, and nitrate leaching. Evidence was drawn from common BNI-producing plants, such as sorghum, rice, and plantain. Evidence shows that BNI can reduce nitrification, and several studies suggest it may improve NUE. However, only one study in this review directly measured nitrate leaching. Simulation evidence also suggests that the timing of BNI compound release may limit its effectiveness in real field conditions, where nitrification often occurs immediately after fertilization. More research in realistic field conditions will be needed to determine the actual effectiveness of BNI for reducing nitrate leaching.

KEYWORDS

Biological nitrification inhibition; Nitrate leaching; Nitrification; Nitrogen use efficiency; Sorgoleone; Sustainable agriculture

1. INTRODUCTION

Nitrogen fertilizers play a central role in modern agriculture. Nitrogen fertilizers can promote rapid vegetative growth, increase chlorophyll production, and boost crop yields and protein content. However, despite these benefits, nitrogen use efficiency (NUE) – the proportion of applied nitrogen that is actually taken up by the crop – remains low. Global NUE in cereal crops is estimated at only around 35%, meaning that more than half of the nitrogen applied as fertilizer is never used by the plant [1]. The nitrogen not taken up by crops is lost through several pathways, including nitrogen leaching and nitrous oxide production. These losses not only reduce NUE, but also cause environmental harm, such as greenhouse gas emissions and water pollution. Climate change will likely make these losses worse [2].

Among these nitrogen loss pathways, nitrogen leaching is a very significant one. Nitrogen leaching describes the process of losing nitrogen through water draining through soil, usually in the form of nitrate [3]. This movement carries the nitrogen out of the reach of plant roots, making it unavailable for uptake and causing it to enter the broader water system. Once in water systems, this excess nitrogen can lead to eutrophication, harm drinking water quality, and affect aquatic and marine biodiversity. Usually, this process occurs during irrigation and rainfall. Because irrigation and/or

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rainfall are unavoidable in agriculture, reducing nitrogen leaching is an important step toward more sustainable farming.

Currently, several approaches to reduce nitrogen leaching have been developed, including precision fertilizer application, controlled-release fertilizers, crop rotation strategies, and chemical nitrification inhibitors [4]. While these methods can be effective in certain cases, the NUE of agriculture has not changed much since 1980, calling for new approaches to reduce nitrate leaching and thus protect human and environmental health.

Using biological nitrification inhibition (BNI) has been proposed as a solution to the problem of nitrogen pollution and thus could be a more sustainable and effective way to reduce nitrogen leaching [5]. BNI is the process by which certain plants produce compounds released from roots that suppress soil nitrification, which in turn could reduce the amount of nitrate available for leaching. Many plants can naturally produce them. Therefore, compared to the other methods, BNI may require less human effort and lower costs.

However, despite having many purported benefits for reducing nitrogen leaching, the extent of how BNI producing plants can affect nitrogen leaching is still understudied. Therefore, this study aims to answer the question: How do BNI producing plants affect nitrogen leaching? To answer this, this study will compare how species with the BNI trait affect nitrate leaching compared to similar plants without the trait, appraise the strength of evidence for how BNI affects nitrate leaching, and determine which species and management strategies are most effective at reducing nitrate leaching.

2. BACKGROUND

Nitrogen is an essential element for all life as a part of proteins and nucleic acids. In agriculture, the amount of nitrogen plants contain strongly influences crop yields. However, not all kinds of nitrogen can be absorbed by plants. In the soil, nitrogen exists in several forms that are constantly being transformed by microorganisms in what is known as the soil nitrogen cycle. Plants take up nitrogen mainly in two inorganic (mineral) forms: ammonium (NH_4^+) and nitrate (NO_3^-). The source of these inorganic forms of nitrogen is either soil organic N, which must be mineralized to form ammonium, or synthetic fertilizers. Both forms can be taken up by plants, but they behave very differently in the soil. Because ammonium is positively charged, it binds to the surfaces of soil particles, especially clays, which tend to be negatively charged. Nitrate, which is negatively charged, does not bind in this way and instead stays dissolved in soil water, making it mobile and easily washed downward. In modern agriculture, nitrogen fertilizers provide an additional source of inorganic nitrogen. It can either directly be ammonium or nitrate, or be nitrogen forms that can be converted into ammonium rapidly, such as urea. These forms of fertilizer-based nitrogen enter the nitrogen cycle and go through processes such as nitrification, plant uptake, and nitrate leaching.

One important transformation in this cycle is nitrification. Nitrification is the process in which microorganisms convert ammonium into nitrate. The nitrification process happens with a pathway that includes two phases. The first phase is when ammonia-oxidizing bacteria (AOB) or ammonia-oxidizing archaea (AOA) oxidize ammonium into nitrite. Then, in the second phase, nitrite is further oxidized by nitrite-oxidizing bacteria to become nitrate. Because nitrate is mobile rather than bound to soil particles, it is the form of nitrogen most susceptible to losses. When rainfall or irrigation occurs, nitrate can move down with the water flow into groundwater or move laterally into surface waters. This process is called nitrogen leaching.

Biological nitrification inhibition (BNI) could be a useful strategy to reduce nitrogen losses, including nitrogen leaching. The process of BNI occurs due to chemical compounds produced by the roots of plants that help to reduce nitrification. More specifically, BNI compounds released from plant roots suppress the soil microorganisms that carry out nitrification, the ammonia-oxidizing bacteria (AOB) and archaea (AOA). The ammonia mono-oxygenase pathway (AMO) happens in both AOA and AOB.

Therefore, most BNI compounds, such as sorgoleone, brachialactone, and 1,9-decanediol work by blocking the AMO pathway. By slowing nitrification, BNI keeps more nitrogen in the soil as ammonium, which is held by soil particles and less likely to leach.

There are multiple plants that have evolved the ability to produce BNI compounds. For example, one of the most studied plants is sorghum [6], which can produce BNI compounds in its roots. Some other examples are rice and Brachiaria humidicola [7, 8]. To plants, BNI provides a mechanism to slow down the nitrification process, therefore reducing nitrogen loss. This process helps plants to be able to access more nitrogen as their nutrients.

BNI compounds in plants are regarded as having potential to reduce nitrification. They have potential to overcome limitations of synthetic nitrification inhibitors, as the latter can be short-lasting, costly, and may cause resistance to develop in nitrifier organisms. However, there are also technical limitations. BNI is restricted to cereals and other grasses; the ability is not present in legumes, which are a source of nitrogen in agricultural systems. To solve these limitations, proponents of BNI have argued for investments in breeding and genetic engineering, which could help the trait become present in other species [9]. In order to determine whether such investments could pay off, a better understanding of the current evidence supporting whether or not BNI could be a good tool for reducing nitrogen pollution is needed.

Several types of indicators could be used to estimate how BNI affects the potential for nitrate leaching. Nitrate leaching can be measured directly in field studies with lysimeters, tools that estimate the amount of drainage occurring in soil and the concentration of nitrate in the soil solution, but since these studies are costly and less common, other, indirect indicators can also be used. NUE is a measure of how much of the nitrogen applied as fertilizer was taken up by the crop. As an indicator of nitrate leaching, the higher NUE is, the less nitrogen is available for loss, which could mean less nitrate leaching. For example, comparing the NUE of plants with or without BNI, or in crops planted following or adjacent to species with BNI capacity, could indicate how efficient BNI is at reducing nitrification and thus how it might reduce nitrate leaching. Another possible indicator is comparing the amount of nitrification that occurs in soils with and without the presence of BNI compounds.

Overall, while BNI could help reduce nitrogen leaching, by reducing nitrification and thus the amount of nitrate available to leach, what is unclear is the extent to which empirical research supports findings about the actual outcome of interest – nitrate leaching – or whether literature mainly focuses on nitrogen cycle processes like nitrification or indirect outcomes like nitrogen use efficiency. It is also unclear the extent to which studies have been done in field settings that represent real agricultural conditions or have mainly been done in controlled environments like labs or greenhouses. By reviewing and critically appraising the evidence, this study aims to compile research on BNI and its relationship with nitrate leaching and synthesize findings to generate a common conclusion about the current state of knowledge.

3. METHODS

In December 2025, Web of Science was searched with keywords related to BNI and nitrogen cycling and nitrogen losses, including combinations of "biological nitrification inhibition" and "nitrate leach*", nitrification, "nitrogen use efficiency", and "nitrogen uptake". The searches returned ~405 papers, which were screened and narrowed to a pool of 22 articles for more thorough screening. From those abstracts, papers were selected in which there was an experiment (lab, greenhouse, or field) involving plants with or without BNI capacity and a measure of nitrification, nitrogen use efficiency, plant nitrogen uptake, or a related measure. From this set, eight papers were examined in depth in a qualitative review.

4. RESULTS

Several studies show that BNI compounds can affect soil nitrification and other nitrogen cycle processes (Table 1; [6], [7], [10]). For example, in both greenhouse and field research, genotypes of sorghum that had higher production of the BNI compound sorgoleone suppressed soil nitrifier activity and reduced soil nitrification and soil nitrous oxide emissions compared to genotypes that produced less sorgoleone, leading to better sorghum growth and biomass production [6]. More specifically, Gao et al. [6] included results coming from three experiments to directly compare high-sorgoleone and low-sorgoleone sorghum genetic stocks. They found that the high-sorgoleone stocks released more hydrophilic BNI compounds from their roots, more strongly suppressed soil nitrifier activity, and produced lower soil nitrification, lower soil nitrous oxide emissions, and lower leaf nitrate levels than the low-sorgoleone stocks, which in turn supported better growth and biomass. Therefore, these results suggest that BNI producing plants can help with the suppression of soil nitrifier activities, leading to a reduced rate of nitrification. Similar effects have been observed not only in sorghum but also in other crops such as rice. For example, Sun et al. [7] found that rice root exudates also contain BNI compounds, such as 1,9-decanediol. In laboratory tests, they showed that 1,9-decanediol can block the ammonia monooxygenase (AMO) pathway, an important step in the nitrification process. Therefore, it can reduce the conversion of ammonium into nitrate. The results of the experiment show that many rice varieties have a strong ability to inhibit nitrification. The highest one reached almost 50%. This provides direct evidence that BNI producing plants can regulate the nitrification process. The study also found that a rice variety's BNI ability and the amount of nitrification inhibitor it released were positively correlated with its ammonium uptake and its preference for ammonium. This indicates that BNI compounds not only influence nitrification, but also influence other nitrogen cycle processes, which improves NUE. Reyes-Escobar et al. [10] focused on BNI compounds combined with biochar. The experiment had 3 groups: One with only BNI, one with BNI and biochar, and one with nothing. Their results showed that the group with only BNI significantly reduced soil nitrate accumulation compared to the group with nothing, which indicates that BNI can have a strong nitrification inhibition ability. Also, the study found that the combination of biochar with BNI improved the effectiveness of these BNI compounds on nitrification inhibition by protecting them from degradation and maintaining a more sustained release in soil. As a result, soils containing the biochar–BNI complexes had a lower nitrate level over time compared to the ones with only BNI. Overall, the findings of Reyes-Escobar et al. [10] provide strong field-based evidence that BNI compounds can significantly inhibit the nitrification process and improve nitrogen use efficiency in agriculture.

Plants with greater capacity for BNI also tended to have higher NUE [8], [11], [12]. Karwat et al. [8] provides evidence that BNI capacity of plants can improve NUE. Their results showed that Brachiaria humidicola genotypes with stronger BNI activity can reduce soil nitrification at a higher rate and lower nitrate leaching losses more efficiently. They also used $\delta^{15}N$ values of plant biomass to infer the integrated impacts of BNI on nitrification, nitrate leaching, and plant nitrogen uptake, showing that lower plant $\delta^{15}N$ values corresponded to plants with more BNI — reflecting uptake from an ammonium pool that retained its original isotopic signature because little ^{15}N-depleted nitrate had been produced and lost. These results show that plants with greater BNI capacity can not only reduce nitrogen losses but also enhance nitrogen uptake, which leads to an increase in nitrogen use efficiency. Gao et al. [6] also supported that plants with BNI capacity tend to have a higher NUE. In this study, high-sorgoleone sorghum genotypes could suppress soil nitrification more effectively than low-sorgoleone genotypes. These results show that plants with a high BNI capacity can reduce nitrogen losses and therefore increase nitrogen uptake. Teutscherová et al. [12] found that high-BNI Urochloa humidicola genotypes increased nitrogen immobilization and caused a higher concentration of ammonium in the soil. This proves that it helped with keeping nitrogen within soil rather than losing it through nitrogen leaching or other ways. With less loss, the NUE will increase because there will

be more nitrogen in soil available for plants to take up. Therefore, the researchers concluded that high BNI producing plants can improve NUE by stabilizing nitrogen in soil for the plant to use.

Direct measurements of changes in nitrate leaching with BNI vs. non-BNI plants were rare; only one study from the literature search showed how a BNI-producing plant could potentially reduce nitrate leaching [11]. Carlton et al. [11] provides strong experimental evidence that plants with a greater BNI capacity can significantly reduce nitrogen losses. They collected intact soil monoliths from a field experiment with two different plant communities, one with perennial ryegrass and white clover, and the other with these species plus plantain forage. Plantain has been seen as a plant with potential BNI ability and can reduce nitrification [11], while the other species are not BNI-producing plants. They applied urine as a source of nitrogen and measured nitrate leaching losses over the course of a growing season. Their results showed that the group with plantain had significantly lower nitrogen losses. Compared to the other group, in December, the plantain group had 82% lower nitrogen leaching losses, and in February, losses were 74% lower. They attributed this reduction mainly to the release of BNI compounds by plantain, which suppressed the activity of AOB, which were measured directly using quantitative polymerase chain reaction (qPCR). As a result, soil with plantain had a higher ammonium concentration and a lower nitrate level. These results show that BNI-producing plants can significantly reduce nitrification and therefore decrease nitrogen losses.

Despite positive effects of BNI on reducing nitrate leaching and reducing nitrification rates, BNI effects on nitrate leaching may also be limited because of a mismatch in the timing of nitrate leaching and BNI-production. Hartman et al. [13] is a simulation study using an ecosystem process model to evaluate the effects of sorghum produced BNI on nitrogen losses. The study confirmed that BNI can reduce nitrification rates and nitrogen losses. However, it also stated that these reductions were minimal. From the study, Hartman et al. concluded that nitrification happens earlier than BNI being produced. This is because most nitrification happens immediately after fertilization, yet BNI starts to be produced after plants' root growth. This causes the nitrification inhibition process to be often too late, which explains why BNI can sometimes be less effective. These findings suggest that although most studies show that BNI can reduce nitrate leaching, its effectiveness in reality might not be as good as expected.

Table 1. Essential experimental papers involving plants with or without BNI capacity and a measure of nitrification, nitrogen use efficiency, plant nitrogen uptake, or a related measure reviewed in this study, and their type of study and key conclusions

Paper	What type of study?	What are key results and conclusions?
Hartman et al. [13]	Simulation study using an ecosystem process model	Nitrification happens earlier than BNI. This is because most nitrification happens immediately after fertilization, yet BNI starts to occur after plants' root growth. This causes the nitrification inhibition to be often too late, which explains why BNI can sometimes be less effective.
Carlton et al. [11]	Field experimental study using lysimeter and soil block	The group with plantain had significantly lower nitrogen losses. Compared to the other group, in December, the plantain group had 82% lower nitrogen leaching losses, and in February, losses were 74% lower.
Teutscherová et al. [12]	Experimental study using two soil samples with different genotypes of U. humidicola	superior short-term microbial ^{15}N immobilization upon N fertilization in soil with high-BNI genotype than with low BNI capacity.
Karwat et al. [8]	Experimental paper with 3 experiments, one of them is long term.	high BNI activity in a plant decreases its $\delta^{15}N$, which therefore decreases the nitrogen losses and increases NUE
Reyes-Escobar et al. [10]	Experimental paper with laboratory and field experiments	The biochar used as matrix to adsorb natural compounds allowed increasing the efficiency of natural extracts; generating a biochar-BNI complex that prolonged the nitrification inhibition at field condition, and consequently could increase the N use efficiency.
Gao et al. [6]	Experimental paper with 3 experiments.	High sorgoleone producing (HS) genetic-stocks showed higher hydrophilic-BNI release from roots and more effectively suppressed soil nitrifier activity, reduced soil-nitrification, soil-N2O emissions, reduced leaf nitrate levels have led to better growth and biomass production compared to LS genetic-stocks.
Sun et al. [7]	Experimental paper on rice root exudates.	BNI and the exudation quantity of nitrification inhibitors in rice are positively correlated with rice ammonium uptake and preference

5. DISCUSSION AND CONCLUSIONS

This review shows that few studies directly measure nitrate leaching in the context of BNI. However, there is clear evidence of the potential to reduce nitrate leaching based on the effects of BNI on nitrification and NUE. There is a clear effect across multiple species that BNI reduces nitrification. Studies involving sorghum, rice, and plantain all showed that BNI producing plants can suppress nitrification in several ways, such as inhibiting the activity of nitrification related microorganisms. Also, several studies suggest that BNI may improve NUE by slowing nitrification and increasing ammonium uptake.

However, there are also uncertainties that were not directly answered by the research papers found in this review. The most important one is the uncertainty about the actual effectiveness in real agricultural settings. For example, BNI compounds may not be released at sufficient concentrations

at the time when significant amounts of nitrification are occurring, such as following fertilizer applications, which is also when nitrate leaching is predominantly occurring. This will cause a reduction of its effect in suppressing nitrate leaching. These findings suggest that the actual effects of BNI on nitrification are affected by other environmental factors, so its effectiveness in real agricultural settings still remains unclear. To answer these open questions, more information is needed. For example: how long do BNI compounds persist in the soil and remain effective at reducing nitrification after BNI-producing plants are no longer there? How quickly are they degraded? What conditions allow them to persist or not? Future research should focus on long-term field experiments conducted under realistic agricultural conditions. For example, a field experiment could compare two groups grown under natural conditions: one planted with BNI-producing plants and one planted without them. By growing the two groups over several growing seasons and measuring nitrogen leaching from each, researchers could directly test how BNI affects leaching in the field. This would provide more direct information regarding the relationship between BNI and nitrogen leaching.

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