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Review

Suppression of soil nitrification by plants

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ABSTRACT

Nitrification, the biological oxidation of ammonium to nitrate, weakens the soil's ability to retain N and facilitates N-losses from production agriculture through nitrate-leaching and denitrification. This process has a profound influence on what form of mineral-N is absorbed, used by plants, and retained in the soil, or lost to the environment, which in turn affects N-cycling, N-use efficiency (NUE) and ecosystem health and services. As reactive-N is often the most limiting in natural ecosystems, plants have acquired a range of mechanisms that suppress soil-nitrifier activity to limit N-losses *via* N-leaching and denitrification. Plants' ability to produce and release nitrification inhibitors from roots and suppress soil-nitrifier activity is termed 'biological nitrification inhibition' (BNI). With recent developments in methodology for *in-situ* measurement of nitrification inhibition, it is now possible to characterize BNI function in plants. This review assesses the current status of our understanding of the production and release of biological nitrification inhibitors (BNIs) and their potential in improving NUE in agriculture. A suite of genetic, soil and environmental factors regulate BNI activity in plants. BNI-function can be genetically exploited to improve the BNI-capacity of major food- and feed-crops to develop next-generation production systems with reduced nitrification and N_2O emission rates to benefit both agriculture and the environment. The feasibility of such an approach is discussed based on the progresses made.

Contents

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1. Introduction

Nitrification, a critical aerobic process that evolved about 2.5 billion years ago, was considered a relatively minor component of the N-cycle until about 50 years ago, when synthetic fertilizer applications in agriculture became widespread [1]. Two groups of soil microorganisms, ammonia-oxidizing bacteria (mainly *Nitrosomonas* spp. and *Nitrosospira* spp.) and ammonia-oxidizing archaea, are largely responsible for the biological oxidation of NH_4^+ to NO_3^- [2,3]. Cationic ammonium is electrostatically held by negatively charged clay surfaces and functional groups of soil organic matter (SOM), and often remains bound to the soil. In contrast, anionic NO_3^- does not bind to the soil and is prone to leaching from the root zone. Several heterotrophic soil bacteria denitrify NO_3^- under anaerobic or partially anaerobic conditions and produce nitrous oxide (N_2O), a colorless gas known as 'laughing gas'. However, N_2O emissions from agricultural systems is no laughing matter as N_2O is a powerful greenhouse gas with global warming potential 300 times greater than that of CO_2, and is the third most important contributor to global warming [4–6]. Nearly 70% of global N_2O emissions come from agricultural ecosystems, where nitrification and denitrification are the major biological processes responsible for its production [7–9]. N_2O levels in the atmosphere are increasing at an alarming rate and are expected to quadruple by 2050 [10–13], unless measures are taken to reduce such emissions.

1.1. Nitrification: A biological process of critical importance for the sustainability of agricultural systems with implications for climate change

Nitrogen fixation, SOM mineralization, immobilization, ammonification, nitrification, and denitrification are the major processes/pathways of the N-cycle in soils (Fig. 1). Nitrification has a relatively minor role in undisturbed ecosystems, whether temperate or tropical as they retain large amounts of N and minimize N-leakages from these systems. Nitrification in some natural systems seems severely restricted, but the underlying mechanism(s) governing N-flow is still poorly understood [14,15]. For example, polyphenols released from leaf litter in certain pine forests can form complexes with dissolved organic N [16]. These organic-N-polyphenol complexes resist soil mineralization, but are absorbed by ecto-mycorrhizae colonizing pine root systems where they are mineralized and supplied to the pine host, thereby tightly regulating N-flow within such ecosystems [17,18]. A range of N conserving mechanisms have evolved in natural ecosystems including direct uptake of organic N by plants (by short-circuiting mineralization) and suppression of nitrification. These mechanisms essentially close the N cycle and facilitate soil-N buildup [18–23].

Unlike most undisturbed ecosystems, modern intensified agricultural systems typically have open N cycles, and have become extremely leaky and inherently inefficient [22,24–28]. While less than 10% of total N undergoes nitrification in undisturbed ecosystems [29], over 95% of total N flows through the nitrification–denitrification pathway in modern production systems [30]. High-nitrifying soil environments in modern production systems are largely responsible for low-N recovery and low-NUE [30,31]. The intensification of agricultural production systems and the decoupling of crop production from livestock operations have disrupted nutrient cycling, depleted SOM stocks, altered soil physical and chemical properties, and driven major shifts in soil microbial activity, resulting in the creation of present high-nitrifying soil environments where NO_3^- accounts for >95% of crop N uptake [10,30–33]. In addition, soil microbial biomass and its nutrient-cycle regulation power has been severely weakened in modern agricultural systems, leading to de-synchrony between soil-N mineralization and plant N demand [34].

Soil nitrification rates have indeed increased several-fold in modern production systems compared to traditional agricultural systems [31,35–37]. Our studies with Alfisols managed under traditional farming practices, i.e. rainfed cropping [Alfisol-rainfed – only single crop is grown during rainy season with limited fertilizer inputs and rotating periodically with legumes] or under irrigated conditions [Alfisol-irrigated – Full irrigation with liberal fertilizer regimes to raise two to three crops per year] over 30 years showed a 5-fold increase in soil nitrification rates in Alfisol-irrigated fields compared to Alfisol-rainfed fields (Subbarao and Sahrawat, Unpublished research, 2013), reinforcing that intensification of agricultural practices resulting in hyper soil-nitrifier activity and accelerated nitrification rates. Despite all the advances in agronomic management of N applications in production agriculture, nearly 70% of N-fertilizer applied to production systems is consequently lost through NO_3^- leaching and gaseous N-emissions (N_2O, NO and N_2) [28,38,39]. The NUE (weight of cereal grain produced per weight of N fertilizer applied) in cereal production systems has accordingly declined from about 80 in 1960s to 20 at present [32], suggesting diminishing returns from N-fertilizer applications. Synthetic nitrification inhibitors were developed in the 1960's, but they have not been widely adopted due to inconsistent performance and lack of economic viability for their use in production agriculture [40]. Urea is the most commonly used nitrogen fertilizer in production agriculture, hydrolyzes (within 24 h from application to the soil by enzyme 'urease' produced by soil bacteria) and releases ammonia, and the nitrogen becomes available to the plant. Urease inhibitors such as NBPT [N-(n-butyl) thiophosphoric triamide, also known as 'agrotarin'] is available and extensively tested in production systems, but has not been adopted due to reasons similar for nitrification inhibitors [30,31,40]. Fertilizer-N use is projected to double and is expected to reach 300 Tg N y^{-1} by 2050 [11,39]. Nitrogen lost from NO_3^- leaching is likely to reach 61.5 Tg N y^{-1} [11], while N_2O emissions are projected to reach 17 Tg N y^{-1} [10,11,41] unless measures are taken to reduce these emissions. These projections suggest that N pollution is reaching a tipping point and that urgent action is needed to improve NUE in production agriculture and minimize N leakages [42].

2. Biological nitrification inhibition (BNI)

2.1. The BNI concept

The ability of certain plant roots to produce and release nitrification inhibitors to suppress soil-nitrifier activity is termed 'biological nitrification inhibition' (BNI). As nitrification is the most important process determining N-cycling efficiency (i.e. proportion of N retained in the ecosystem during a complete cycling loop), restricting nitrification will minimize N-leakage and facilitate N-flow through NH_4^+ assimilation pathways [30]. Most plants and microbes have the ability to utilize NH_4^+ or NO_3^- as mineral-N source [43]; yet, few studies have integrated plant utilization of these N-forms on ecosystem functioning [44]. Suppressing soil-nitrifier activity thus, should not limit the availability of inorganic-N for plant growth or soil microbial activity. Moreover,