Nitrogen management in grasslands and forage-based production systems – Role of biological nitrification inhibition (BNI)

G.V. SUBBARAO¹, I.M. RAO², K. NAKAHARA¹, Y. ANDO¹, K.L. SAHRAWAT³, T. TESFAMARIAM¹, J.C. LATA³, S. BOUDSOQC², J.W. MILES², M. ISHITANI² AND M. PETERS²

¹Japan International Research Center for Agricultural Sciences (JIRCAS), Ohwashi, Tsukuba, Ibaraki, Japan. www.jircas.affrc.go.jp
²Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia. www.ciat.cgiar.org
³International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, Andhra Pradesh, India. www.jircas.affrc.go.jp
⁴UPMC-Bioemco, École Normale Supérieure, Paris, France. www.biologie.ens.fr/bioemco
⁵INRA, UMR Eco&Soils, Montpellier SupAgro-CIRAD-INRA-IRD, Montpellier, France. www.5.montpellier.inra.fr/ecosols_eng

Keywords: Brachiaria grasses, grassland productivity, global warming, nitrogen losses, nitrous oxide emissions, nitrogen-use efficiency.

Abstract

Nitrogen (N), the most critical and essential nutrient for plant growth, largely determines the productivity in both extensive and intensive grassland systems. Nitrification and denitrification processes in the soil are the primary drivers of generating reactive N (NO₃⁻, N₂O and NO), largely responsible for N loss and degradation of grasslands. Suppressing nitrification can thus facilitate retention of soil N to sustain long-term productivity of grasslands and forage-based production systems. Certain plants can suppress soil nitrification by releasing inhibitors from roots, a phenomenon termed ‘biological nitrification inhibition’ (BNI). Recent methodological developments [e.g. bioluminescence assay to detect biological nitrification inhibitors (BNIs) from plant-root systems] led to significant advances in our ability to quantify and characterize BNI function in pasture grasses. Among grass pastures, BNI capacity is strongest in low-N environment grasses such as Brachiaria humidicola and weakest in high-N environment grasses such as Italian ryegrass (Lolium perenne) and B. brizantha. The chemical identity of some of the BNIs produced in plant tissues and released from roots has now been established and their mode of inhibitory action determined on nitrifying Nitrosomonas bacteria. Synthesis and release of BNIs is a highly regulated and localized process, triggered by the presence of NH₄⁺ in the rhizosphere, which facilitates release of BNIs close to soil-nitrifier sites. Substantial genotypic variation is found for BNI capacity in B. humidicola, which opens the way for its genetic manipulation. Field studies suggest that Brachiaria grasses suppress nitrification and N₂O emissions from soil. The potential for exploiting BNI function (from a genetic improvement and a system perspective) to develop production systems, that are low-nitrifying, low N₂O-emitting, economically efficient and ecologically sustainable, is discussed.

Resumen

El nitrógeno (N), el nutrient más crítico y esencial para el crecimiento de las plantas, es determinante para la productividad de las pasturas, tanto de tipo extensivo como intensivo. Los procesos de nitrificación y denitrificación en el suelo son los principales responsables de la generación de formas de N reactiva (NO₃⁻, N₂O y NO) y, como consecuencia, de la pérdida de N y la degradación de las pasturas. Por tanto, la supresión de la nitrificación puede facilitar la retención de N en el suelo necesario para mantener, a largo plazo, la productividad de pastizales y sistemas de producción basados en forrajes. Algunas plantas pueden suprimir la nitrificación en el suelo mediante la liberación de sustancias inhibidoras desde sus raíces, un fenómeno llamado ‘inhibición biológica de la nitrificación’ (BNI, por su sigla en

Correspondence: G.V. Subbarao, Japan International Research Center for Agricultural Sciences, 1-1 Ohwashi, Tsukuba, Ibaraki 305-8686, Japan.
E-mail: Subbarao@jircas.affrc.go.jp

www.tropicalgrasslands.info
Introducción

Las pastizales son el mayor usuario de tierra, ocupando 3.2 billones de hectáreas de las 4.9 billones de hectáreas de tierra agrícola mundial (Steinffeld et al. 2006). Además, una proporción significativa de la tierra cultivada (0.5 billones de hectáreas) se utiliza para la producción de pastos y cultivos de granos (e.g. falso trigo, centeno, maíz y soja) para apoyar la producción ganadera intensiva (Steinffeld y Wassenaar 2007; Herrero et al. 2010, 2011). La mineralización de materia orgánica en el suelo (MOS) es el principal N en el sistema de pastizales. Para pastos intensivos, el N aportado por fertilizantes puede llegar a 200-600 kg/N/ha/año, con solo 30% recuperada por el ganado y el animal entrando en el sistema, mientras que el 70% restante se pierde en formas reactivas de N (i.e. NO₃⁻, NO₂⁻, NO) (Galloway et al. 2009). La eficiencia de uso del N (NUE) en sistemas de pastizales (cereales o lúpulo) se puede recoger de 5 a 10%, dependiendo de si el ganado o el cereales es el sistema de producción (van der Hoek 1998). Los animales de pastoreo tienden a retener aproximadamente el 5% del N ingerido (excepto el N que se consuma en los excrementos) en sus cuerpos y son eliminados en forma de orina, que contribuye al efecto de invernadero del dióxido de nitrógeno (Hahn y Verchot 2000; Zhu et al. 2013). La nitrificación y la denitrificación son los principales factores para la emisión de N₂O, el gas de efecto invernadero más poderoso que CO₂ (Hahn y Crutzen 1982). Como un catión, NH₄⁺ se une a las superficies de minerales de canto de la SOM, lo que reduce el N₂O⁺ por leaching. En contraste, el N₂O⁺ no se une al suelo y se expulsa al suelo de la raíz. 

N pérdidas en sistemas agrícolas afectan el entorno global y contribuyen significativamente a calentamiento global

Debido al desarrollo de sistemas que nitrifican pastizales (donde NO₃⁻ representa >95% del N ingerido), la pastura intensiva y la producción de alimentos a partir de grano pasto, pueden llegar a ser extremadamente " leaks " de forma inherente (Subbarao et al. 2012); cerca de 70% del 150 Mt de N fertilizante aplicado anualmente a los sistemas agrícolas a escala global se pierden en N₂O, NO y NO₃⁻ (Tilman et al. 2001 y 2007); y NO₃⁻ producido anualmente por pastizales. Según el modelo de pastizales (Worthington y Danks 1992), la mayor parte del N se pierde a través de la nitrificación y la pérdida de gaseosa N (NO₂⁻, NO y N₂), causando daño al medio ambiente y pérdida económica (Tilman et al. 2002; Steinffeld y Wassenaar 2007; Herrero et al. 2011; Subbarao et al. 2013).

Las pruebas recientemente desarrolladas, por ej., muestras de bioluminiscencia para detectar inhibidores biológicos de la nitrificación (BNI), han permitido mejorar la posibilidad de cuantificar y caracterizar la función de los BNIs en gramíneas forrajeras. Dentro de las gramíneas, tiene la mayor capacidad de BNI; se ha encontrado en especies de pastos bajos en N como Brachiaria humidicola, y la más baja en N para especies de pastos del género Lolium perenne y B. brizantha. Actualmente se conoce la identidad química de algunos BNIs producidos en tejidos de plantas y liberados en las raíces, igualmente su modo de acción inhibitory sobre la nitrificación de las bacterias Nitrosomonas. La síntesis y liberación de los BNIs es un proceso altamente regulado y localizado, estimulado por la presencia de NH₄⁺ en la rizósfera, lo que facilita la liberación de los BNIs cerca de los sitios de nitrificación en el suelo. En B. humidicola se ha encontrado una amplia variación genotípica en la capacidad de BNI, lo que abre un camino para su manipulación genética. Estudios a nivel de campo sugieren que las gramíneas del género Brachiaria reducen la nitrificación y la emisión de N₂O del suelo. Se discute el potencial de explotar la función de BNI, desde la perspectiva de mejoramiento genético y de sistema, para desarrollar sistemas de producción con baja nitrificación y baja emisión de N₂O, y que sean económicamente eficientes y ecológicamente sostenibles.

Nitrificación abre varias vías para la pérdida de N y debilita la capacidad de retención del suelo en sistemas de pastizales

La nitrificación, la oxidación biológica de NH₄⁺ a NO₃⁻, abre varias vías para la producción de N₂O y NO, generadas a través de nitrifier-denitrification o denitrificación heterotrofa (Davidson y Verchot 2000; Zhu et al. 2013). La nitrificación y la denitrificación son los principales factores para las emisiones de N₂O, el gas de efecto invernadero más poderoso que CO₂ (Hahn y Crutzen 1982). Como un cation, NH₄⁺ se une a las superficies de minerales de canto de la SOM, que reduce el N₂O⁺ por leaching. En contraste, el N₂O⁺ no se une al suelo y es expulsado fuera del rango de raíz. El N fertilizer enters pastures principalmente como N fertilizers (in intensive systems) or is derived from SOM-mineralization (in extensive systems) or hydrolysis of
urea N from urine excreted from grazing animals, where NH$_4^+$ is produced either through SOM-mineralization-ammonification or urea hydrolysis, as the first product of inorganic N. Heterotrophic soil microorganisms convert NH$_4^+$ into microbial N, i.e. immobilization, and pasture roots and nitrifying bacteria compete for this NH$_4^+$ as an N source (Figure 1). Nitrogen flow into microbial immobilization or plant uptake is desirable. However, N flows into nitrification pathways generate reactive N forms (NO$_3^-$, N$_2$O and NO), that are not retained by the soil, and are lost to the environment, leading to the degradation of grassland systems.

Restricting the N flow to the nitrification pathway by inhibiting soil nitrifier activity facilitates NH$_4^+$ uptake by plants; this also allows N flow into the microbial pool (Hodge et al. 2000). The immobilization and mineralization loop of the N cycle dominates to keep soil N cycling within the system, and creates a slow-release N pool to sustain grassland productivity in such systems (Figure 1). Most plants have the ability to use NH$_4^+$ or NO$_3^-$ as their N source (Haynes and Goh 1978; Boudsocq et al. 2012). Reducing nitrification rates in agricultural systems does not alter the intrinsic ability of plants to absorb N, but does increase retention time of N in the root zone as NH$_4^+$, which is less mobile and less energetically costly for uptake and assimilation than NO$_3^-$, providing additional time for plants to absorb N. Many of the advantages, associated with inhibiting nitrification to improve productivity and NUE of intensive grassland systems and feed-grain production systems, have been demonstrated using chemical nitrification inhibitors (Subbarao et al. 2006a; Dennis et al. 2012).

**Biological nitrification inhibition (BNI)**

*The BNI concept*

The ability to produce and release nitrification inhibitors from plant roots to suppress soil nitrifier activity is termed ‘biological nitrification inhibition’ (Figure 1).

![Biological Nitrification Inhibition (BNI)](image)

**Figure 1.** Schematic representation of the biological nitrification inhibition (BNI) interfaces with the N cycle. The BNI exuded by roots inhibits nitrification that converts NH$_4^+$ to NO$_3^-$ in ecosystems with large amounts of BNI (e.g. brachialactone), such as in *Brachiaria* grasses, the flow of N from NH$_4^+$ to NO$_3^-$, via NO$_2^-$, is restricted, and it is NH$_4^+$ and microbial N rather than NO$_3^-$ that accumulates in the soil. In systems with little or no BNI, such as modern agricultural systems, nitrification occurs rapidly, leaving little time for plant roots to absorb NO$_3^-$; thus NO$_3^-$ is lost from the system through denitrification and leaching; (adapted from Subbarao et al. 2012).
Nitrification largely determines the N-cycling efficiency (i.e. proportion of N that stays in the ecosystem during a complete N-cycling loop); the BNI function has the potential to improve agronomic NUE (Subbarao et al. 2012; 2013b). Recent modeling studies coupled with in-situ measures suggest that tropical grasses, which inhibit nitrification, exhibit a 2-fold greater productivity than those that lack such ability (Lata 1999; Boudsocq et al. 2012).

**BNI characterization in pasture grasses**

Recent methodological advances have facilitated the detection and quantification of nitrification inhibitors from intact plant roots using a recombinant *Nitrosomonas* construct (Subbarao et al. 2006b). Nitrification inhibitors released from roots measured as ‘BNI activity’, are expressed in ATU (allylthiourea unit) and this ability is termed BNI capacity (Subbarao et al. 2007b). Root systems of tropical pasture grasses showed a wide range in BNI capacity. *Brachiaria humidicola*, a grass adapted to low-N production environments of South American savannas, showed the greatest BNI capacity (range from 15 to 50 ATU/g root dry wt/d) (Subbarao et al. 2007b). By contrast, *Lolium perenne*, *B. brizantha* and *Panicum maximum*, that are adapted to high-N environments, showed the least BNI capacity (2–5 ATU/g root dry wt/d) (Figure 2). Sorghum is the only field crop that showed a significant BNI capacity (5–10 ATU/g root dry wt/d) among the cereal and legume crops evaluated (Subbarao et al. 2007b; 2013b).

The BNI capacity of root systems arises from their ability to release 2 categories of BNIs: (a) hydrophobic BNIs; and (b) hydrophilic BNIs. These BNI fractions differ in their mobility in the soil and their solubility in water; the hydrophobic BNIs may remain close to the root as they could be strongly adsorbed on the soil particles, increasing their persistence. The mobility of the hydrophobic BNIs is via diffusion across a concentration gradient; thus this form is likely to be confined to the rhizosphere (Raynaud 2010; Subbarao et al. 2013a). In contrast, the hydrophilic BNIs may move further from the point of release due to their solubility in water, and this may improve their capacity to control nitrification beyond the rhizosphere (Subbarao et al. 2013a). The relative contributions of hydrophobic BNIs and hydrophilic BNIs to the BNI capacity may differ among plant species. For *Brachiaria* grasses, both fractions make equal contributions to the BNI capacity; for sorghum, the hydrophobic BNIs play a dominant role in determining the BNI capacity, whereas in wheat, hydrophilic BNIs determine the root system’s inhibitory capacity (G.V. Subbarao and T. Tsehaye, unpublished data).

For *Brachiaria* spp., the amount of inhibitors released from root systems could be substantial. Based on the BNI activity release rates observed (17–50 ATU/g root dry wt/d) and assuming the average live root biomass of a long-term grass pasture at 1.5 t/ha (Rao 1998), it was estimated that BNI activity of 2.6 x 10^9–7.5 x 10^9 ATU/ha/d is potentially released (Subbarao et al. 2009a). This amounts to an inhibitory potential equivalent to that achieved by the application of 6.2–18.0 kg of nitrpyrin/ha/yr, which is large enough to have a significant influence on the functioning of the nitrifier population and nitrification rates in the soil. Field studies indicate a 90% decline in soil ammonium oxidation rates due to extremely small populations of nitrifiers (ammonia-oxidizing bacteria, AOB, and archaea, AOA, determined as amoA genes) within 3 years of establishment of *B. humidicola* (Figure 3). Nitrous oxide emissions were suppressed by >90% in field plots of *B. humidicola* compared with soybean, which lacks BNI capacity in its root systems (Subbarao et al. 2009a).

**Chemical identities of BNIs and their mode of inhibitory action**

The major nitrification inhibitor released from the roots of *B. humidicola* is a cyclic diterpene, named ‘brachialactone’ (Subbarao et al. 2009a). This compound has a dicycloprene (a,d) cyclooctane skeleton (5-8-5 ring system) with a γ-lactone ring bridging one of the 5-membered rings and the 8-membered ring (Figure 4).
the HAO enzymatic pathway. About 60–90% of the inhibitory activity released from the roots of *B. humidicola* is due to brachialactone. Release of brachialactone is a regulated plant function, triggered and sustained by the availability of NH$_4^+$ in the root environment (Subbarao et al. 2007a; 2009a). Brachialactone release is restricted to those roots that are directly exposed to NH$_4^+$, and not the entire root system, suggesting a localized release response (Subbarao et al. 2009a).

**Genetic improvement of BNI capacity of pasture grasses**

Significant genetic variability (ranging from 7.1 to 46.3 ATU/g root dry wt/d) exists for BNI capacity in *B. humidicola*, indicating a significant potential for genetic manipulation of BNI capacity by conventional plant breeding (Subbarao et al. 2007b; 2009b). Recent findings suggest substantial genetic variability for brachialactone release among *B. humidicola* germplasm accessions, nearly 10-fold differences, suggesting the potential for breeding *Brachiaria* genotypes with high brachialactone capacity. Efforts are underway to develop molecular markers for brachialactone release capacity in *Brachiaria* spp.

**Perspectives**

Sustainable intensification of grasslands and feed-crop production systems is needed to meet the global demands for meat and milk, particularly in developing countries. As the demand for meat and milk is expected to double by 2050 (Herrero et al. 2009), there will be further efforts to intensify grasslands and feed-crop-based systems. Most increases in productivity are, however, achieved through massive inputs of industrially produced N fertilizer. Nearly 70% of the 150 Mt N applied to global agricultural systems is lost, largely due to the high nitrifying nature of soil environments (Tilman et al. 2001; Subbarao et al. 2013b). As nitrification and denitrification are the primary biological drivers of NO$_3^-$, N$_2$O and NO production (i.e. reactive N forms largely responsible for environmental pollution), suppressing nitrification is critical to reduce N losses and to retain soil N for longer periods in the grassland systems. The BNI function in forage grasses and feed-crops such as sorghum can be exploited using genetic and crop- and/or production system-based management to design low-nitrifying agronomic environments to improve NUE. In addition, the high BNI capacity in *Brachiaria* spp. can be utilized for the benefit of feed-crop systems such as maize, that receive most of the N fertilization but do not have inherent BNI capacity in their root systems. This

---

**Figure 3.** Soil ammonium oxidation rates in field plots planted to tropical pasture grasses (differing in BNI capacity) and soybean (lacking BNI capacity in roots); grasses: covering 3 years from establishment (September 2004–November 2007), soybean: 6 seasons of cultivation over 3 years. Con – control plots (plant free); Soy – soybean; Pm – Panicum maximum; BMul – Brachiaria hybrid cv. Mulato (apomictic hybrid that contains germplasm from *B. ruziziensis*, *B. decumbens* and *B. brizantha*, but NOT from *B. humidicola*); Bh-679 – *B. humidicola* CIAT 679 (standard cultivar Tully); Bh-16888 – *B. humidicola* accession CIAT 16888. Values are means ± s.e. of 3 replications; (adapted from Subbarao et al. 2009a).

**Figure 4.** Chemical structure of brachialactone, the major nitrification inhibitor isolated from root exudates of *Brachiaria humidicola*; (from Subbarao et al. 2009a).
could be achieved by integrating _Brachiaria_ pastures with high BNI capacity and maize production using agro-pastoral systems (Subbarao et al. 2013b). In grazed grassland systems, most of the plant protein N is excreted by livestock (through urine) and thus returned to the soil. Grassland systems that retain N excreted by livestock are likely to maintain/sustain productivity over time. The BNI function could be most effective in controlling nitrification in grassland systems if genetically manipulated, either by conventional plant breeding or by genetic engineering. Most grasses develop extensive root systems and are perennial (Rao et al. 2011); if this is combined with high BNI capacity, these grassland systems can potentially suppress soil nitrifier activity to retain and use N more efficiently than at present. As grazing animals usually deposit urine and dung in a random, patchy manner, soil N is redistributed. The patchy distribution makes it difficult to control nitrification using synthetic nitrification inhibitors. The BNI function in forage grasses could be more effective in controlling nitrification to sustain system productivity and to protect these systems from degradation.

**Acknowledgments**

The research on BNI at CIAT is supported by BMZ-GIZ, Germany; MADR, Colombia; MOFA, Japan; and Sida, Sweden.

**References**

Boudsocq S; Nibovet A; Lata JC; Raynaud X; Loeuille N; Mathieu J; Blouin M; Abbadie L; Barot S. 2012. Plant preference for ammonium versus nitrate: A neglected determinant of ecosystem functioning? American Naturalist 180:60−69.


Dennis SJ; Cameron KC; Di HJ; Moir JL; Staples V; Sills P; Richards KG. 2012. Reducing nitrate losses from grazed grassland in Ireland using a nitrification inhibitor (DCD). Biology and the Environment 112B:79−89.

Galloway JN; Townsend AR; Erisman JW; Bekunda M; Zai Z; Freney JR; Martinelli LA; Seitzinger SP; Sutton MA. 2008. Transformation of the nitrogen cycle: Recent trends, questions and potential solutions. Science 320:889−892.

Galloway JN; Dentener F; Burke M; Dumont E; Bouwman AF; Kohn RA; Mooney HA; Seitzinger S; Kroeze C. 2009. The impact of animal production systems on the nitrogen cycle. In: Steinfeld H; Mooney HA; Schneider F; Neville LE, eds. Livestock in a changing landscape. Vol. 1. Island Press, Washington, DC, USA. p. 83−95.


Herrero M; Thornton PK; Gerber P; Reid RS. 2009. Livestock, livelihoods and the environment: Understanding the trade-offs. Current Opinion in Environmental Sustainability 1:111−120.

Herrero M; Thornton PK; Notenbaert AM; Wood S; Msangi S; Freeman HA; Bossio D; Dixon J; Peters M; van de Steeg J; Lynam J; Parthasarathy Rao P; Macmillan S; Gerard B; McDermott J; Seré C; Rosegrant M. 2010. Smart investments in sustainable food production: Revisiting mixed crop-livestock systems. Science 327:822−825.

Herrero M; Gerber P; Vellinga T; Garnett T; Leip A; Opiro C; Westhoek HJ; Thornton PK; Olesen J; Hutchings N; Montgomery H; Soussana JF; Steinfeld H; McAllister TA. 2011. Livestock and greenhouse gas emissions: The importance of getting the numbers right. Animal Feed Science and Technology 166:779−782.

Hodge A; Robinson D; Fitter AH. 2000. Are microorganisms more effective than plants at competing for nitrogen? Trends in Plant Science 5:304−308.


Rao IM; Miles J; Wenzl P; Louw-Gaume A; Cardoso JA; Ricarte J; Polania J; Rincón J; Hoyos V; Frossard E; Wagatsuma T; Horst W. 2011. Mechanisms of adaptation of brachiaria grasses to abiotic stress factors in the tropics. Plenary paper presented at the III International Symposium on Forage Breeding, 7−11 November 2011. Embrapa (Empresa Brasileira de Pesquisa Agropecuária), Bonito, MS, Brazil. p. 361−383.


Steinfeld H; Gerber P; Wassenaar T; Castel V; Rosales M; de Haan C. 2006. Livestock’s long shadow: Environmental issues and options. FAO (Food and Agriculture Organization of the United Nations), Rome, Italy. [http://www.fao.org/docrep/010/a0701e/a0701e00.HTM](http://www.fao.org/docrep/010/a0701e/a0701e00.HTM).


[www.tropicalgrasslands.info](http://www.tropicalgrasslands.info)
Subbarao GV; Ito O; Sahrawat KL; Berry WL; Nakahara K; Ishikawa T; Watanabe T; Suenaga K; Rondon M; Rao IM. 2006a. Scope and strategies for regulation of nitrification in agricultural systems – Challenges and opportunities. Critical Reviews in Plant Sciences 25:303–335.


Subbarao GV; Wang HY; Ito O; Nakahara K; Berry WL. 2007a. NH$_4^+$ triggers the synthesis and release of biological nitrification inhibition compounds in Brachiaria humidicola roots. Plant and Soil 290:245–257.

Subbarao GV; Rondon M; Ito O; Ishikawa T; Rao IM; Nakahara K; Lascano C; Berry WL. 2007b. Biological nitrification inhibition (BNI) – Is it a widespread phenomenon? Plant and Soil 294:5–18.

Subbarao GV; Nakahara K; Hurtado MP; Ono H; Moreta DE; Salcedo AF; Yoshihashi AT; Ishikawa T; Ishitani M; Ohnishi-Kameyama M; Yoshida M; Rondon M; Rao IM; Lascano CE; Berry WL; Ito O. 2009a. Evidence for biological nitrification inhibition in Brachiaria pastures. Proceedings of the National Academy of Sciences of the United States of America 106:17302–17307.

Subbarao GV; Kishii M; Nakahara K; Ishikawa T; Ban T; Tsujimoto H; George TS; Berry WL; Hash CT; Ito O. 2009b. Biological nitrification inhibition (BNI) – Is there potential for genetic interventions in the Triticeae? Breeding Science 59:529–545.

Subbarao GV; Sahrawat KL; Nakahara K; Ishikawa T; Kishii M; Rao IM; Hash CT; George TS; Srinivasa Rao P; Nardi P; Bonnett D; Berry W; Suenaga K; Lata JC. 2012. Biological nitrification inhibition – A novel strategy to regulate nitrification in agricultural systems. Advances in Agronomy 114:249–302.

Subbarao GV; Nakahara K; Ishikawa T; Ono H; Yoshida M; Yoshihashi T; Zhu Y; Zakir HAKM; Deshpande SP; Hash CT; Sahrawat KL. 2013a. Biological nitrification inhibition (BNI) activity in sorghum and its characterization. Plant and Soil 366:243–259.

Subbarao GV; Sahrawat KL; Nakahara K; Rao IM; Ishitani M; Hash CT; Kishii M; Bonnett DG; Berry WL; Lata JC. 2013b. A paradigm shift towards low-nitrifying production systems: The role of biological nitrification inhibition (BNI). Annals of Botany 112:297–316.

Tilman D; Fargione J; Wolff B; D’Antonio C; Dobson A; Howarth R; Shindler D; Schlesinger WH; Simberloff D; Swackhamer D. 2001. Forecasting agriculturally driven global environmental change. Science 292:281–284.


Zhu X; Burger M; Doane TA; Horwath WR. 2013. Ammonia oxidation pathways and nitrifier denitrification are significant sources of N$_2$O and NO under low oxygen availability. Proceedings of the National Academy of Sciences of the United States of America 110:6328–6333.

© 2013

Tropical Grasslands—Forrajes Tropicales is an open-access journal published by Centro Internacional de Agricultura Tropical (CIAT). This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 3.0 Unported License. To view a copy of this license, visit http://creativecommons.org/licenses/by-nc-sa/3.0/

www.tropicalgrasslands.info