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Phenotyping of *Urochloa humidicola* grass hybrids for agronomic and environmental performance in the Piedmont region of the Orinoquian savannas of Colombia

Daniel M. Villegas[1] | Ashly Arévalo[1] | Mauricio Sotelo[1] | Jonathan Nuñez | Danilo Moreta[1,2] | Idupulapati Rao[1] | Manabu Ishitani[1] | Guntur V. Subbarao[3] | Jacobo Arango[1]

[1]International Center for Tropical Agriculture (CIAT), Cali, Colombia

[2]Cornell University, Ithaca, New York, USA

[3]Japan International Research Center for Agricultural Sciences, Tsukuba, Japan

Correspondence
Jacobo Arango, International Center for Tropical Agriculture (CIAT), Cali, Colombia.
Email: j.arango@cgiar.org

Present address
Jonathan Nuñez, Department of Environmental Systems Science, ETH Zürich, Zürich, Switzerland.

Danilo Moreta, Cornell University, Ithaca, New York, USA.

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Abstract

In the low fertility acid soils of the Orinoquian savannas of Colombia, *Urochloa humidicola* cv. Tully or Humidicola is one of the most widely planted tropical forage grasses for improving livestock productivity. Low nutritional quality of this grass limits sustainable livestock production in this region. In this study, we conducted a phenotypic evaluation under field and greenhouse conditions of one of the first hybrid populations of *U. humidicola* generated from the forage breeding program of CIAT. Our objective was to identify a set of new hybrids of *U. humidicola* that combine improved productivity and nutritional quality plus the biological nitrification inhibition (BNI) trait/ability to reduce nitrogen (N) losses via leaching and nitrous oxide (N_2O) emissions. To this end, we tested 118 hybrids (planted in pots) in the greenhouse for over 6 months and measured potential nitrification rates (NR) using soil microcosm incubation. NR values observed ranged from 0.27 to 5.75 mg N-NO_3^- kg soil^{-1} day^{-1}. Later, 12 hybrids with different levels of NR were selected and field-tested in the Orinoquia region over a 4 years period (2013–2017) for dry matter production, nutrition quality (crude protein, *in vitro* digestibility and fibres content) and NR in each year. In the rainy season of 2018, two hybrids with superior agronomic performance and contrasting field level NR (Uh08/1149 and 0450) were subjected to analysis of soil-borne N_2O emissions after fertilization during 13 days. The NR values recorded were not directly correlated with the forage quality parameters evaluated, however, the two grasses with the lowest NR values were among those with the highest biomass production, crude protein content, and N uptake. The grass hybrid Uh08/1149 and the germplasm accession CIAT 16888 were found as materials with superior forage value, with production of 14.1 and 14.6 tons dry matter ha^{-1} year^{-1} (up to 8% higher than the cv. Tully), crude protein of 11.5 and 9.1% per cut (up to 20% higher than the cv. Tully), and N uptake of 31.6 and 25.7 kg N ha^{-1}

Daniel M. Villegas and Ashly Arévalo these authors share their first authorship.

cut^{-1} (up to 30% higher than the cv. Tully). Additionally, these two grasses are likely to exhibit high-BNI ability, with potential to improve N use efficiency in managed pastures.

KEYWORDS
acid soil, *Brachiaria*, forage breeding, forage quality, N uptake, nitrification, nitrous oxide

1 | INTRODUCTION

Grasses of the genus *Urochloa* (syn. *Brachiaria*) are by far the most widely planted forages in the Neotropics, with estimations of 9 M ha (million hectares) in *Urochloa* grasses in Colombia (DANE, 2020), and of 80 to 100 M ha in Brazil (de Oliveira et al., 2004; Jank et al., 2014). The success of these African grasses in improving livestock productivity in Latin America has been related to their wider adaptation range, mainly to acidic soils with low available nitrogen (N) and phosphorus (P), high aluminium (Al) content, and also to their suitability for integration into diverse production systems given their tolerance to shade and compatibility to associate with a range of legume species (Fisher & Kerridge, 1996; Miles et al., 2004; Rao et al., 1996).

The Orinoquian savannas are the largest grassland area of Colombia with 18 M ha, composed of 13 M ha of high plains and dissected plateau, and 5 M ha of flooded savannas (Recio et al., 2011). These savanna areas have an animal inventory of less than 6 M animals. On average, about three to 10 hectares are needed to feed one animal, which raises the need to sustainably intensify animal production. In Orinoquia, 52% of the land is covered by native savanna vegetation and 30% by introduced grasses, mostly *Urochloa* spp. (Álvarez & Rincón, 2010). However, it has been widely acknowledged that these introduced grasses have not expressed their full productive potential due to inadequate infrastructure, management and policies that influenced their integration into human-intervened crop-livestock systems (Ayarza et al., 2022; Rao et al., 2015; Tapasco et al., 2019).

The commercial cultivars of *Urochloa* are adapted to the soil and climate conditions of Latin American lowlands. However, there are still some production constraints to most cultivars. *U. humidicola* is among the most important species for animal production within this genus, and the area used for seed production of this grass in Brazil is only surpassed by *U. brizantha* cv. Marandu (Jank et al., 2014). Currently, there are two commercial cultivars: the cv. Tully CIAT 679 (also cv. Humidicola or 'Dulce') and the cv. Llanero CIAT 6133 (previously described as *U. dictyoneura* [Cook & Schultze-Kraft, 2015]). This species is highly adapted to low fertility acid soils with high Al toxicity together with tolerance to waterlogging, spittlebug (Hemiptera: Cercopidae, a major pest in tropical grasslands), and higher stocking rates (Pardo & Perez, 2010). However, it is also considered a 'poor-quality' grass (Lapointe & Miles, 1992), mainly in terms of low crude protein content, high lignin, low digestibility, and its forage quality decreases rapidly over time (Lascano & Euclides, 1996). Therefore, research efforts are in progress in terms of both germplasm selection and plant breeding aiming to develop more suitable cultivars with improved forage quality and productivity for improving livestock production.

In 2006 the International Center for Tropical Agriculture (CIAT) started the breeding program on *U. humidicola* based on the genetic resources of CIAT's germplasm bank, which were collected from East Africa (Burundi, Tanzania, Ethiopia, Rwanda) and Southern Africa (Zimbabwe, Zambia, South Africa and other unknown locations), targeting to improve nutrition quality, spittlebug resistance, seed production, and tolerance to multiple abiotic stresses.

Urochloa grasses have been highlighted for having a variety of ecological strategies that improve nutrient cycling and nutrient use efficiency in tropical agroecosystems (Baptistella et al., 2020; Villegas, Velasquez, et al., 2020b). One of the most remarkable is biological nitrification inhibition (BNI) (Subbarao et al., 2009), which is the plant's ability to module soil nitrifier communities to inhibit nitrification, reduce the pace at which ammonium (NH_4^+) is transformed into nitrate (NO_3^-) in the soil, and avoid N losses in the form of nitrous oxide (N_2O) emissions (Byrnes et al., 2017) and potentially NO_3^- leaching. With the overarching goal to develop a grass variety with enhanced agronomic as well as environmental performance, in this study we evaluated one of the first hybrid populations of *U. humidicola* developed by the breeding program of CIAT for differences in forage biomass production, nutritional quality and emissions of N_2O from soil in the Orinoquia region of Colombia.

2 | MATERIALS AND METHODS

The evaluation of the *U. humidicola* collection was carried out in two phases. First, a greenhouse screening of a breeding population of hybrids was done prioritizing the nitrification rates (NR) of soil as a criterion to select contrasting genotypes for further evaluation (Nunez et al., 2018; Villegas, Arevalo, et al., 2020a). Second, a field trial was established with contrasting hybrids at a research station in the Piedmont region of the Orinoquian savannas of Colombia to evaluate their agronomic and environmental performance under such conditions.

2.1 | Greenhouse screening

To evaluate genotypic differences in the expression of the BNI trait, in December 2012 a population of *U. humidicola* hybrids from the breeding population of CIAT (Uh08) was evaluated in the greenhouse at CIAT in Palmira, Colombia (3°30′03.1″ N 76°21′25.4″ W). The

Uh08 population was the first population generated by the breeding program on *U. humidicola*. It originated from a recombination block in an open pollination field of a set of 14 sexual hybrids and 19 germplasm accessions from CIAT's genebank that were compatible in ploidy ($2n = 6x = 36$). Although the Uh08 was not generated to breed the BNI capacity of the grasses, the list of parent germplasm accessions included certain genotypes that showed contrasting BNI capacity based on later studies (Nunez et al., 2018; Subbarao et al., 2007; Subbarao et al., 2009).

A set of 118 hybrids of the Uh08 population and five control genotypes were planted in pots of 3 kg of acid soil, collected from the Taluma Agrosavia (formerly Corpoica) research station, located near Puerto Gaitan, Colombia (4°22′00″ N, 72°13′33″ W). The soil is classified as an Oxisol with pH of 4.9, clay content of 42%, total N of 1.1 g kg^{-1}, and C/N ratio of 12.4. The experiment was laid out in a randomized complete block design with three replicates. The controls used in the study included three of the parental *U. humidicola* germplasm accessions: CIAT 26146, 26149, and 16888 (high-BNI). The accession CIAT 679 (cv. Tully) was included as it is the most widely planted grass in the region, and it displays a high BNI performance. Bare soil pots (i.e., without plants) were considered to serve as no-BNI treatment.

2.1.1 | Soil nitrification rates

Genotypic differences in BNI were evaluated in the hybrid population by estimating soil nitrification rates 6 months after planting by the soil microcosm incubation method (Nunez et al., 2018). To this end, rhizosphere soil samples were collected 1 day after N fertilization (100 kg N ha^{-1}) supplied in the form of liquid ammonium sulphate. This high rate of N application was expected to trigger the BNI activity that could facilitate the rapid identification of differences in soil nitrification rates among the tested genotypes (Subbarao et al., 2006).

The soil samples were air-dried for 48 h, ground and sieved to a particle size of 2 mm. Mineral N was extracted using 5 g of soil with KCl 1 M (1:10 w/v), shaking for 30 min, and filtering in Whatman paper No 2. The concentrations of NH_4^+ and NO_3^- were determined colorimetrically following the method described in D. Villegas, Arevalo, et al. (2020a). Soil subsamples were incubated in aerated amber flasks at 25°C for 11, 19 and 27 days, and NH_4^+ and NO_3^- concentrations were measured at each sampling time. Potential nitrification rates of soil were calculated as the slope of NO_3^- concentration and incubation time of 11, 19 and 27 days.

2.2 | Field trial

2.2.1 | Study site

The field evaluation of 12 hybrids, selected following the BNI screening done under greenhouse conditions, took place during 2013 to 2018 in the Agrosavia La Libertad research station located in Villavicencio, Colombia, in the eastern plains at 338 masl (4°03′46″ N, 73°27′47″ W) in the Piedmont region (foothills landscape). During the evaluation period the site presented a mean temperature of 26.5°C, relative humidity of 81% and annual precipitation of 2368 mm. The soil type in this area is an Oxisol classified as typic Haplustox with high terraces (Orduz-Rodríguez et al., 2011), with pH of 5.5, clay content of 42%, in g kg^{-1}: 27.31 organic matter, 1.1 total N; in cmol kg^{-1}: 2.06 Ca, 0.78 Mg, 0.06 Na, 0.18 K; in mg kg^{-1}: 20.85 Bray II-P, 0.89 Cu, 2.12 Zn, 2.63 Mn, 16.64 Fe, 33.60 S, 0.18 B; and C:N ratio of 12.4. Before the establishment of the field trial, the site had continuous maize cropping for more than 8 years.

2.2.2 | Experimental design

In 2013 a field trial was established with 16 different forage grasses and a bare soil (i.e., treatments) in plots of 16 m^2 (4 × 4 m). The plots were laid out in randomized complete blocks with three replications, with 1 m distance between plots inside one block, and 2 m between blocks. The treatments consisted of a set of 12 apomictic hybrids of *U. humidicola* from the breeding population (Uh08); three *U. humidicola* germplasm accessions from the genebank of CIAT: 16888, 26146, 26149; and the commercial cv. Tully (CIAT 679). A bare soil treatment (three plots without plants) was included as a no-BNI control for soil nitrification and N_2O measurements. Before the establishment of the trial, lime was applied at a rate of 500 kg ha^{-1}, and fertilizer was applied only once at 12 days after sowing supplying (in kg ha^{-1}) 100 N, 25 P, 50 K, 50 Ca, 15 Mg, 10 S, 0.5 B, and 2.6 Zn. The sowing density was 16 plants per plot (1 plant m^{-2}). The plants grew for 3 months until adequate coverage of the plots before the first evaluation.

2.2.3 | Dry matter production and nutrition quality

To measure plant biomass production and nutrition quality, three assessments were done every year from 2014 to 2017, one in the dry season (mid-November to mid-March, with 60–150 mm monthly precipitation) and two in the rainy season (mid-March to mid-November, 400–550 mm). Before every evaluation, the whole trial was standardized by cutting the plants at 10 cm height from soil level. After 35 days of pasture regrowth in the rainy season, and at 60 days in the dry season, three PVC frames of 0.25 m^2 were randomly placed in each plot and aboveground plant biomass was harvested by cutting the forage at 10 cm height. The samples were oven-dried at 60°C for at least 48 h until constant mass and total dry matter content was determined.

In order to assess any potential trade-off between BNI and forage quality, a forage subsample was ground using a Retsch SM 100 mill and sieved to 1 mm particle size. The nutritional quality parameters of forage biomass were measured following the established protocols for crude protein (CP) (Krom, 1980; Searle, 1984), in vitro dry matter digestibility (IVDMD) (Tilley & Terry, 1963), acid detergent fibre (ADF) and neutral detergent fibre (NDF) contents (Goering & Van Soest, 1970).

2.2.4 | Nitrification rates and nitrous oxide emissions from soil

Every year from 2014 to 2017 during the rainy season topsoil samples (0–10 cm) were collected using a soil auger and following a grid-like sampling method in each field plot (cores collected from four quadrants and the centre). Nitrification rates were then determined following the same methodology that was described for the greenhouse experiment.

During the fifth year of the study, in the rainy season of 2018, the emissions of N_2O from soil were measured by selecting hybrids with the most contrasting NR of soil in the field (Uh08/1149, and 0450), using the CIAT 679 cv. Tully as control genotype, and the bare soil as no-BNI/plant control. In every plot, two closed static chambers of 27 cm diameter (made with PVC) were installed. Each chamber consisted of a 10 cm height ring, burying the first 5 cm in the soil and a 10 cm height cap, which was placed over the rings and sealed with a rubber band only during measurements. The monitory period was of 13 consecutive days, which accounted for a baseline measurement before N-fertilizer application (100 kg ha^{-1}) as liquid ammonium sulphate and followed by 12 measurements at daily intervals every morning from 8:00 to 10:00 AM. For every N_2O sampling, the static chambers were closed for 10 min to allow the gas to accumulate in the headspace and N_2O concentration in the gas sample was measured every 20 s using a portable FTIR multigas analyzer Gasmet DX4040 (Teutscherova et al., 2019; Villegas, Arevalo et al., 2020a). Accumulated emissions were calculated for each treatment by linear interpolation of the emissions of N_2O during the sampling period. Along with N_2O concentrations, soil samples were taken every second day to determine the amount of NH_4^+ and NO_3^- in the soil and their change over time. Mineral N extraction and colorimetric determination of NH_4^+ and NO_3^- were carried out as described before for the greenhouse experiment.

2.3 | Data analysis

Statistical differences among treatments for the variables of biomass production, nutrition quality, NR and cumulative emissions of N_2O from soil were assessed through ANOVA and Tukey's HSD test at $p < .05$ for multiple comparisons in R v4.4. All figures were constructed using the Sigmaplot Software v12.

3 | RESULTS

3.1 | Greenhouse screening

3.1.1 | Soil nitrification rates

A wide range of potential NR values was observed among the genotypes evaluated in the greenhouse study (Figure 1). In the grass controls the mean of the NR value ranged from 0.28 to 4.82 mg N-NO_3^- kg $soil^{-1}$ day^{-1}, being the lowest and highest values observed in *U. humidicola* CIAT 16888 and CIAT 26149, respectively. The parental control CIAT 26146 showed an intermediate NR value of (1.5 mg N-NO_3^- kg $soil^{-1}$ day^{-1}). The uncultivated treatment (bare soil) showed NR of 5.41 mg N-NO_3^- kg $soil^{-1}$ day^{-1}, being the highest NR among the controls and second among all the samples measured. In the hybrid population, the NR values recorded ranged from 0.27 to 5.75 mg N-NO_3^- kg $soil^{-1}$ day^{-1} being the lowest and highest values observed within Uh08/0420 and Uh08/1253, respectively.

The selection of hybrids with different levels of BNI for field evaluation was made considering the distribution of the NR values among the hybrid population. The hybrids located in the first and fourth quartiles were considered low and high NR hybrids, respectively; and the hybrids located in the second and third quartiles were considered an intermediate NR group. The limits for each NR group were (in mg N-NO_3^- kg $soil^{-1}$ day^{-1}), low: <0.92; intermediate 0.92–1.84, high: >1.84. The selected hybrids were then established in the field as mentioned in Section 2.2.

3.2 | Field trial

3.2.1 | Plant biomass production and forage quality

The annual production of forage dry matter (DM) of the grass hybrids evaluated in the field ranged from 11.4 to 14.1 t DM ha^{-1} $year^{-1}$ (Table 1), with a mean value of 12.5 t DM ha^{-1} $year^{-1}$. Two hybrids Uh08/1149 and 1155 stood out among the hybrid population with annual biomass production of 14.1 and 13.6 t DM ha^{-1} $year^{-1}$ respectively, both being higher than the value of cv. Tully, which showed DM production of 13.5 t DM ha^{-1} $year^{-1}$, although statistical differences were not found. The grass with the highest DM production was the high BNI control CIAT 16888, with 14.6 t DM ha^{-1}. Substantial seasonal variation in DM production over the year was observed in all the grasses evaluated, with reductions of 58% on average in the hybrids and 56% in the controls in the dry versus, the rainy season.

The average CP content per cut in the hybrid population was 9.17%, with hybrids Uh08/1149, 0450, 0700, and 0675 showing comparable or superior CP content than the cv. Tully (9.6%), with values of 11.5, 9.8, 9.5, and 9.4 respectively (Table 1). The Uh08/1149 was not only the grass with the highest CP content, but also the only one that surpassed the threshold of 10% on a yearly basis. In the dry season, it also surpassed by more than 2% compared to the second-best grass with the highest CP (7.5%), and by 3% compared to the average of all the hybrids evaluated (6.8%). Moreover, the CP value of Uh08/1149 in the dry season was higher than that of most grasses in the rainy season.

All the hybrids evaluated surpassed the IVDMD value observed within the cv. Tully (56%). Two hybrids, Uh08/0450 and 1149 showed IVDMD of 60.3 and 59.8%, respectively whereas the high BNI control CIAT 16888 accession showed the highest IVDMD with 60.7%. The Uh08/1149 hybrid exhibited the lowest NDF (68.7%) and intermediate levels of ADF (37.7%), whereas the CIAT 16888 accession was among the genotypes with the highest values for both parameters. (Table S1).

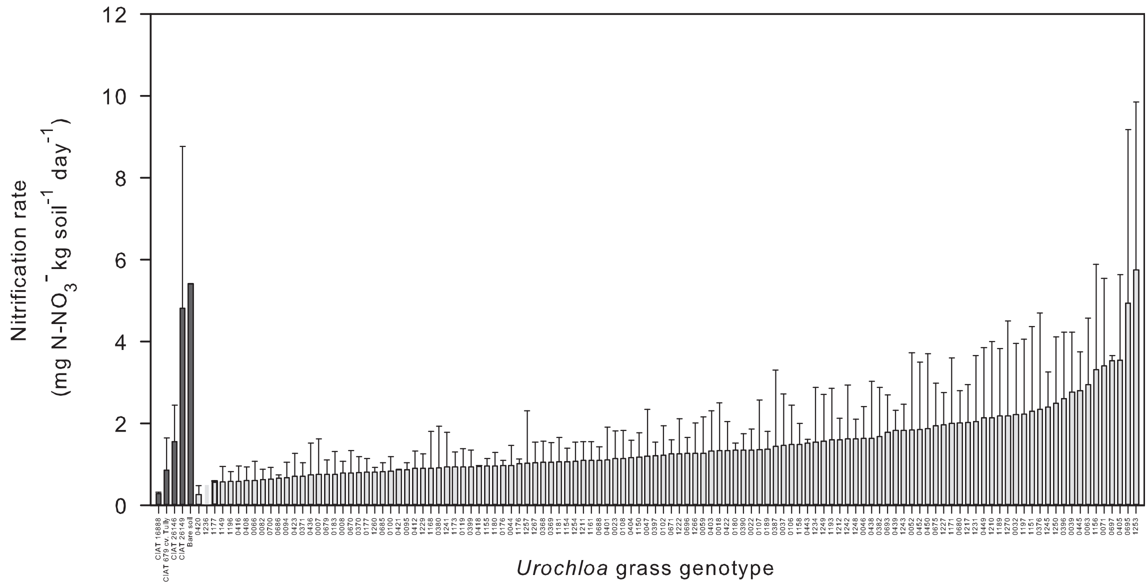

FIGURE 1 Potential soil nitrification rates of a population of 118 apomictic *U. humidicola* hybrids (light coloured bars) and five controls with known BNI activity (dark coloured bars) grown in pots for more than 6 months under greenhouse conditions at CIAT, Colombia. Values represent the mean and standard error of the mean from three replications

TABLE 1 Shoot plant biomass production, crude protein, N uptake and nitrification rates of 16 *Urochloa* forage grasses evaluated in dry and rainy season in the Piedmont region of Orinoquian savannas of Colombia from 2014 to 2017. Depicted values are mean with standard error of the mean in parentheses. Different letters denote statistical differences according to Tukey's HSD test ($\alpha = 0.05$)

	Biomass production (t DM ha^{-1})			Crude protein (%)				
Forage grass	Dry season[1] (cut^{-1})	Rainy season[2] (cut^{-1})	Total[3] (year^{-1})	Dry season[1] (cut^{-1})	Rainy season[2] (cut^{-1})	Average[3] (cut^{-1})	N uptake (kg N ha^{-1} cut^{-1})	Nitrification rates (mg N-NO$_3^-$ kg soil^{-1} day^{-1})
Uh08/0022	0.6 (0.2)	1.4 (0.4)	11.4 (3.4) a	6.1 (1.3)	9.6 (1.7)	8.8 (1.6) a	19.8 (7.3) a	2.3 (1.6) a
Uh08/0422	0.6 (0.2)	1.5 (0.4)	12.4 (3.4) a	7.3 (1.0)	9.4 (1.8)	9.0 (1.6) ab	22.5 (9.1) ab	2.9 (1.7) a
Uh08/0450	0.6 (0.2)	1.5 (0.4)	12.2 (3.8) a	7.4 (0.9)	10.5 (2.2)	**9.8 (1.9) ab**	**24.1 (9.1) ab**	**5.1 (1.5) a**
Uh08/0675	0.6 (0.3)	1.5 (0.4)	12.4 (3.7) a	7.3 (0.9)	10.0 (1.3)	9.4 (1.2) ab	22.6 (6.9) ab	2.7 (1.4) a
Uh08/0680	0.7 (0.4)	1.5 (0.4)	12.6 (3.9) a	6.0 (1.0)	9.3 (2.1)	8.5 (1.9) a	20.9 (8.5) a	2.0 (1.3) a
Uh08/0696	0.6 (0.2)	1.6 (0.5)	12.8 (4.0) a	7.0 (0.9)	9.0 (1.5)	8.5 (1.4) a	20.3 (6.1) a	2.3 (1.3) a
Uh08/0700	0.5 (0.1)	1.5 (0.5)	12.1 (4.3) a	7.5 (1.1)	10.1 (1.9)	9.5 (1.7) ab	20.8 (6.7) a	2.0 (0.8) a
Uh08/1149	0.5 (0.2)	1.8 (0.6)	**14.1 (5.2) a**	9.7 (1.3)	12.1 (1.6)	**11.5 (1.6) b**	**31.6 (12.6) b**	**1.9 (1.1) a**
Uh08/1155	0.7 (0.2)	1.7 (0.5)	**13.5 (4.5) a**	5.8 (0.8)	9.4 (1.8)	8.6 (1.5) a	21.4 (6.8) ab	2.6 (1.8) a
Uh08/1243	0.5 (0.2)	1.7 (0.6)	12.9 (5.0) a	6.5 (0.5)	9.6 (1.5)	8.9 (1.3) ab	22.3 (9.3) ab	3.1 (2.5) a
Uh08/1248	0.7 (0.2)	1.5 (0.4)	12.2 (3.7) a	5.9 (1.2)	9.2 (1.9)	8.5 (1.8) a	19.5 (7.0) a	2.0 (0.9) a
Uh08/1250	0.6 (0.2)	1.5 (0.4)	**11.9 (3.3) a**	5.9 (1.3)	9.1 (2.2)	8.4 (2.0) a	18.7 (6.2) a	2.1 (1.1) a
UhCIAT/16888	0.7 (0.3)	1.8 (0.7)	**14.6 (5.5) a**	6.7 (1.4)	9.8 (1.9)	9.1 (1.8) ab	**25.7 (9.6) ab**	2.4 (1.2) a
UhCIAT/26146	0.7 (0.2)	1.5 (0.4)	12.4 (3.4) a	6.4 (0.8)	9.5 (1.5)	8.9 (1.4) a	20.5 (5.9) a	3.0 (1.5) a
UhCIAT/26149	0.8 (0.2)	1.4 (0.3)	12.0 (2.9) a	7.0 (1.0)	8.9 (1.6)	8.5 (1.5) a	18.6 (5.2) a	3.1 (1.3) a
UhCIAT/679 cv. Tully	0.6 (0.2)	1.7 (0.6)	**13.5 (5.1) a**	7.0 (1.0)	10.3 (1.1)	9.6 (1.1) ab	**24.4 (8.8) ab**	**1.9 (1.0) a**

Note: Bold values represent data highlighted in the results Section 3.2.1.
[1]Pasture recuperation time in the dry season was of 60 days.
[2]Pasture recuperation time in the rainy season was of 35 days.
[3]Calculated weighing the biomass production by season in nine cuts per year. Two cuts in the dry season and seven cuts in the rainy season.

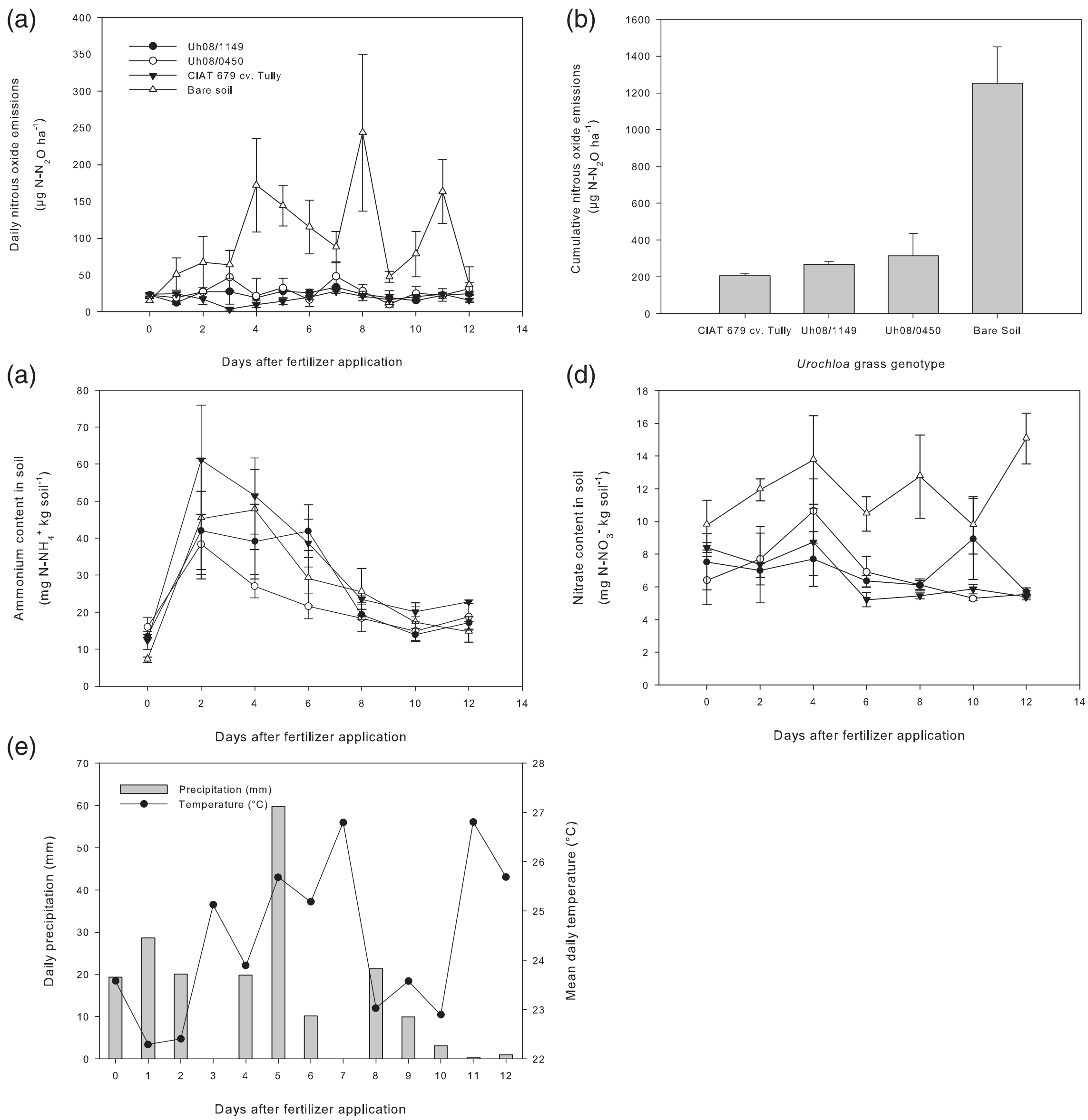

FIGURE 2 (a) Daily and (b) cumulative nitrous oxide emissions in *Urochloa* forage grasses and bare soil control evaluated in the rainy season in the Piedmont region of Orinoquian savannas of Colombia. (c) Ammonium and (d) nitrate content in soil and (e) precipitation and temperature conditions recorded during the 13 days of measurement period. Depicted values are the mean and standard error of the mean. Different letters denote statistical differences according to the Tukey's HSD test ($\alpha = 0.05$)

The N uptake in shoot biomass in the grass hybrids was on average 22 kg N ha^{-1} cut^{-1}. Whereas within the cv. Tully, it was 24.4 kg N ha^{-1} cut^{-1} and 25.7 in the CIAT 16888. The highest N uptake recorded in the hybrid population was that of Uh08/1149 with 31.6 kg N ha^{-1} cut^{-1}, which is 30% higher than that of the cv. Tully, followed by Uh08/450, with 24.1 kg N ha^{-1} cut^{-1}.

3.2.2 | Soil nitrification rates and N_2O emissions

The mean of soil nitrification rates (NR) recorded in the field were in the range of 1.9–5.1 mg N-NO_3^- kg $soil^{-1}$ day^{-1} (Table 1). The grasses Uh08/1149 and cv. Tully presented the lowest NR value with 1.9 mg N-NO_3^- kg $soil^{-1}$ day^{-1}, whereas the majority of the grasses were in the range of 2.0–3.1 mg N-NO_3^- kg $soil^{-1}$ day^{-1}, and the Uh08/450 hybrid showed the highest NR value with 5.1 mg N-NO_3^- kg $soil^{-1}$ day^{-1}. The NR values were not directly correlated with the forage quality parameters evaluated of plant biomass (Person's correlation coefficient [CC] $= -0.19$, $p = .47$), crude protein (CC $= 0.05$, $p = .86$), N uptake (CC $= 0.004$, $p = .98$) (Figure S1). However, the two grasses with the lowest NR values (cv. Tully and Uh08/1149) were among those with the highest biomass production, CP content, and N uptake (Table 1; Figure S1).

The accumulated N_2O emissions over the 12 days were highest in the bare soil plots (1252 μg N_2O-N ha^{-1}), followed by the

Uh08/0450, Uh08/1149, and the cv. Tully (Figure 2a,b). The bare soil plots emitted four to six times the amount of N_2O by all the grass treatments. The emissions recorded within the cv. Tully, and Uh08/1149 were about 52% and 17% lower than that observed from the highest N_2O emitting grass Uh08/0450. However, statistically significant differences were not observed between the grasses evaluated.

During the N_2O measurement period, the concentration of NH_4^+ and NO_3^- in the soil differed among grass treatments. The concentrations of NH_4^+ in the soil showed a maximum peak at 2 days after fertilization (DAF), and gradually decreased until 10–12 DAF when they reached similar levels as before fertilization (Figure 2c). In contrast, NO_3^- fluctuated constantly over the 12 days in a pattern similar to that of daily precipitation (Figure 2d,e). The average concentration of NH_4^+ in soil over the 12 days period was the highest within the cv. Tully, and the lowest within the Uh08/0450, whereas NO_3^- level was the highest within the bare soil plots and the lowest within the cv. Tully.

4 | DISCUSSION

4.1 | Suitability of the hybrids for the eastern plains of Colombia

The Orinoquia region of Colombia has difficult conditions for the cultivation of crops and pastures because of the low soil base content, low pH, and high aluminium saturation (Leon & Rincón, 2010). To this end, between 1960 and 1990 a series of evaluations performed by different Colombian research institutions identified *Andropogon gayanus*, *U. decumbens*, *U. brizantha*, and *U. humidicola* as the species better adapted to the agroecological characteristics of the region. Among them, *U. humidicola* stood out not only because of its tolerance to the already mentioned soil conditions, but also to flooding, drought, and burning. In addition, this species has the ability to accumulate high amounts of carbon in the soil via its deep root system (Ayarza et al., 2022; Fisher et al., 1994). However, it has also been considered a forage of moderate-to-low nutrition quality, affecting the cattle's voluntary intake and animal weight gain (Pardo & Perez, 2010).

In the present study, we evaluated a breeding population of 118 *U. humidicola* hybrids, which were grown in pots for about 6 months and based on this screening we selected 12 hybrids to evaluate their agronomic and environmental performance under field conditions over 4 years time. Our aim was to identify at least one grass genotype with improved nutrition quality combined with high BNI capacity potential.

In the Piedmont region of the Colombian Orinoquian savannas, Pardo and Perez (2010) suggested that with the application of maintenance P and K inputs, the expected annual dry matter (DM) production of *U. humidicola* is between 7 and 8 t DM ha^{-1}. The Piedmont region receives a higher amount of annual rainfall (Álvarez & Rincón, 2010), about 3300 mm with more cloudy days than that of the high plains region (2200 mm) and this can impact dry matter production. In the Orinoquian high plains, Fisher and Kerridge (1996) reported annual DM yields of 11.7 and 14.5 t DM ha^{-1} with cv. Llanero (CIAT 6133) and cv. Tully (CIAT 679) respectively. Salinas and Gualdrón (1982) observed an annual yield of 11.9 t DM ha^{-1} under management conditions similar to that of our experiment (0.5 t ha^{-1} of lime and 17 kg ha^{-1} of P fertilizer). On the other hand, in the acidic soils of Brazilian Cerrado, with a longer dry season than that of the Colombian Orinoquia Fisher and Kerridge (1996) reported *U. humidicola* annual yields of 7.4–13.8 t DM ha^{-1}. The soils of Cerrados of Brazil may have less limitation for root development than the soils of the Orinoquia region of Colombia (Ayarza et al., 2022).

The plant biomass production recorded for the hybrids of the Uh08 in the field was in the range of 11.4–14.1 t DM ha^{-1} year^{-1}, located in the higher-end of the yields reported in the literature of acid soils of Colombia and Brazil (Fisher & Kerridge, 1996; Pardo & Perez, 2010; Salinas & Gualdrón, 1982). Out of the 12 hybrids evaluated, the Uh08/1149 hybrid stood out because of its plant DM production, which provided around 600 kg of additional feed per year than the most planted grass in the region, the cv. Tully. Apart from producing more biomass, the Uh08/1149 also outperformed the cv. Tully in various nutrition quality parameters, with 4.4% higher IVDMD, 3.4% lower NDF, and 2% more CP, allowing to harvest additional 7.2 kg of N per hectare per cut in its shoot biomass (30% increase). This suggests that the genotypes identified in this study may positively impact livestock productivity because an increase in IVDMD of the grass has a significant effect on improving animal liveweight gain (Lascano & Euclides, 1996). Although the main focus of this study was on the hybrids of *U. humidicola* from the breeding program, it is worth noting the germplasm accession CIAT 16888, which presented the highest DM production among all the grasses evaluated with 14.6 t DM ha^{-1} year^{-1}, the highest IVDMD (60.7%), and second-highest N uptake 25.7 kg N ha^{-1} year^{-1}. The CP, NDF and ADF profile of this grass was not as outstanding as in other grasses.

In the Piedmont region of Orinoquia, Rincón et al. (2018) evaluated the CP content of grazed *U. humidicola* cv. Llanero (CIAT 6133) during the rainy season after 21 days of recuperation, and the values observed were 8.4% with zero-N maintenance fertilization, and 9.9% with 100 kg N ha^{-1}. These CP values are closer to those of the cv. Tully, as the CP value in the rainy season after 35 days of recuperation was 10.3%.

It is widely accepted that pastures' quality, particularly CP and IVDMD decreases over time, therefore it is noteworthy that the CP content of the Uh08/1149 hybrid in the dry season with a recuperation time of 60 days (9.7%) was comparable to that of cvs. Llanero (9.9%) and Tully (10.3%) in the rainy season with a shorter recuperation time of 21 and 35 days. This finding is particularly relevant as the dry season in the Orinoquia, although it is relatively short (~3 months), it has dramatic effects on the amount and quality of the pastures available to cattle. Indeed, it is common that farmers have to either buy hay from other regions of Colombia, or sell their cows at low prices because it is not possible to feed them with the available resources on the farm.

The stolon-forming growth habit of *U. humidicola* has been considered favourable to control soil erosion, however, its dominance is also seen as a difficulty for association with various legume species with erect growth habit (Pardo & Perez, 2010). But one advantage of the Uh08/1149 hybrid is that although it forms stolons, it does not cover 100% of the land where it is planted. This brings the opportunity for improving pasture management by associating the Uh08/1149 hybrid either with other grasses or with more persistent herbaceous legumes such as *Arachis pintoi* or *Desmodium heterocarpon* in mixed pastures (Fisher & Kerridge, 1996).

4.2 | BNI and N_2O emissions of forage grasses

We ranked the genotype Uh08/0450 as a low BNI hybrid and Uh08/1149 as a high BNI hybrid according to the observed NR value. Furthermore, both genotypes showed the highest N uptake among the forages evaluated. This suggests that the observed differences in NR was not related to depletion of the inorganic N substrate pool via plant uptake but likely to contrasting BNI activity between the hybrids. In addition, the low BNI hybrid also shows a higher N_2O emission compared to the high BNI hybrid. This provides support for our categorization because the role of high BNI capacity in reducing soil N_2O emissions has already been confirmed in different tropical grasses (Byrnes et al., 2017; de Klein et al., 2022; Villegas, Arevalo, et al., 2020a).

Studies on the mechanisms driving the BNI capacity of the cv. Tully have revealed that Brachialactone and its isomers (an organic inhibitor released by roots), inhibit soil nitrifiers and reduce the oxidation of NH_4^+ into NO_3^- (Egenolf et al., 2020; Subbarao et al., 2009). The BNI capacity has been proposed as a strategy to conserve N in nutrient-limiting environments (Subbarao et al., 2012). Indeed, the soil mineral N transformations during the N_2O sampling period revealed that in cv. Tully and Uh08/1149 the soil NH_4^+ content was continuously higher than that of Uh08/0450 at the same level of fertilizer application (Figure 2c), and this observation is consistent with the BNI concept and its validation under field conditions (Subbarao et al., 2012).

Subbarao et al. (2007) suggested that BNI is a genetically variable trait. The hybrid population of *U. humidicola* was generated from the genetic recombination of 14 sexual hybrids and 19 germplasm accessions from CIAT's genebank. Among the list of germplasm accessions that gave origin to that population, the CIAT 16888 was found, which has exhibited high BNI activity, even surpassing that of CIAT 679 (cv. Tully) in the study of Subbarao et al. (2009), and this was supported by the NR measured in the greenhouse screening, displaying lower NR value than the cv. Tully. Therefore, the genetic background of CIAT 16888 is likely to have been a source of high BNI for the population as observed within the Uh08/1149hybrid.

4.3 | Final remarks

The livestock sector of the Colombian Orinoquian savannas confronts highly heterogeneous conditions in terms of soil fertility, forage species, and pasture and cattle management. In this study we presented the development of a hybrid population of *U. humidicola*, a grass adapted to diverse agroecological conditions but with low nutritional quality. In a two-phase evaluation project (greenhouse and field) with 4 years of field assessment (i.e., 12 evaluations), we identified one hybrid (Uh08/1149) with superior agronomic performance than the commercially available cv. Tully, which is the most planted grass in the region, without significantly increasing the soil N_2O emissions after fertilization, likely because of high BNI capacity. Likewise, the CIAT 16888 germplasm accession showed high agronomic performance, which also based on previous studies, has been acknowledged as a high BNI grass. Both the Uh08/1149 hybrid and the CIAT 16888 germplasm accession are promising grasses that provide forage of high value with high N uptake ability, which could be further evaluated under grazing (animal trampling and palatability) to determine whether these two grasses are viable options for release as new materials to the forages market for sustainable intensification of livestock production in the Colombian Orinoquia.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Daniel M. Villegas https://orcid.org/0000-0001-6801-3332

Jacobo Arango https://orcid.org/0000-0002-4828-9398

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