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Incongruous variation of denitrifying bacterial communities as soil N level rises in Canadian canola fields

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ABSTRACT

Soil N fertilization stimulates the activity of the soil bacterial species specialized in performing the different steps of the denitrification processes. Different responses of these bacterial denitrifiers to soil N management could alter the efficiency of reduction of the greenhouse gas N_2O into N_2 gas in cultivated fields. We used next generation sequencing to show how raising the soil N fertility of Canadian canola fields differentially modifies the diversity and composition of nitrite reductase (*nirK* and *nirS*) and nitrous oxide reductase (*nosZ*) gene-carrying denitrifying bacterial communities, based on a randomized complete blocks field experiment. Raising soil N levels increased up to 60% the ratio of the *nirK* to *nirS* genes, the two nitrite reductase coding genes, in the Brown soil and up to 300% in the Black soil, but this ratio was unaffected in the Dark Brown soil. Raising soil N levels also increased the diversity of the bacteria carrying the nitrite reductase gene *nirK* (Simpson index, $P = 0.0417$ and Shannon index, 0.0181), and changed the proportions of the six dominant phyla hosting *nirK*, *nirS*, and *nosZ* gene-carrying bacteria. The level of soil copper (Cu) and the abundance of *nir*K gene, which codes for a Cu-dependent nitrite reductase, were positively related in the Brown ($P = 0.0060$, $R^2 = 0.48$) and Dark Brown (0.0199, $R^2 = 0.59$) soils, but not in the Black soil. The level of total diversity of the denitrifying communities tended to remain constant as N fertilization induced shifts in the composition of these denitrifying communities. Together, our results indicate that higher N fertilizer rate increases the potential risk of nitrous oxide (N_2O) emission from canola fields by promoting the proliferation of the mostly adaptive N_2O-producing over the less adaptive N_2O-reducing bacterial community.

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1. Introduction

The problem of greenhouse gas (GHG) emissions from human activity is attracting the attention of the research community, policymakers, and the society as a whole (IPCC, 2006). Nitrous oxide (N_2O) is the third most important GHG after carbon dioxide (CO_2) and methane (CH_4), contributing 8% of the total global GHG emissions (IPCC, 2007). This potent has a lifetime in the atmosphere twice as long as CO_2 with a global warming potential 310 times higher (Forster et al., 2007). Globally, over 40% of total N_2O emissions are from human activity, mainly from agriculture (EPA, 2010). About 70% of the N_2O emissions in the U.S.A. are attributable to the management of agricultural soils fertility (EPA, 2011). Modern crop production largely relies on fertilizers (Gorfer et al., 2011; Cui et al., 2013) and the inefficient use of N fertilizers by crops results in the denitrification of a large proportion of the N added to cultivated soils. Nitrogen fertilizer is a major source of nitrous oxide emissions leading to global climate change (Hofstra and Bouwman, 2005).

The production of canola (*Brassica napus* and *Brassica rapa*) has increased 3.4 times globally between 1995 and 2012 (FAOSTAT, 2012), as canola oil is used for human consumption and the production of biodiesel. The annual production of canola has increased sharply in the past decade in Canada, passing from 6.8 million tonnes in 2003 to 18.0 million tonnes in 2013. Canola crops require large inputs of N fertilizer (Karamanos et al., 2005). The release of high-yielding hybrid cultivars in recent years has raised the amounts of N fertilizer applied in canola fields (Cutforth et al., 2009). Increased N fertilizer rates in canola production increases the carbon footprint of canola products (Gan et al., 2012). Therefore, it is important to understand the influence of N fertilization on the process of denitrification in canola fields.

Denitrification is an anaerobic respiration process in which NO_3^- and NO_2^- serve as electron acceptors. These N forms are

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reduced stepwise into the gaseous intermediates NO and N_2O, and the end product N_2 (Zumft, 1997). Many soil microorganisms have denitrifying capabilities (Hayatsu et al., 2008). Denitrifying bacteria are typically identified through culture-independent approaches because many of them are unculturable or difficult to grow in culture (Yoshida et al., 2009).

In soils, the denitrifiers form a phylogenetically diverse functional group (Philippot et al., 2007), and the corresponding genes are involved in the process of denitrification, rather than the microorganisms carrying out this process. Nitrite reductase is an enzyme catalyzing the reduction of NO_2^- to NO. There are two classes of nitrite reductases: the cytochrome cd_1-containing nitrite reductase coded by the gene *nirS* and the Cu-dependent nitrite reductase coded by the gene *nirK* (Braker et al., 2000). The reduction of N_2O to the innocuous gas N_2 is catalyzed by the enzyme nitrous oxide reductase encoded in the gene *nosZ* (Hoeren et al., 1993). It is crucial to understand the influence of soil N level on *nirS*, *nirK* and *nosZ* gene-carrying bacteria, so that the optimized fertilization program in canola production can be developed with the goal of increasing crop productivity while reducing N_2O and N_2 emissions.

The objective of this study was to determine the effect of varying soil N availability on the community of denitrifiers inhabiting the rhizosphere of canola in western Canada. We tested the hypothesis that increased N application in canola field can cause shifts in the abundance and taxonomic composition of the denitrifying bacterial communities of canola rhizosphere. This hypothesis was tested in three pedoclimatic zones. Next generation sequencing technology, pyrosequencing, an advanced molecular tool are useful in the analysis of soil microbial diversity (Yang et al., 2012) and the distribution of the functional genes (Lindström et al., 2004), was used to measure both the impacts of N fertilization on the taxonomic composition of denitrifying bacterial communities and on the relative abundance of the genes controlling the denitrification process in the soil.

2. Materials and methods

2.1. Experimental design and field management

A field experiment was conducted on research farms located in three different pedoclimatic zones of the Canadian prairie: in a Brown Chernozem of the Semiarid Prairie at Swift Current, in a Dark Brown Chernozem at Scott, and in a Black Chernozem of the Parkland at Indian Head, SK, Canada. Brown, Dark Brown and Black Chernozem soils have been evolved under the influences of different precipitation regions. The soil climate of Brown Chernozem is from sub-humid to semiarid, that of Dark Brown Chernozem is semiarid and that of Black Chernozem is sub-humid (Soil Classification Working Group, 1998). At each pedoclimatic zone, three soil N levels, no N (0 kg N ha^{-1}), medium (60 kg N ha^{-1}), and high (120 kg N ha^{-1}), were randomized in four complete blocks, for a total of 36 plots. Soils first received the recommended levels of P, K and S through the application of 75 kg ha^{-1} of 17-22-0-13 in Brown Chernozem zone, 120 kg ha^{-1} of 5-25-26-8 in Dark Brown Chernozem zone, and 50 kg ha^{-1} of 11-51-0-0 in Black Chernozem zone based on soil nutrient tests. Then, the N fertilizer treatments were applied, i.e., 0, 130 and 260 kg ha^{-1} of urea, to create the no N, medium, and high N level treatments in Brown and Dark Brown Chernozem zones, and the rates of 0, 118 and 249 kg ha^{-1} of urea were applied at Black Chernozem zone. All fertilizers were banded 40 mm beside and 30 mm below the seed rows. The hybrid canola cultivar 'InVigor L150' was seeded at the rate of 8.8, 8.1 and 6.3 kg ha^{-1} at Brown, Dark Brown and Black Chernozem zones, respectively, to establish plant stands with a density of 150 plant m^{-2}. Details on experimental locations and field management are presented in Table 1.

2.2. Soil sampling and analyses

Rhizosphere soil samples were taken at the 50% flowering stage of canola from each plot. Five individual canola plants were selected randomly, debris on the soil surface were removed, and the selected plants were dug out, to a depth of 25 cm. Bulk soil was removed by shaking, and the five root systems collected from each plot were pooled in a labeled plastic bag. All 36 samples were kept in a cooler on ice during sampling and transportation from the fields to the laboratory, and kept in a cold room at 4 °C overnight. The rhizosphere soil was brushed from the roots and homogenized by sieving through 2-mm to produce one rhizosphere sample per plot. Each rhizosphere soil sample was parsed into two subsamples. One set of subsamples was placed in small plastic bags and stored at −20 °C for molecular analysis, and the other set was air dried for chemical analyses. Soil nitrate and ammonium were determined by KCl extraction (Hamm et al., 1970; Gentry and Willis, 1988), available soil P and K by $NaHCO_3$ extraction (Hamm et al., 1970), available soil S by $CaCl_2$ extraction (Hamm et al., 1973), available soil Cu and Fe by diethylenetriaminepentaacetic acid (DTPA) (Carter and Gregorich, 2006), and soil organic carbon was determined by combustion in a NA1500Carlo Erba NCS Analyzer (Fisons Instruments, Danvers, MA, USA), as reported by Baccanti and Colombo (1992). All soil analyses were conducted in the Chemistry Laboratory of the Semiarid Prairie Agricultural Research Centre of Agriculture and Agri-Food Canada.

Table 1
Field management details at the three experimental locations.

Location	Soil type	Soil texture	Coordinates	Seeding		Fungicide		Herbicide		Insecticide	
				Date	Rate (kg ha^{-1})	(g a.i. ha^{-1})	Date	(g a.i. ha^{-1})	Date	(g a.i. ha^{-1})	Date
Swift Current	Brown	Loam to silt	50° 18' N, 107° 41' W	May 9	8.8						
						98.9 pyraclostrobin + 242 boscalid	July 5	500 glufosinate ammonium + 14.8 clethodim	June 07	1424 carbaryl	July 11
Scott	Dark Brown	Loam	52°29' N, 108°95' W	May 16	8.1	None	None	500 glufosinate ammonium + 14.8 Clethodim	June 12	None	None
Indian Head	Black	Heavy clay	50°53' N, 103°66' W	May 13	6.3	None	None	500 glufosinate ammonium + 14.8 clethodim + 206 clopyralid	June 12	None	None

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