

Grain Legumes in Northern Great Plains: Impacts on Selected Biological Soil Processes

Newton Z. Lupwayi* and Ann C. Kennedy

ABSTRACT

Cropping systems in the Northern Great Plains have shifted from fallow-based to legume-based systems. The introduction of grain legumes has impacted soil organisms, including both symbiotic and nonsymbiotic N-fixing bacteria, pathogens, mycorrhizae and fauna, and the processes they perform. These changes occur through effects of legume seed exudates, rhizosphere exudates, and decomposing crop residues. The legume-*Rhizobium* symbiosis results in dinitrogen (N₂) fixation that adds plant available N into the soil system. It is estimated that about 171 million kg N₂ was fixed by field pea (*Pisum sativum* L.), lentil (*Lens culinaris* Medik.), dry bean (*Phaseolus vulgaris* L.), and chickpea (*Cicer arietinum* L.) crops in the Canadian Prairies in 2004, representing 7% of the total fertilizer-N (2580 million kg) used by Canadian prairie farmers in that year. Similarly, an estimated 40 million kg N₂ was fixed by field pea, lentil, and dry bean (including chickpea) crops in U.S. agroecosystems in 2004. Some of the fixed N₂ is recycled for the benefit of nonlegume crops grown after grain legumes. Many other associations benefit from the legume in a cropping system, including mycorrhizal associations that improve plant nutrient and water uptake, changes in the pathogen load and disease development, and overall changes in the soil community. Legumes contribute to greenhouse gas (N₂O and CO₂) emissions during nitrification and denitrification of fixed N. However, because less fertilizer-N is used in legume-based cropping systems, overall greenhouse gas emissions are usually less than those in fertilized monoculture cereals. Therefore, grain legumes in Northern Great Plains have positive effects on agriculture by adding and recycling biologically fixed N₂, enhancing nutrient uptake, reducing greenhouse gas emissions by reducing N fertilizer use, and breaking nonlegume crop pest cycles.

CEREAL-FALLOW ROTATIONS have historically been the predominant cropping system in the semiarid Canadian Prairies and Northern Great Plains of the United States, mainly to reduce the risk of crop failure resulting from soil moisture deficits (Spratt et al., 1975; Grant et al., 2002). It has long been recognized that fallow-based rotations reduce soil organic matter, primarily because little plant C is returned to the soil, but also due to increased soil erosion during the fallow phase (see Janzen, 2001, for a historical perspective of concerns about organic matter loss). Soils in southern Saskatchewan and the Palouse region of the U.S. Pacific Northwest, lost about 50% of the original organic matter after more than 80 yr of wheat-fallow cropping (Campbell and Souster, 1982; Papendick and Parr, 1997; Schnitzer et al., 2006). With the advent of conservation tillage systems (minimum- or zero-tillage) in the 1970s, more soil moisture was conserved than what

was possible under conventional-tillage. Continuous cropping became a viable option for producers because soil moisture was conserved in such tillage systems; consequently, fallow acreages in Canada and the United States began to decline (Fig. 1). Since monoculture cereal cropping often results in pest buildup (Pedersen and Hughes, 1992; Bailey et al., 2001), other crops were sought to include in rotations, as crop diversification was required (see Tanaka et al., 2002, for a historical perspective of cropping systems). Pulse crops became attractive rotation crops, and their acreages increased (Fig. 2). In the Canadian Prairies, field pea is grown on the greatest acreage, while lentil, chickpea, and dry bean are also grown but to a lesser extent (Fig. 2a). In the U.S. Northern Great Plains, dry bean, including chickpea, are the most common, but field pea and lentil are also grown (Fig. 2b).

The introduction of these pulse crops to the previously fallow-based agricultural systems of the Northern Great Plains has many implications, including changes in soil biology and the resultant biological processes. In this paper we discuss the effects of pulse crops on soil microbiological and faunal relationships and some of the processes that occur during, or as a result of, these interactions. The interactions occur mostly in the zone around legume seeds (spermosphere) at planting, around roots (rhizosphere), and inside roots (in nodules or endophytically) during crop growth, and within and near decomposing crop residues (detritusphere) after harvest. In this paper, these zones of activity are described first, followed by a general discussion of the importance of soil biota in sustainable agriculture and the effects that legumes have. The impact of grain legumes on N₂ fixation, N uptake, N cycling, greenhouse gas emissions, and biological pest control are then discussed. Examples from the Northern Great Plains are cited when available, otherwise examples from outside the region are given to illustrate some points. Similarly, examples on grain legumes will be cited where available, otherwise points will be illustrated using other legumes as examples.

MAJOR ZONES OF INTERACTION BETWEEN LEGUMES AND SOIL ORGANISMS

The spermosphere, rhizosphere, root nodules, and detritusphere are the major zones of interaction between legumes and soil microorganisms. The spermosphere is the soil zone surrounding, and influenced by, seeds. The size of the spermosphere is thought to extend anywhere from 5 to 10 mm from the seed (Short and Lacy, 1976; Stanghellini and Hancock, 1971). The term *pathozone* was coined to indicate the zone of influence of the spermosphere in terms of pathogen chemotaxis

N.Z. Lupwayi, Agriculture & Agri-Food Canada, Box 29, Beaverlodge, AB, Canada T0H 0C0; and A.C. Kennedy, USDA-ARS, 217 Johnson Hall, Washington State Univ., Pullman, WA 99164-6421. Received 8 Nov. 2006. *Corresponding author (LupwayiN@agr.gc.ca).

Published in Agron. J. 99:1700–1709 (2007).

Symposium Papers
doi:10.2134/agronj2006.0313s

© American Society of Agronomy
677 S. Segoe Rd., Madison, WI 53711 USA



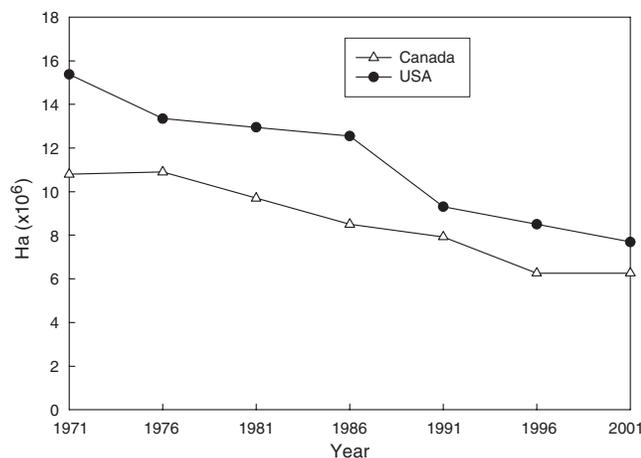


Fig. 1. Land area occupied by summer fallow in Canada and United States from 1971 to 2001. Source of data: Statistics Canada (1999) and USDA (2002), with permission.

(Short and Wyllie, 1978; Gilligan and Bailey, 1997). For field pea, the spermosphere, if defined by the greatest distance that *Fusarium solani* f. sp. *pisi* germinated, is not more than 7 mm. The legume seed is an excellent location for microbial and macrofaunal growth and colonization. A seed progresses from a dormant, nonmetabolic state to, almost instantly, an explosive physiological response with concomitant microbial activity. The carbon released from the imbibing seed provides rich, readily available nutrients to the soil microflora. Exudates and mucilage are in abundant supply and in a constant state of flux in the spermosphere. There are many different types of interactions that can occur once imbibition of water by the seed begins. Some of the interactions are universal and occur across all species, and others are more species- and cultivar-specific (Nelson, 2004; Roberts and Ellis, 1989). These differences can change with seed and seedling maturation (Chanway et al., 1991). Exudation is greater at the emerging radicle than any other place on the seed. The influence will be felt by the entire plant as the microbial community on the seed can be passively carried along as the extending root pushes through soil for long distances. These interactions in the spermosphere can be significant to the plant, as well as the microbial community, as it sets up for the longer term and the effects of the more-influential rhizosphere microflora (Scher et al., 1984).

The rhizosphere is the volume of soil adjacent to, and influenced by, the plant root (Hiltner, 1904) and can extend to more than 5 mm away from the root. The root influences the rhizosphere through release of a variety of organic compounds which serve as sources of energy and nutrients for soil macro- and microbiota. The term *rhizosphere effect* describes the enhanced microbial growth and population densities in the rhizosphere, due to increased soluble C and nutrients, compared with the surrounding bulk soil (Elliott et al., 1984). These organic compounds are deposited in the rhizosphere through root exudation, sloughing-off of root cap cells, secretion of root mucilage, and senescence of root epidermis (Nguyen, 2003). Root exudates include carbohy-

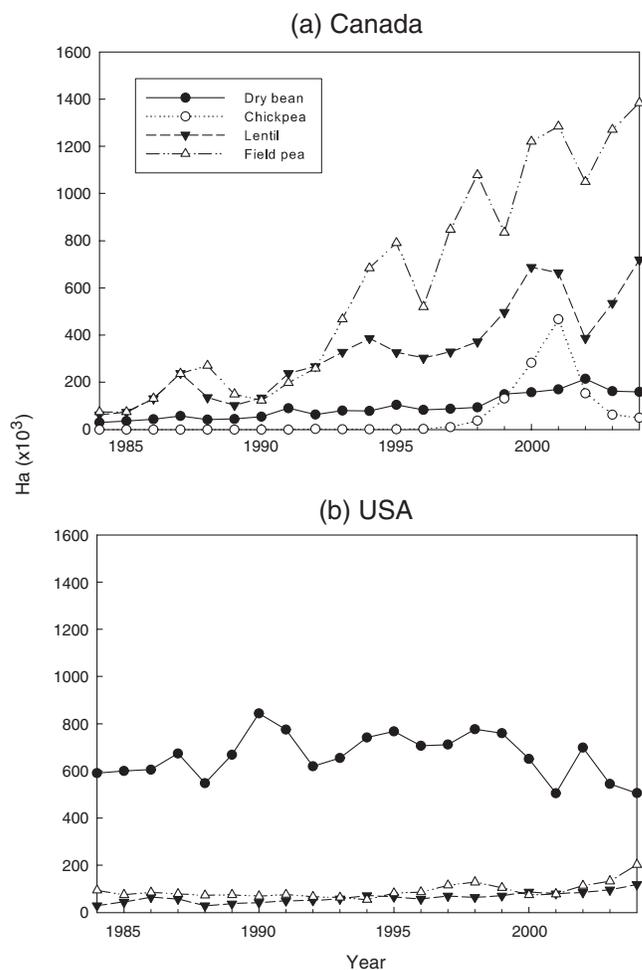


Fig. 2. Land area occupied by grain legume crops in Canada and United States from 1984 to 2004. Source of data: FAO (2005), with permission.

drates, amino acids and amides, aliphatic acids, aromatic acids, phenolic compounds, fatty acids, sterols, vitamins, enzymes, and purines/nucleosides (Dakora and Phillips, 2002; Bertin et al., 2003).

One of the most widely studied beneficial plant-microbe interactions is the symbiotic relationship between legumes and *Rhizobium* spp. (The terms *Rhizobium* or rhizobia are here-in used collectively for the genera *Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Mesorhizobium*, *Allorhizobium*, and *Azorhizobium*, unless specified otherwise.) Interactions between rhizobia and legume roots result in formation of root nodules, in which rhizobia use energy from the host plant to transform (fix) atmospheric N_2 into plant-available forms of N. Before *Rhizobium* can form nodules in legume roots to fix N_2 , the bacterium must be attracted to the roots through bidirectional host-bacterium communication (signaling). Legume root exudates contain chemical compounds, including flavonoids, that attract rhizobia to root hairs (Dakora and Phillips, 2002). Flavonoids are also involved in host specificity of rhizobia. They induce rhizobia to express *nod* genes that are essential for nodulation and host range. These genes encode enzymes that are involved in the synthesis and secretion of host-

specific nodulation signals called Nod factors (Geurts et al., 2005). These factors, which are lipo-chito-oligosaccharides, signal back to the plant and induce deformation of the root hair that results in infection and formation of the root nodule.

After legume crop harvest, residues returned to soil are colonized by soil microorganisms because the residues are a source of C (and other nutrients) for microbial growth and respiration. The litter (crop residue) and the adjacent soil modified by the presence of litter have been called the detritosphere (Gaillard et al., 2003; Poll et al., 2006). The magnitude of the increase in abundance and activity of microorganisms in the detritosphere depends on the biochemical composition of the residues (Gaillard et al., 2003) and environmental factors (e.g., soil temperature and moisture).

SIGNIFICANCE OF SOIL BIOTA AND EFFECTS OF LEGUMES

Soil biota have a profound but often subtle effect on agriculture. The presence of a large and diverse soil microbial and faunal community is crucial to the productivity of any agroecosystem, regardless of management. The soil biota are responsible for many soil processes, which can include residue decomposition, nutrient cycling, organic matter transformations, degradation of agrochemicals, and building soil tilth and structure (Wood, 1991; Swift and Anderson, 1993). Beneficial soil organisms can enhance plant performance by increasing mineral solubilization (Chabot et al., 1996), N₂ fixation (Chemining'wa and Vessey, 2006), production of plant hormones (Brown, 1972; Zahir et al., 2003), and suppression of harmful pathogens (Janvier et al., 2007). Often these organisms can be manipulated to produce beneficial effects for agriculture and the environment; for example, inoculation with rhizobia to increase plant-available N in legumes (Van Kessel and Hartley, 2000; Vessey, 2004), mycorrhizal associations to assist nutrient uptake (Sylvia, 1998; Vazquez et al., 2002; Feng et al., 2003), or biological control of plant pests to reduce chemical inputs (Cook and Baker, 1983; Paulitz, 1991). Soil biotic processes are key in producing and reducing greenhouse gases (Davidson, 1991; Drinkwater et al., 1998). However, their contributions to the complete nutrient budget are not totally understood.

The type and functional characteristics of the species in agroecosystems may be as important as the number of species (Grime, 1997; Hopper and Vitousek, 1997). Microfauna (e.g., protozoa and microbe-feeding nematodes) graze on microflora, and mesofauna (e.g., Collembola and oribatid mites) feed on certain soil fungi. These interactions affect nutrient cycling. Mineralization of N has been found to increase in the presence of microbial grazers due to release of ammonium from consumed rhizosphere bacteria (Alphei et al., 1996). Increasing the density of Collembola has been shown to reduce clover (*Trifolium subterraneum* L.) infection by arbuscular mycorrhizae, P uptake, and growth (Larsen and Jakobsen, 1996). Addition of low C:N ratio organic material (e.g., legume green manure) to soil increases the biomass of bacterivorous (bacteria-feeding) nematodes early in the decomposition process, whereas addition of high C:N ratio organic material (e.g., cereal straw) stimulates fungivorous nematodes late in the decomposition process (Ferris and Matute, 2003; Georgieva et al., 2005). Because of these observations, it has been suggested that nematodes may be useful indicators of substrate quality and nutrient release during residue decomposition (Griffiths, 1994).

The benefits of including a legume in a crop rotation are numerous and have been used for thousands of years to improve crop yields. Legumes in rotation may break a disease cycle, add N and C, and alter the biology of the system. Crop species diversity, cropping intensity, and crop rotation affect microbial activity and diversity (Thomas and Kevan, 1993). The plant community composition may, in fact, drive the soil biotic community (Halvorson et al., 2005). In Saskatchewan, Biederbeck et al. (2005) examined microbial populations and enzyme activities after 6 yr of monoculture wheat, fallow-wheat, or legume green manure-wheat rotations. In almost all cases (except urease activity), microbial populations and enzyme activities were higher in legume-based rotations than in fallow-wheat rotation or monoculture wheat (Table 1). Similarly, in fields with prior history of forage legumes in the crop rotation in Ontario, there were increases in activities of the soil enzymes dehydrogenase, urease, glutaminase, phosphatase, arylsulfatase, and β -glucosidase (Bergstrom et al., 1998). While these examples are from forage or cover crop legumes, it appears likely that rotations containing

Table 1. Effects of legume green manure on soil microbial populations and enzyme activities in the 0- to 10-cm depth after 6 yr (sampled after the wheat phase of the rotations). (Reprinted with modification from Biederbeck et al., 2005, with permission from Elsevier).†

Crop rotation	Organisms g ⁻¹ dry soil		Enzyme activity			
	Bacteria ($\times 10^6$)‡	Fungi ($\times 10^3$)‡	Urease $\mu\text{g U}_h \text{g}^{-1} \text{h}^{-1}$	Dehydrogenase $\mu\text{g TPF g}^{-1} \text{h}^{-1}$	Phosphatase $\mu\text{g PNP g}^{-1} \text{h}^{-1}$	Arylsulfatase $\mu\text{g PNP g}^{-1} \text{h}^{-1}$
Fallow-wheat	16.8e	58d	36.8c	47.3e	537e	30.2e
Wheat-wheat	27.5d	66d	76.3a	63.7d	665d	42.3d
Lentil-wheat	73.0a	130ab	57.0b	109.1a	978a	97.8a
Flatpea-wheat	54.1c	103c	49.3bc	85.6c	833c	73.5c
Vetch-wheat	67.7ab	112bc	55.8b	98.4ab	908b	85.1b
Field pea-wheat	63.4bc	142a	47.5bc	89.1bc	955ab	90.3ab

† Flatpea = *Lathyrus tingitanus* L.; U_h = hydrolyzed urea; TPF = Triphenyl formazan formed; PNP = p-nitrophenol released.

‡ Multiply the reported numbers by this to obtain the actual numbers.

grain legumes will also result in greater microbial activity. In Alberta, microbial diversity of soils under wheat (*Triticum aestivum* L.) preceded by red clover (*Trifolium pratense* L.) or field pea was higher than in wheat preceded by summer fallow or continuous wheat (Lupwayi et al., 1998). A no-till corn (*Zea mays* L.)-soybean [*Glycine max* (L.) Merr.] rotation in Missouri had higher populations of earthworm [*Aporrectodea trapezoids* (Dugés)] than a no-till wheat-corn rotation (Hubbard et al., 1999). Different crops in a rotation, including legumes, were shown to stimulate nonpathogenic strains of *Fusarium oxysporum*, which leads to suppression of Fusarium wilt (Edel et al., 1997).

Legumes may exhibit different effects on the soil biota due to the fact that plants and their seed and root exudates drive the soil biotic activity and community structure near the seed and root. Legume exudates differ in amount and composition from the exudates of other crop species, thus the rhizosphere communities may be different (Duineveld et al., 1998; Ibekwe and Kennedy, 1998; Ohtonen et al., 1999). Field pea and oat (*Avena sativa* L.) seeds exude very different profiles of amino acids, with field pea excreting 22 amino acids while oat excreted only 14 (Powell and Matthews, 1981). Legumes like lupin (*Lupinus albus* L.) and chickpea exude large amounts of organic acids into the rhizosphere, particularly in low-P soils, and these acid exudates mobilize P from pools of otherwise unavailable soil P (Veneklaas et al., 2003). Differences between legumes and other crops in the biochemical composition of their residues also affect the composition of decomposer soil biota. Changes in the diversity and function of the members in a soil food web will influence the productivity of a soil (Thomas and Kevan, 1993). Some of the microbiological processes that are influenced by legume crops include N₂ fixation, N cycling, nutrient uptake, greenhouse gas emissions, and biological pest control.

NITROGEN FIXATION

Grain legumes, in symbiosis with rhizobia, fix up to 450 kg N₂ ha⁻¹ (Unkovich and Pate, 2000). On the lower end of this scale are chickpea (0–141 kg ha⁻¹), dry bean (0–165 kg ha⁻¹), and lentil (5–191 kg ha⁻¹), and on the upper end are lupin (*Lupinus* spp.) (19–327 kg ha⁻¹), faba bean (*Vicia faba* L.) (12–330 kg ha⁻¹) and soybean (0–450 kg ha⁻¹). In the Canadian prairies, Biederbeck et al. (1996) estimated that field pea fixed 90 kg N₂ ha⁻¹, lentil fixed 56 kg ha⁻¹, and dry bean fixed 30 kg ha⁻¹ in 1994. In Saskatchewan, five chickpea varieties fixed an average of 26 kg N₂ ha⁻¹ per year in three seasons (Thavarajah et al., 2005). If these N₂ fixation rates are multiplied by the respective land areas occupied by these crops in 2004 (Fig. 2a), it is estimated that 124.5, 40.3, 4.8, and 1.3 million kg N₂ were fixed by field pea, lentil, dry bean, and chickpea crops, in that order, in Canadian prairie agroecosystems in 2004. Similarly, 18.2, 6.6, and 15.2 kg N₂ were fixed by field pea, lentil, and dry bean (including chickpea) crops, in that order, in U.S. agroecosystems in 2004 if the same N₂ fixation rates are assumed. In Canada, the total 171 million kg N₂ fixed by pulse crops

in 2004 represented 6.6% of the total fertilizer-N (2580 million kilograms) used by prairie farmers in that year (Canadian Fertilizer Institute, 2005).

The increase in pulse acreages in the Northern Great Plains has led to reexamination of inoculant formulations and methods of delivery for N₂-fixing bacteria. Direct application of peat powder inoculant to seed was the most common method until an easier method of seed application with liquid inoculants was introduced (Hynes et al., 1995). Research has since shown that soil inoculation (i.e., direct application of inoculant to the soil in the vicinity of the legume seed) is usually more effective than seed inoculation (Kyei-Boahen et al., 2002; Clayton et al., 2004a, 2004b; Gan et al., 2005a, 2005b). The advantage of using granular inoculants is especially pronounced under soil stress conditions like soil acidity, low soil moisture, or cool, wet soils. Under moisture stress, granular inoculant applied to the soil was more effective in maintaining field pea yield than seed-applied inoculants (Miller et al., 2002). Under cool, wet conditions in the spring, the rhizobial population in field pea rhizosphere continued to increase when granular inoculant was used, but with the seed-applied liquid inoculant, the populations declined for a period of time before recovering (Hynes et al., 2001). If soil inoculation is more effective than seed inoculation, the effectiveness of soil inoculation with liquid inoculant is also worth investigating.

The distribution and diversity of specific strains of N₂-fixing bacteria vary with environmental conditions and presence or absence of legume hosts (Strain et al., 1994). Management, the environment, as well as the plant community, can influence *Rhizobium*, and thus impact the diversity of this group of microorganisms (Turco and Bezdicek, 1987; Hirsch et al., 1993; Strain et al., 1994; Ferreira et al., 2000). Crop rotations in Brazil containing soybean resulted in higher populations and greater diversity and activity of *Bradyrhizobium* than those without soybean, even though more than 15 yr had passed since inoculation (Ferreira et al., 2000). However, research in the Canadian prairies has shown that field pea tend to respond to inoculation even in soils that contain infective and effective indigenous strains of *Rhizobium leguminosarum* bv. *viciae*, (Chemining'wa and Vessey, 2006).

NITROGEN CYCLING

Nitrogen is recycled mostly during decomposition of above- and belowground crop residues. Nitrogen cycling is mainly mediated by soil microorganisms, and the rate and pattern of N release from crop residues is regulated by soil microbial activity and residue quality. Environmental conditions like soil moisture and temperature affect N mineralization by influencing soil microbial activity (Vigil and Kissel, 1995; Agehara and Warncke, 2005). Mineralization of N is usually positively correlated with residue N concentration and negatively correlated with C:N, lignin:N and polyphenol:N ratios (Lupwayi and Haque, 1999; Lupwayi et al., 2006).

Most of the N in legume crops is in the grain and is removed from the farm at harvest in the high-protein legume seeds. This removal of N through grain harvest

means that (i) little N is returned to the soil with pulse crop residues (e.g., 22 kg N ha⁻¹ in field pea residues in northwestern Alberta, Soon and Clayton, 2002); and (ii) the crop residues have wide C:N, lignin:N, and polyphenol:N ratios, and therefore decompose slowly, which means that the little N that they contain is released even more slowly or immobilized by the decomposing microflora. For example, field pea cut at flowering stage had an average C:N ratio of 20 and lignin:N ratio of 2, but the residues after grain harvest had a C:N ratio of 63 and a lignin:N ratio of 14 (Lupwayi et al., 2006). The difference between fixed N and N contained in the harvested grain (i.e., the amount of fixed N that remains after crop harvest) is the N balance, which can be positive (net N credit) or negative (net N deficit). In the Canadian prairies, Biederbeck et al. (1996) estimated net N credits of 18 kg N ha⁻¹ for field pea, 9 kg ha⁻¹ for lentil, and 0 kg ha⁻¹ for dry bean in 1994. In a rotational benefits study in Manitoba, field pea provided the largest and most consistent apparent N benefit (11–14 kg N ha⁻¹ per 1000 kg grain yield) to the following wheat crop, the benefits of chickpea and common bean were inconsistent, and soybean provided virtually no benefit (Przednowek et al., 2004).

Net N credits do not indicate how much of the crop residue N will actually be released to the crops(s) grown after a grain legume crop. ¹⁵Nitrogen studies have shown that a succeeding crop can recover 2 to 26% of the N applied through grain legume residues (Mohr et al., 1998; Giller et al., 1997; Fillery, 2001). Bremer and Van Kessel (1992) estimated that only 7% of N in lentil straw was mineralized in the following growing season and concluded that lentil straw was not a significant source of soil N. Soon and Arshad (2002) and Lupwayi et al. (2006) reported net N mineralization from pea straw of 6 kg N ha⁻¹ and 4 to 18 kg N ha⁻¹, respectively. However, N benefits from pulse crop residues are usually still greater than those from cereal residues, where N is mostly immobilized. The N contribution by decomposing legume roots is usually not added to these estimates due to methodological difficulties.

Nitrogen sparing is another way in which legume crops contribute N to intercropped or rotation crops. Since part of their N requirement is met by N₂ fixation, legumes utilize less of the available soil N than cereals, thereby sparing or conserving inorganic N for the intercrop or following crop (Chalk et al., 1993; Herridge et al., 1995). However, N sparing is not universal because legumes sometimes take up as much or even more soil inorganic N than comparable nonlegume crops (Unkovich and Pate, 2000).

Even when legume crop residues result in short-term N immobilization, they increase soil organic matter when used in crop rotations. Soil organic matter improves the soil physical structure that may reduce soil erosion and increase water and nutrient retention. Grain legumes also increase biological diversity in ecosystems.

NUTRIENT UPTAKE

Mycorrhizae

Mycorrhizae are nonpathogenic fungi that form symbiotic associations with plant roots. Mycorrhizal fungi

associate with roots of pulse crops, and terms like *mycorrhizosphere* (Linderman, 1988) and *hyphosphere* (Li et al., 1991) have been used to describe portions of the rhizosphere in which this association occurs (Linderman, 1988). The beneficial relationship between the two can increase the uptake of nutrients and water in plants, and can influence N₂ fixation in legumes by improving host nutrition (Ocampo, 1986). Hamel (2004) has reviewed the impact of mycorrhizae on crop N and P nutrition. This relationship in turn can also influence other microorganisms in the community by altering nutrient status and other interactions (Johnson et al., 1992). Mycorrhizal associations have the greatest impact on plant growth in stressed environments, P-deficient soils, eroded sites, and acidic or reclaimed lands (Barea, 1991). Crop rotations, especially those with legumes, can increase root colonization by mycorrhizae (Douds et al., 1997). Cover crops, such as vetches (*Vicia* spp.), have been shown to increase the vesicular arbuscular mycorrhizae (VAM) inoculum potential for subsequent crops (Boswell et al., 1998; Galvez et al., 1995). Borie et al. (2002) demonstrated that lupin residues increased mycorrhizal colonization of wheat more than wheat residues, and mycorrhizal wheat acquired more P but less Zn, Cu, Mn, and Al in an acid soil. The interaction involving mycorrhizal fungi and rhizobia may also influence plant growth by increasing N and P acquisition (Xavier and Germida, 2002).

Endophytic Rhizobia

Roots of nonlegume crops grown in rotation with legumes contain endophytic rhizobia. When barley (*Hordeum vulgare*), wheat, and canola (*Brassica rapa* L.) were each grown in monoculture or in rotation with field pea in northern Alberta, populations of endophytic rhizobia up to 7244 cells g⁻¹ root DM were observed in field pea-based rotations, but <10 cells g⁻¹ root DM were observed in monoculture (Lupwayi et al., 2004a). These endophytic rhizobia and other bacteria have been found to increase yields of nonlegume crops (Biswas et al., 2000; Riggs et al., 2001), but there is no conclusive evidence that the benefits involve symbiotic N₂ fixation (James, 2000; Yanni et al., 2001). These bacteria increase yields by stimulating plant growth, increasing disease resistance, or improving the plant's ability to withstand environmental stresses like drought (Dobbelaere et al., 2003). The rhizobia act as plant growth-promoting rhizobacteria (PGPR) that have been shown to expand the root architecture of the crop, enabling it to accumulate more N, P, K, Ca, Mg, Na, Zn, and Mo than control plants (Yanni et al., 2001). Therefore, rhizobia contribute to the rotational benefits of legumes in cropping systems in more ways than fixing N. Even in legumes, seed treatment with rhizobia has been shown to reduce disease incidence. In field experiments in southern Alberta, treatment of field pea and lentil seed with *Rhizobium leguminosarum* bv. *viciae* reduced the incidence of damping-off, a disease caused by soilborne pathogens *Pythium* spp. (Huang and Erickson, 2007). However, the relative roles of crop protection and crop

nutrition in the effects of rhizobia (as PGPR) on non-legume crops require clarification.

GREENHOUSE GAS EMISSION

Legumes contribute to N₂O emissions because the atmospheric N₂ fixed by the legume during *Rhizobium* symbiosis is nitrified and denitrified like fertilizer-N (Rochette et al., 2004). Also, rhizobia in root nodules are capable of denitrification as well as N₂ fixation. While high rates of denitrification by *Rhizobium* species have been shown in laboratory studies, losses of N occurring in the field due to denitrification by these species are inconsistent or not well documented (O'Hara and Daniel, 1985). Therefore, the ecological implications of denitrification by rhizobia are not well understood.

Greenhouse gases (mainly CO₂ and N₂O) are also produced during microbial utilization of organic compounds in the spermosphere, rhizosphere, and detritosphere. Nitrous oxide emissions, in particular, occur during nitrification (in well aerated soil) or denitrification (in poorly aerated soil) of soil N from inorganic or organic sources. The time of gas sampling in relation to the time of residue placement is important in assessing the effects of legume residues on greenhouse gas emissions. When sampling was done only in the following crop in rotation (i.e., months after residue placement in the preceding season), Lupwayi et al. (1999) reported less CO₂ evolution in plots preceded by legume crops than in monoculture wheat. When sampling started at the time of residue placement, results showed a peak of CO₂ evolution within weeks of placement, and the peak was greater and earlier with legume (especially green manure) residues than other residues (Lupwayi et al., 2004b). Similar results were reported by Schomberg and Steiner (1997) and Sarrantonio (2003). Huang et al. (2004) and Toma and Hatano (2007) found that both N₂O and CO₂ emissions were negatively correlated with the C to N ratio of crop residues (i.e., pulse crop residues may produce more N₂O and CO₂ than cereal residues if the pulse residue C to N ratio is narrower than that of cereal residue). When crop rotations that included legume crops were compared with rotations that had no legume crops in research results collated from N₂O measurements in Alberta, Saskatchewan, Ontario, and Quebec over a 10-yr period, Helgason et al. (2005) reported higher N₂O emissions from systems with field pea in rotation than from nonlegume systems even though the non-legume plots received substantially more N fertilization than did the legume system.

Since legume crops are grown with little or no fertilizer-N, emissions of N₂O are expected to be less in a legume crop than in a fertilized cereal crop even though legume root exudates may result in increased gas emissions. This was the case in the Canadian study quoted above (Helgason et al., 2005) when emissions were compared in paired legume (receiving 0 or 5 kg ha⁻¹ fertilizer-N yr⁻¹) vs. nonlegume (receiving 0–190 kg N ha⁻¹ yr⁻¹) crops. In Quebec, Rochette et al. (2004) reported greater N₂O emissions under fertilized timothy grass (*Phleum pratense* L.) than under alfalfa and soybean, and Gregorich et al. (2005) found similar results (legume-based systems vs. fertilized annual crops) in eastern Canada and northeastern United States. In addition, the reduced use of fertilizer-N in legume-based cropping systems means less burning of fossil fuel (CO₂ emission) in manufacturing, transporting, and applying fertilizer-N. In Saskatchewan, Zentner et al. (2001) reported 24% less total energy requirement in a lentil-wheat rotation compared with a wheat-wheat system because lentil N reduced fertilizer-N requirements for subsequent wheat. In Michigan, Robertson et al. (2000) calculated the global warming potentials associated with several fertilizer-based and legume-based cropping systems by weighting each gas (CO₂, N₂O, and CH₄) emitted in each cropping system on the basis of its potency as a greenhouse gas, and aggregating the results. In a corn-soybean-wheat rotation, the tilled and fertilized system had a net GWP of 114, the organic with legume cover crop system 41, and the no-till fertilized system 14 CO₂ equivalents (g m⁻² yr⁻¹) (Table 2). The difference between the first two systems was mainly due to fossil fuel required to produce fertilizer-N and the use of lime. Using similar accounting on a 20-yr field experiment in Ontario, Meyer-Aurich et al. (2006) reported that diversifying corn rotations with soybean and wheat underseeded with red clover (corn-corn-soybean-wheat_{red clover} rotation) resulted in mitigation of about 1300 kg CO₂ equivalents per hectare per year, and that adding alfalfa into a corn rotation (corn-corn-alfalfa-alfalfa rotation) could mitigate more than 2000 kg CO₂ equivalents per hectare per year. The contribution of legumes to greenhouse gas emissions were more than offset by reduced emissions from less fertilizer manufacture and use, and increased soil carbon sequestration. Crews and Peoples (2004) also concluded that obtaining N from legumes is potentially more sustainable than from industrial sources. Therefore, the effects of legumes on greenhouse gas emissions depend on the level at which they are examined (i.e., crop level, farm

Table 2. Relative greenhouse gas global warming potentials (GWPs in g CO₂ equivalents m⁻² yr⁻¹, based on Intergovernmental Panel on Climate Change conversion factors) for different management systems of a corn-soybean-wheat rotation in Michigan from 1991 to 1999. Source: Robertson et al. (2000).

Management	CO ₂				N ₂ O	CH ₄	Net GWP
	Soil C	Fert. N	Lime	Fuel			
Corn-legume-wheat rotation	0	27	23	16	52	-4	114
Conventional-tillage	0	27	23	16	52	-4	114
Organic with legume cover	-29	0	0	19	56	-5	41
No-tillage	-110	27	34	12	56	-5	14

Table 3. Greenhouse gas emissions from legume and nonlegume crops at crop, farm, or national levels.

Level	Source of N ₂ O or CO ₂ emission	Legume crop vs. fertilized cereal crop (in-crop)	Legume crop rotation vs. cereal crop rotation
Crop or crop rotation	1. Fertilizer (inorganic N)	legume < cereal (Rochette et al., 2004; Helgason et al., 2005)	legume < cereal
	2. Crop residues (organic N)	legume = cereal (if both grown after the same nonlegume) [†]	legume > cereal (Lupwayi et al., 2004b; Helgason et al., 2005)
Farm	Fertilizer application	legume < cereal	legume < cereal (Zentner et al., 2001)
National	Fertilizer manufacture and transportation	legume < cereal	legume < cereal (Robertson et al., 2000; Meyer-Aurich et al., 2006)

[†] Decomposition of residues of the preceding nonlegume crop will emit similar amounts of gases in either crop.

level, or national level, Table 3). It is clear that the reduced use of N fertilizers in legume crops results in less gas emissions than fertilized nonlegume crops at farm and national levels due to reduced fuel use in manufacturing, transportation, and application of the fertilizer.

BIOLOGICAL PEST CONTROL

Legume and nonlegume losses from disease and injury, which can be due to bacteria, fungi, viruses, protozoa, nematodes, and other macrofauna, are found throughout agricultural ecosystems. They can have a large impact on plant growth and can be a determining factor in plant productivity (Burdon, 1987). Soilborne pathogens may affect plant competitiveness and plant succession (Van der Putten and Peters, 1997).

The production of amino acids by legume seeds is thought to play a part in the success of plant beneficial microorganisms; however, not all spermosphere environments support biocontrol agents. The biocontrol efficacy of *Pseudomonas putida* N1R on *Pythium ultimum* was due to the competitiveness of the *P. putida* N1R for the seed exudates. Damping off caused by *Pythium* did not succeed when N1R could interfere with the stimulation of *Pythium* by the exudates (Paulitz, 1991). *Pseudomonas cepacia* was an effective biocontrol agent against *Pythium ultimum* when the bacterium was applied to seed and colonized the spermosphere (Parke, 1990). Long-chain saturated fatty acids from seeds stimulate the germination of sporangia of *Pythium ultimum* (Nelson, 1990). *Enterobacter cloacae*, a biocontrol agent used to suppress *Pythium*, reduces the response of *Pythium* to the germinating seed by metabolizing long-chain fatty acid seed exudates (Nelson, 1990). The inactivation of the pathogen by *E. cloacae* occurs with many different plant species, but was not evident with corn or field pea due to their high rate of exudation relative to other plant species. The presence of high levels of sugars may reduce the metabolism of the long-chain fatty acids, and thus reduce the biocontrol efficacy (Kageyama and Nelson, 2003). Legumes have been shown to stimulate several nonpathogenic strains of *F. oxysporum*. An increase in the nonpathogenic strains reduces the impact of *Fusarium* wilt (Edel et al., 1997).

Growing the same crop continuously on the same piece of land fosters buildup of pests (pathogens, insects, and weeds) to which the crop is susceptible. Rotating crops with nonhost crops interrupts the pest cycle. For cereals, rotations with legumes are particularly attrac-

tive because the legumes are likely to contribute N to the soil-plant system as well as interrupt pathogen cycles. In Saskatchewan, sporulation of the soilborne pathogen *Cochliobolus sativus*, which causes common root rot in cereals, on several hosts sampled in the fall was found to be in the order: cereal crops > pulse crops > oilseed crops, forage grasses, and forage legumes (Duczek et al., 1996). Stevenson and Van Kessel (1996) found that the incidence of wheat common root rot had a score of 0.99 (on a 0–4 scale) in a field pea-wheat rotation compared with 3.19 in wheat monoculture. Bailey et al. (2001) found similar results. Downy brome (*Bromus tectorum* L.) weed populations in Alberta were lower in lentil-based and canola-based wheat rotations than in continuous wheat, possibly due to the greater use of selective herbicides in these rotations (Blackshaw et al., 1994). These pest control benefits of legumes do not always occur, and opposite effects on *Pythium* spp. have been reported in wheat in Australia (Pankhurst et al., 1995). However, the increased microbial diversity and activity in legume spermosphere, rhizosphere, or detritosphere usually promotes biological pest control (Janvier et al., 2007).

CONCLUSIONS

The impacts of grain legumes on soil biota begin from the time seed is planted and continue after crop harvest. The altered soil biology has mostly beneficial effects to agriculture by adding and recycling biologically fixed N₂, enhancing nutrient uptake, reducing greenhouse gas emissions by reducing N fertilizer use, and breaking crop pest cycles. Soil inoculation with granular rhizobial inoculant seems to be more effective in increasing N₂ fixation than seed inoculation, but there is need to also investigate soil inoculation using liquid inoculant. Most studies on the contribution of pulse crops to the N economy of the following crop are conducted in only one subsequent crop. Multiyear studies are required to show whether net N immobilization (if it occurs) in the first year of residue decomposition changes to net N mineralization in later years as the C:N ratio narrows. The role of N rhizodeposition in contribution of N to subsequent crops needs further study because usually only contributions from aboveground legume residues are quantified. The increased microbial diversity and activity when legume crops are grown usually mitigates disease through enhanced biological pest control. However, there is need to separate pest control effects resulting from broken pest cycles or increased biological

activity from those resulting from pesticides used in the legume phase of crop rotations. It is also unclear how many years the pest control benefits last after a legume crop. Grain legume crops have increased the sustainability of the wheat-dominated cropping systems of the Northern Great Plains, but further research in the issues outlined here will enhance their impact.

REFERENCES

- Agehara, S., and D.D. Warncke. 2005. Soil moisture and temperature effects on nitrogen release from organic nitrogen sources. *Soil Sci. Soc. Am. J.* 69:1844–1855.
- Alpei, J., M. Bonkowski, and S. Scheu. 1996. Nematoda and Lumbricidae in the rhizosphere of *Hordelemus europaeus* (Poaceae): Faunal interactions, response of microorganisms and effects on plant growth. *Oecologia* 106:111–126.
- Bailey, K.L., G.P. Lafond, P.R. Watson, and D.A. Derksen. 2001. Effect of tillage and crop rotation on root and foliar diseases of wheat and pea in Saskatchewan from 1991 to 1998. *Can. J. Plant Sci.* 81: 789–803.
- Barea, J.M. 1991. Vesicular-arbuscular mycorrhizae as modifiers of soil fertility. *Adv. Soil Sci.* 15:2–40.
- Bergstrom, D.W., C.M. Monreal, and D.J. King. 1998. Sensitivity of soil enzyme activities to conservation practices. *Soil Sci. Soc. Am. J.* 62:1286–1295.
- Bertin, C., X. Yang, and L.A. Weston. 2003. The role of root exudates and allelochemicals in the rhizosphere. *Plant Soil* 256:67–83.
- Biederbeck, V.O., R.P. Zentner, and C.A. Campbell. 2005. Soil microbial populations and activities as influenced by legume green fallow in a semiarid climate. *Soil Biol. Biochem.* 37: 1775–1784.
- Biederbeck, V.O., W.A. Rice, C. van Kessel, L.D. Bailey, and E.C. Huffman. 1996. Present and potential future nitrogen gains from legumes in major soil zones of the prairies. p. 441–455. *In* Soils and Crops 1996 Proceedings. University of Saskatchewan.
- Biswas, J.C., J.K. Ladha, and F.B. Dazzo. 2000. Rhizobia inoculation improves nutrient uptake and growth of lowland rice. *Soil Sci. Soc. Am. J.* 64:1644–1650.
- Blackshaw, R.E., F.J. Larney, C.W. Lindwall, and G.C. Kozub. 1994. Crop production and tillage effects on weed populations on the semi-arid Canadian prairies. *Weed Technol.* 8:231–237.
- Borie, F., Y. Redel, R. Rubio, J.L. Rouanet, and J.M. Barea. 2002. Interactions between crop residue application and mycorrhizal development and some soil–root interface properties and mineral acquisition by plants in an acidic soil. *Biol. Fertil. Soils* 36:151–160.
- Boswell, E.P., R.T. Koide, D.L. Shumway, and H.D. Addy. 1998. Winter wheat cover cropping, VA mycorrhizal fungi and maize growth and yield. *Agric. Ecosyst. Environ.* 67:55–65.
- Bremer, E., and C. van Kessel. 1992. Plant available nitrogen from lentil and wheat residues during a subsequent growing season. *Soil Sci. Soc. Am. J.* 56:1155–1160.
- Brown, M.E. 1972. Plant growth substances produced by microorganisms of soil and rhizosphere. *J. Appl. Bacteriol.* 35:443–451.
- Burdon, J.J. 1987. Diseases and plant population biology. Cambridge Univ. Press, New York.
- Campbell, C.A., and W. Souster. 1982. Loss of organic matter and potentially mineralizable N from Saskatchewan soils due to cropping. *Can. J. Soil Sci.* 62:651–656.
- Canadian Fertilizer Institute. 2005. Canadian fertilizer information system: Retail sales statistics—fertilizer year ended June 30th, 2004. Available at www.cfi.ca/files/publications/statistical_documents/CFIS_Retail_2004.PDF [posted 10 May 2004; accessed 2 Apr. 2007; verified 18 Sept. 2007]. Canadian Fertilizer Institute, Ottawa, ON.
- Chabot, R., H. Antoun, and M.P. Cescas. 1996. Growth promotion of maize and lettuce by phosphate-solubilizing *Rhizobium leguminosarum* biovar *phaseoli*. *Plant Soil* 184:311–321.
- Chalk, P.M., C.J. Smith, S.D. Hamilton, and P. Hopmans. 1993. Characterization of the N benefit of a grain legume (*Lupinus angustifolius* L.) to a cereal (*Hordeum vulgare* L.) by an *in situ* ¹⁵N isotope dilution technique. *Biol. Fertil. Soils* 15:39–44.
- Chanway, C.P., R.R. Turkington, and F.B. Holl. 1991. Ecological implications of specificity between plants and spermosphere microorganisms. *Adv. Ecol. Res.* 21:121–169.
- Chemining'wa, G.N., and J.K. Vessey. 2006. The abundance and efficacy of *Rhizobium leguminosarum* bv. *Viciae* in cultivated soils of the eastern Canadian prairie. *Soil Biol. Biochem.* 38:294–302.
- Clayton, G.W., W.A. Rice, N.Z. Lupwayi, A.M. Johnston, G.P. Lafond, C.A. Grant, and F. Walley. 2004a. Inoculant formulation and fertilizer nitrogen effects on field pea: Nodulation, nitrogen fixation and nitrogen partitioning. *Can. J. Plant Sci.* 84:79–88.
- Clayton, G.W., W.A. Rice, N.Z. Lupwayi, A.M. Johnston, G.P. Lafond, C.A. Grant, and F. Walley. 2004b. Inoculant formulation and fertilizer nitrogen effects on field pea: Crop yield and quality. *Can. J. Plant Sci.* 84:89–96.
- Cook, R.J., and K.F. Baker. 1983. The nature and practice of biological control of plant pathogens. *Am. Phytopathological Soc., St. Paul, MN.*
- Crews, T.E., and M.B. Peoples. 2004. Legume versus fertilizer sources of nitrogen: Ecological tradeoffs and human needs. *Agric. Ecosyst. Environ.* 102:279–297.
- Dakora, F.D., and D.A. Phillips. 2002. Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant Soil* 245: 35–47.
- Davidson, E.A. 1991. Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems. p. 219–235. *In* J.E. Rogers and W.B. Whitman (ed.) Microbial production and consumption of greenhouse gases “methane, nitrogen oxides, and holomethanes.” ASM Press, Am. Soc. of Microbiology, Washington, DC.
- Dobbelaere, S., J. Vanderyeden, and Y. Okon. 2003. Plant growth-promoting effects of diazotrophs in the rhizosphere. *Crit. Rev. Plant Sci.* 22:107–149.
- Douds, D.D., Jr., L. Galvez, M. Franke-Snyder, C. Reider, and L.E. Drinkwater. 1997. Effect of compost addition and crop rotation point upon VAM fungi. *Agric. Ecosyst. Environ.* 65:257–266.
- Drinkwater, L.E., P. Wagoner, and M. Sarrantonio. 1998. Legume-based cropping systems have reduced carbon and nitrogen losses. *Nature* 396:262–265.
- Duczek, L.J., L.L. Jones-Flory, S.L. Reed, K.L. Bailey, and G.P. Lafond. 1996. Sporulation of *Bipolaris sorokiniana* on the crowns of crop plants grown in Saskatchewan. *Can. J. Plant Sci.* 76:861–867.
- Duineveld, B.M., A.S. Rosado, J.D. van Elsas, and J.A. van Veen. 1998. Analysis of the dynamics of bacterial communities in the rhizosphere of the chrysanthemum via denaturing gradient gel electrophoresis and substrate utilization patterns. *Appl. Environ. Microbiol.* 64:4950–4957.
- Edel, V., C. Steinberg, N. Gautheron, and C. Alabouvette. 1997. Populations of non-pathogenic *Fusarium oxysporum* associated with roots of four plant species compared to soil-borne populations. *Phytopathology* 87:693–697.
- Elliott, L.F., G.M. Gilmour, J.M. Lynch, and D. Tittmore. 1984. Bacterial colonization of plant roots. p. 1–16. *In* R.L. Todd and J.E. Giddens (ed.) Microbial–plant interactions. SSSA, Madison, WI.
- FAO. 2005. FAOSTAT data, 2005. [updated 20 Dec. 2004]. Food and Agriculture Organization, Rome.
- Feng, G., Y.C. Song, X.L. Li, and P. Christie. 2003. Contribution of arbuscular mycorrhizal fungi to utilization of organic sources of phosphorus by red clover in a calcareous soil. *Appl. Soil Ecol.* 22:139–148.
- Ferreira, M.C., D. de S. Andrade, K.M. de O. Chueire, S.M. Takemura, and M. Hungria. 2000. Tillage method and crop rotation effects on the population sizes and diversity of *Bradyrhizobia* nodulating soybean. *Soil Biol. Biochem.* 32:627–637.
- Ferris, H., and M.M. Matute. 2003. Structural and functional succession in the nematode fauna of a soil food web. *Appl. Soil Ecol.* 23:93–110.
- Fillery, I.R.P. 2001. The fate of biologically fixed nitrogen in legume-based dryland farming systems: A review. *Aust. J. Exp. Agric.* 41:361–381.
- Gaillard, V., C. Chenu, and S. Recous. 2003. Carbon mineralization in soil adjacent to plant residues of contrasting biochemical quality. *Soil Biol. Biochem.* 35:93–99.
- Galvez, L., D.D. Douds, Jr., P. Wagoner, L.R. Longnecker, L.E. Drinkwater, and R.R. Janke. 1995. An overwintering cover crop increases inoculum of VAM fungi in agricultural soil. *Am. J. Alter. Agric.* 10:152–156.

- Gan, Y., K.G. Hanson, R.P. Zentner, F. Selles, and C.L. McDonald. 2005a. Response of lentil to microbial inoculation and low rates of fertilization in the semiarid Canadian prairies. *Can. J. Plant Sci.* 85:847–855.
- Gan, Y., F. Selles, K.G. Hanson, R.P. Zentner, B.G. McConkey, and C.L. McDonald. 2005b. Effect of formulation and placement of *Mesorhizobium* inoculants for chickpea in the semiarid Canadian prairies. *Can. J. Plant Sci.* 85:555–560.
- Georgieva, S., S. Christensen, and K. Stevnbak. 2005. Nematode succession and microfauna-microorganism interactions during root residue decomposition. *Soil Biol. Biochem.* 37:1763–1774.
- Geurts, R., E. Federova, and T. Bisseling. 2005. Nod factor signaling genes and their function in the early stages of *Rhizobium* infection. *Curr. Opin. Plant Biol.* 8:346–352.
- Giller, K.E., G. Cadisch, C. Ehaliotis, E. Adams, W.D. Sakala, and P.L. Mafongonya. 1997. Building soil nitrogen capital in Africa. p. 151–192. *In* R.J. Buresh et al. (ed.) *Replenishing soil fertility in Africa*. SSSA Spec. Publ. 51. SSSA and ASA, Madison, WI.
- Gilligan, C.A., and D.J. Bailey. 1997. Components of pathozone behaviour. *New Phytol.* 75:475–490.
- Grant, C.A., G.A. Peterson, and C.A. Campbell. 2002. Nutrient considerations in diversified cropping systems in the northern Great Plains. *Agron. J.* 94:186–198.
- Gregorich, E.G., P. Rochette, A.J. VandenBygaart, and D.A. Angers. 2005. Greenhouse gas contributions of agricultural soils and potential mitigation practices in Eastern Canada. *Soil Tillage Res.* 83:53–72.
- Griffiths, B.S. 1994. Microbial-feeding nematodes and protozoa in soil: Their effects on microbial activity and nitrogen mineralization in decomposing hotspots and rhizosphere. *Plant Soil* 164:25–33.
- Grime, J.P. 1997. Biodiversity and ecosystem function: The debate deepens. *Science* 277:1260–1261.
- Halvorson, J.J., J.L. Smith, and A.C. Kennedy. 2005. Lupine effects on soil development and function during early primary succession at Mount St. Helens. p. 243–254. *In* V.H. Dale et al. (ed.) *Ecological responses to the 1980 eruptions of Mount Saint Helens*. Springer-Verlag, New York.
- Hamel, C. 2004. Impact of arbuscular mycorrhizal fungi on N and P cycling in the root zone. *Can. J. Soil Sci.* 84:383–395.
- Helgason, B.L., H.H. Janzen, M.H. Chantigny, C.F. Drury, B.H. Ellert, E.G. Gregorich, R.L. Lemke, E. Patty, P. Rochette, and C. Wagner-Riddle. 2005. Toward improved coefficients for predicting direct N₂O emissions from soil in Canadian agroecosystems. *Nutr. Cycling Agroecosyst.* 72:87–99.
- Herridge, D.F., H. Maecellos, W.L. Felton, G.L. Turner, and M.B. Peoples. 1995. Chickpea increases soil N fertility in cereal systems through nitrate sparing and N₂ fixation. *Soil Biol. Biochem.* 27:545–551.
- Hiltner, L. 1904. Über neuere Erfahrungen und Probleme auf dem Gebiet der Bodenbakteriologie und unter besonderer Berücksichtigung der Gründung und Brache. (In German.) *Arb. Dtsch. Landwirtschaft. Ges. Berlin* 98:59–78.
- Hirsch, P.R., M.J. Jones, S.P. McGrath, and K.E. Giller. 1993. Heavy metals from past applications of sewage sludge decrease the genetic diversity of *Rhizobium leguminosarum* biovar *trifolii* populations. *Soil Biol. Biochem.* 25:1485–1490.
- Hopper, D.U., and P.M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302–1305.
- Huang, H.C., and R.S. Erickson. 2007. Effect of seed treatment with *Rhizobium leguminosarum* bv. *viciae* on *Pythium* damping-off, seedling height, root nodulation, root biomass, shoot biomass, and seed yield of pea and lentil. *J. Phytopathol.* 155:31–37.
- Huang, Y., J. Zou, X. Zheng, Y. Wang, and X. Xu. 2004. Nitrous oxide emissions as influenced by amendment of plant residues with different C:N ratios. *Soil Biol. Biochem.* 36:973–981.
- Hubbard, V.C., D. Jordan, and J.A. Stecker. 1999. Earthworm response to rotation and tillage in a Missouri claypan soil. *Biol. Fertil. Soils* 29:343–347.
- Hynes, R.K., D.C. Jans, E. Bremer, N.Z. Lupwayi, W.A. Rice, G.W. Clayton, and M.M. Collins. 2001. *Rhizobium* population dynamics in pea rhizosphere after application of different inoculant formulations. *Can. J. Microbiol.* 47:595–600.
- Hynes, R.K., K.A. Kraig, D. Covert, R.S. Smith, and R.J. Rennie. 1995. Liquid rhizobial inoculants for lentil and field pea. *J. Prod. Agric.* 8:547–552.
- Ibekwe, A.M., and A.C. Kennedy. 1998. Phospholipid fatty acid profiles and carbon utilization patterns for analysis of microbial community structure under field and greenhouse conditions. *FEMS Microbiol. Ecol.* 26:151–163.
- James, E.K. 2000. Nitrogen fixation in endophytic and associative symbiosis. *Field Crops Res.* 65:197–209.
- Janvier, C., F. Villeneuve, C. Alaabouvette, V. Edel-Hermann, T. Mateille, and C. Steinberg. 2007. Soil health through soil disease suppression: Which strategy from descriptors to indicators? *Soil Biol. Biochem.* 39:1–23.
- Janzen, H.H. 2001. Soil science on the Canadian Prairies—Peering into the future from a century ago. *Can. J. Soil Sci.* 81:489–503.
- Johnson, N.C., D. Tilman, and D. Wedin. 1992. Plant and soil controls on mycorrhizal fungal communities. *Ecol.* 73:2034–2042.
- Kageyama, K., and E.B. Nelson. 2003. Differential inactivation of seed exudate stimulation of *Pythium ultimum* sporangium germination by *Enterobacter cloacae* influences biological control efficacy on different plant species. *Appl. Environ. Microbiol.* 69:1114–1120.
- Kyei-Boahen, S., A.E. Slinkard, and F.L. Walley. 2002. Evaluation of rhizobial inoculation methods for chickpea. *Agron. J.* 94:851–859.
- Larsen, J., and I. Jakobsen. 1996. Effects of mycophagous Collembola on the symbiosis between *Trifolium subterraneum* and three arbuscular mycorrhizal fungi. *New Phytol.* 133:295–302.
- Li, X.L., E. George, and H. Marschner. 1991. Phosphorus depletion and pH decrease at the root–soil and hyphae–soil interfaces of VA mycorrhizal white clover fertilized with ammonium. *New Phytol.* 119:397–404.
- Linderman, R.G. 1988. Mycorrhizal interactions with the rhizosphere microflora: The mycorrhizosphere effect. *Phytopathology* 78:366–370.
- Lupwayi, N.Z., G.W. Clayton, K.G. Hanson, W.A. Rice, and V.O. Biederbeck. 2004a. Endophytic rhizobia in barley, wheat and canola roots. *Can. J. Plant Sci.* 84:37–45.
- Lupwayi, N.Z., G.W. Clayton, J.T. O'Donovan, K.N. Harker, T.K. Turkington, and W.A. Rice. 2004b. Soil microbiological properties during decomposition of crop residues under conventional and zero tillage. *Can. J. Soil Sci.* 84:411–419.
- Lupwayi, N.Z., G.W. Clayton, J.T. O'Donovan, K.N. Harker, T.K. Turkington, and Y.K. Soon. 2006. Nitrogen release during decomposition of crop residues under conventional and zero tillage. *Can. J. Soil Sci.* 86:11–19.
- Lupwayi, N.Z., G.W. Clayton, and W.A. Rice. 1999. Soil microbial biomass and carbon dioxide flux under wheat as influenced by tillage and crop rotation. *Can. J. Soil Sci.* 79:273–280.
- Lupwayi, N.Z., and I. Haque. 1999. *Leucaena* hedgerow intercropping and cattle manure application in the Ethiopian highlands. I. Decomposition and nutrient release. *Biol. Fertil. Soils* 28:182–195.
- Lupwayi, N.Z., W.A. Rice, and G.W. Clayton. 1998. Soil microbial diversity and community structure under wheat as influenced by tillage and crop rotation. *Soil Biol. Biochem.* 30:1733–1741.
- Meyer-Aurich, A., A. Weersink, K. Janovicek, and B. Deen. 2006. Cost-efficient rotation and tillage options to sequester carbon and mitigate GHG emissions from agriculture in eastern Canada. *Agric. Ecosyst. Environ.* 117:119–127.
- Miller, P.R., B.G. McConkey, G.W. Clayton, S.A. Brandt, J.A. Staricka, A.M. Johnston, G.P. Lafond, B.G. Schatz, D.D. Baltzenberger, and K.E. Neill. 2002. Pulse crop adaptation in the northern Great Plains. *Agron. J.* 94:261–272.
- Mohr, R.M., H.H. Janzen, E. Bremer, and M.H. Entz. 1998. Fate of symbiotically-fixed ¹⁵N₂ as influenced by method of alfalfa termination. *Soil Biol. Biochem.* 30:1359–1367.
- Nelson, E.B. 1990. Exudate molecules initiating fungal responses to seeds and roots. *Plant Soil* 129:61–73.
- Nelson, E.B. 2004. Microbial dynamics and interactions in the spermosphere. *Annu. Rev. Phytopathol.* 42:271–309.
- Nguyen, C. 2003. Rhizodeposition of organic C by plants: Mechanisms and controls. *Agronomie* 23:375–396.
- Ocampo, J.A. 1986. Vesicular-arbuscular mycorrhizal infection of “host” and “non-host” plants: Effect on the growth responses of the plants and the competition between them. *Soil Biol. Biochem.* 18:607–610.
- O'Hara, G.W., and R.M. Daniel. 1985. Rhizobial denitrification: A review. *Soil Biol. Biochem.* 17:1–9.

- Ohtonen, R., H. Fritze, T. Pennanen, A. Jumpponen, and J. Trappe. 1999. Ecosystem properties and microbial community changes in primary succession on a glacier forefront. *Oecologia* 119:239–246.
- Pankhurst, C.E., H.J. McDonald, and B.G. Hawke. 1995. Influence of tillage and crop rotation on the epidemiology of *Pythium* infections of wheat in a red-brown earth of South Australia. *Soil Biol. Biochem.* 27:1065–1073.
- Papendick, R.I., and J.F. Parr. 1997. No-till farming: The way of the future for a sustainable dryland agriculture. *Ann. Arid Zone* 36: 193–208.
- Parke, J.L. 1990. Population dynamics of *Pseudomonas cepacia* in the pea spermosphere in relation to biocontrol of *Pythium*. *Phytopathology* 80:1307–1311.
- Paulitz, T.C. 1991. Effect of *Pseudomonas putida* on the stimulation of *Pythium ultimum* by seed volatiles of pea and soybean. *Phytopathology* 81:1282–1287.
- Pedersen, E.A., and G.R. Hughes. 1992. The effect of crop rotation on development of the septoria disease complex on spring wheat in Saskatchewan. *Can. J. Plant Pathol.* 14:152–158.
- Poll, C., J. Ingwersen, M. Stemmer, M.H. Gerzabek, and E. Kandeler. 2006. Mechanisms of solute transport affect small-scale abundance and function of soil microorganisms in the detritusphere. *Eur. J. Soil Sci.* 57:583–595.
- Powell, A.A., and S. Matthews. 1981. A physical explanation for solute leakage from dry pea embryos during imbibition. *J. Exp. Bot.* 32: 1045–1050.
- Przednowek, D.W.A., M.H. Entz, B. Irvine, D.N. Flatten, and J.R. Thiessen. 2004. Rotational yield and apparent N benefits of grain legumes in southern Manitoba. *Can. J. Plant Sci.* 84: 1093–1096.
- Riggs, P.J., M.K. Chelius, A.L. Iniguez, S.M. Kaepler, and E.W. Triplett. 2001. Enhanced maize productivity by inoculation with diazotrophic bacteria. *Aust. J. Plant Physiol.* 28:829–836.
- Roberts, E.H., and R.H. Ellis. 1989. Water and seed survival. *Ann. Bot. (Lond.)* 63:39–52.
- Robertson, G.P., E.A. Paul, and R.R. Harwood. 2000. Greenhouse gases in intensive agriculture: Contributions of individual gases to the radiative forcing of the atmosphere. *Science* 289:1922–1925.
- Rochette, P., D.A. Angers, G. Belanger, M.H. Chantigny, D. Prevoist, and G. Levesque. 2004. Emission of N₂O from alfalfa and soybean crops in eastern Canada. *Soil Sci. Soc. Am. J.* 68:493–506.
- Sarrantonio, M. 2003. Soil response to surface-applied residues of varying carbon–nitrogen ratios. *Biol. Fertil. Soils* 37:175–183.
- Scher, F.M., M. Dupler, and R. Baker. 1984. Effect of synthetic iron chelates on population densities of *Fusarium oxysporum* and the biological control agent *Pseudomonas putida* in soil. *Can. J. Microbiol.* 30:1271–1275.
- Schomberg, H.H., and J.L. Steiner. 1997. Estimating crop residue decomposition coefficients using substrate-induced respiration. *Soil Biol. Biochem.* 29:1089–1097.
- Schnitzer, M., D.F.E. McArthur, H.R. Schulten, L.M. Kozak, and P.M. Huang. 2006. Long-term cultivation effects on the quantity and quality of organic matter in selected Canadian prairie soils. *Geoderma* 130:141–156.
- Short, G.E., and M.L. Lacy. 1976. Factors affecting pea seed and seedling rot in soil. *Phytopathology* 66:188–192.
- Short, G.E., and T.D. Wyllie. 1978. Inoculum potential of *Macrophomina phaseolina*. *Phytopathology* 68:188–192.
- Soon, Y.K., and M.A. Arshad. 2002. Comparison of the decomposition and N and P mineralization of canola, pea and wheat residues. *Biol. Fertil. Soils* 36:10–17.
- Soon, Y.K., and G.W. Clayton. 2002. Eight years of crop rotation and tillage effects on crop production and N fertilizer use. *Can. J. Soil Sci.* 82:165–172.
- Spratt, E.D., J.H. Strain, and B.J. Gorby. 1975. Summer fallow substitutes for western Canada. *Can. J. Plant Sci.* 55:477–484.
- Stanghellini, M.E., and J.G. Hancock. 1971. Radial extent of the bean spermosphere and its relation to the behavior of *Pythium ultimum*. *Phytopathology* 61:165–168.
- Statistics Canada. 1999. Canada Year Book, 1999. Statistics Canada, Ottawa, ON.
- Stevenson, F.C., and C. van Kessel. 1996. A landscape-scale assessment of the nitrogen and non-nitrogen rotation benefits of pea. *Soil Sci. Soc. Am. J.* 60:1797–1805.
- Strain, S.R., K. Leung, T.S. Whittam, F.S. de Bruijn, and P.J. Bottomley. 1994. Genetic structure of *Rhizobium leguminosarum* biovar *trifolii* and *viciae* populations found in two Oregon soils under different plant communities. *Appl. Environ. Microbiol.* 60:2772–2778.
- Swift, M.J., and J.M. Anderson. 1993. Biodiversity and ecosystem function in agricultural systems. p. 15–41. *In* E.D. Schulze and H.A. Mooney (ed.) *Biodiversity and ecosystem function*. Springer-Verlag, Berlin.
- Sylvia, D.M. 1998. Mycorrhizal symbioses. p. 408–426. *In* D.M. Sylvia et al. (ed.) *Principles and applications of soil microbiology*. Prentice Hall, NJ.
- Tanaka, D.L., J.M. Krupinsky, M.A. Liebig, S.D. Merrill, R.E. Ries, J.R. Hendrickson, H.A. Johnson, and J.D. Hanson. 2002. Dynamic cropping systems: An adaptable approach to crop production in the Great Plains. *Agron. J.* 94:957–961.
- Thavarajah, D., R.A. Ball, and J.J. Schoenau. 2005. Nitrogen fixation, amino acid, and ureide associations in chickpea. *Crop Sci.* 45: 2497–2502.
- Thomas, V.G., and P.G. Kevan. 1993. Basic principles of agroecology and sustainable agriculture. *J. Agric. Environ. Ethics* 5:1–18.
- Toma, Y., and R. Hatano. 2007. Effect of crop residue C:N ratio on N₂O emissions from Gray Lowland soil in Mikasa, Hokkaido, Japan. *Soil Sci. Plant Nutr.* 53:198–205.
- Turco, R.F., and D.F. Bezdicsek. 1987. Diversity within two serogroups of *Rhizobium leguminosarum* native to soils in the Palouse of Eastern Washington. *Ann. Appl. Biol.* 111:103–114.
- Unkovich, M.J., and J.S. Pate. 2000. An appraisal of recent field measurements of symbiotic N₂ fixation by annual legumes. *Field Crops Res.* 65:211–228.
- USDA. 2002. Major uses of land in the United States. Available at <http://www.ers.usda.gov/Briefing/LandUse/majorlandusechapter.htm> [updated 18 Oct. 2005; accessed 24 Apr. 2007; verified 19 Sept. 2007]. USDA-Economic Research Service, Washington, DC.
- Van der Putten, W.H., and B.A.M. Peters. 1997. How soil-borne pathogens may affect plant competition. *Ecol.* 78:1785–1795.
- Van Kessel, C., and C. Hartley. 2000. Agricultural management of grain legumes: Has it led to an increase in nitrogen fixation? *Field Crops Res.* 65:165–181.
- Vazquez, M.M., J.M. Barea, and R. Azcon. 2002. Influence of arbuscular mycorrhizae and a genetically modified strain of *Sinorhizobium* on growth, nitrate reductase activity and protein content in shoots and roots of *Medicago sativa* as affected by nitrogen concentrations. *Soil Biol. Biochem.* 34:899–905.
- Veneklaas, E.J., J. Stevens, G.R. Cawthray, S. Turner, A.M. Grigg, and H. Lambers. 2003. Chickpea and white lupin rhizosphere carboxylates vary with soil properties and enhance phosphorus uptake. *Plant Soil* 248:187–197.
- Vessey, J.K. 2004. Benefits of inoculating legume crops with rhizobia in the Northern Great Plains. Available at www.plantmanagementnetwork.org/cm/. Crop Manage.
- Vigil, M.F., and D.E. Kissel. 1995. Rate of nitrogen mineralized from incorporated crop residues as influenced by temperature. *Soil Sci. Soc. Am. J.* 59:1636–1644.
- Wood, M. 1991. Biological aspects of soil protection. *Soil Use Manage.* 7:130–136.
- Xavier, L.J.C., and J.J. Germida. 2002. Response of lentil under controlled conditions to co-inoculation with arbuscular mycorrhizal fungi and rhizobia varying in efficacy. *Soil Biol. Biochem.* 34: 181–188.
- Yanni, Y.G., R.Y. Rizk, F.K. Abd-El-Fattah, A. Squartini, V. Corich, A. Giacomini, F. de-Bruijn, J. Rademaker, F.J. Maya, P. Ostrom, M. Vega-Hernandez, R.I. Hollingsworth, E. Martinez-Molina, P. Mateos, E. Velazquez, J. Wopereis, E. Triplett, M. Umali-Garcia, J.A. Anarna, B.G. Rolfe, J.K. Ladha, J. Hill, R. Mujoo, P.K. Ng, and F.B. Dazzo. 2001. The beneficial plant growth-promoting association of *Rhizobium leguminosarum* bv. *trifolii* with rice roots. *Aust. J. Plant Physiol.* 28:845–870.
- Zahir, Z.A., M. Arshad, and W.T. Frankenberger, Jr. 2003. Plant growth promoting rhizobacteria: Applications and perspectives in agriculture. *Adv. Agron.* 81:97–168.
- Zentner, R.P., C.A. Campbell, V.O. Biederbeck, P.R. Miller, F. Selles, and M.R. Fernandez. 2001. In search of a sustainable cropping system for the semiarid Canadian Prairies. *J. Sustain. Agric.* 18: 117–135.