
Critical Reviews in Plant Sciences
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/bpts20

# Plant Life History and Residue Chemistry Influences Emissions of $CO_2$ and $N_2O$ From Soil - Perspectives for Genetically Modified Cell Wall Mutants

Shamim Gul [a b] & Joann Whalen [a]

[a] Department of Natural Resource Sciences, Macdonald Campus , McGill University , 21 111 Lakeshore Road, Ste-Anne-de-Bellevue, Quebec , H9X 3V9 , Canada

[b] Department of Botany , University of Balochistan , Saryab Road, Quetta , Balochistan , Pakistan

Published online: 29 Apr 2013.

To cite this article: Shamim Gul & Joann Whalen (2013): Plant Life History and Residue Chemistry Influences Emissions of $CO_2$ and $N_2O$ From Soil - Perspectives for Genetically Modified Cell Wall Mutants, Critical Reviews in Plant Sciences, 32:5, 344-368

To link to this article: http://dx.doi.org/10.1080/07352689.2013.781455

*Critical Reviews in Plant Sciences*, 32:344–368, 2013

ISSN: 0735-2689 print / 1549-7836 online
DOI: 10.1080/07352689.2013.781455

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# Plant Life History and Residue Chemistry Influences Emissions of $CO_2$ and $N_2O$ From Soil – Perspectives for Genetically Modified Cell Wall Mutants

**Shamim Gul[1,2] and Joann Whalen[1]**

[1]*Department of Natural Resource Sciences, Macdonald Campus, McGill University, 21 111 Lakeshore Road, Ste-Anne-de-Bellevue, Quebec H9X 3V9, Canada*

[2]*Department of Botany, University of Balochistan, Saryab Road, Quetta, Balochistan, Pakistan*



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Address correspondence to Dr. Shamim Gul, Lecturer, Department of Botany, University of Balochistan, Saryab Road, Quetta, Balochistan, Pakistan, Cell Phone # +923362005882. E-mail: shamim.gul@mail.mcgill.ca

**Vascular plants have lignified tissues that transport water, minerals, and photosynthetic products throughout the plant. They are the dominant primary producers in terrestrial ecosystems and capture significant quantities of atmospheric carbon dioxide ($CO_2$) through photosynthesis. Some of the fixed $CO_2$ is respired by the plant directly, with additional $CO_2$ lost from rhizodeposits metabolized by root-associated soil microorganisms. Microbially-mediated mineralization of organic nitrogen (N) from plant byproducts (rhizodeposits, dead plant residues) followed by nitrification generates another greenhouse gas, nitrous oxide ($N_2O$). In anaerobic soils, reduction of nitrate by microbial denitrifiers also produces $N_2O$. The plant-microbial interactions that result in $CO_2$ and $N_2O$ emissions from soil could be affected by genetic modification. Down-regulation of genes controlling lignin biosynthesis to achieve lower lignin concentration or a lower guaiacyl:syringyl (G:S) ratio in above-ground biomass is anticipated to produce forage crops with greater digestibility, improve short rotation woody crops for the wood-pulping industry and create second generation biofuel crops with low ligno-cellulosic content, but unharvested residues from such crops are expected to decompose quickly, potentially increasing $CO_2$ and $N_2O$ emissions from soil. The objective of this review are the following: 1) to describe how plants influence $CO_2$ and $N_2O$ emissions from soil during their life cycle; 2) to explain how plant residue chemistry affects its mineralization, contributing to $CO_2$ and $N_2O$ emissions from soil; and 3) to show how modification of plant lignin biosynthesis could influence $CO_2$ and $N_2O$ emissions from soil, based on experimental data from genetically modified cell wall mutants of *Arabidopsis thaliana*. Conceptual models of plants with modified lignin biosynthesis show how changes in phenology, morphology and biomass production alter the allocation of photosynthetic products and carbon (C) losses through rhizodeposition and respiration during their life cycle, and the chemical composition of plant residues. Feedbacks on the soil environment (mineral N concentration, soil moisture, microbial communities, aggregation) affecting $CO_2$ and $N_2O$ emissions are described. Down-regulation of the Cinnamoyl CoA Reductase 1 (*CCR1*) gene is an excellent target for highly digestable forages and biofuel crops, but *A. thaliana* with this mutation has lower plant biomass and fertility, prolonged vegetative growth and plant residues that are more susceptible to biodegradation, leading to greater $CO_2$ and $N_2O$ emissions from soil in the short term. The challenge in future crop breeding efforts will be to select tissue-specific genes for lignin biosynthesis that meet commercial demands without compromising soil $CO_2$ and $N_2O$ emission goals.**

**Keywords** carbon cycle, carbon sequestration, decomposition, genetically modified crop, mineralization, soil microbial community

## I. INTRODUCTION

Increasing emission of greenhouse gases (GHG) such as $CO_2$ and $N_2O$ is of environmental concern. The contribution of $CO_2$ and $N_2O$ to global warming is 60% and 6%, respectively (Dalal and Allen, 2008). The $CO_2$ concentration has increased from approximately 280 ppm to 380 ppm since 1750 (Dalal and Allen, 2008) and this value is increasing by 1.8 ppm $yr^{-1}$ (Tans, 2012). The $N_2O$ concentration increased from 270 ppb to 319 ppb during the same period (Dalal and Allen, 2008) and is increasing linearly by approximately 0.26% $yr^{-1}$ (IPCC, 2007). Over a 100 year time frame, the global warming potential of $N_2O$ is 298 times greater than $CO_2$ and it also contributes to destruction of the stratospheric ozone layer (Ravishankara *et al.*, 2009). Increasing $CO_2$ concentration is mainly from human activities such as fossil fuel combustion, cement production, land use change and agricultural practices whereas the increased $N_2O$ emission is predominantly due to greater use of N fertilizer in agriculture (Dalal and Allen, 2008).

Vascular plants influence emissions of $CO_2$ and $N_2O$ from soil during their growth and when their dead residues are incorporated in soil (Figure 1). Considering the $CO_2$ emissions first, we begin with photosynthesis, a chemical reaction that fixes $CO_2$ into organic compounds in green plants. About 30 to 50% of the fixed $CO_2$ is respired daily and returns to the atmosphere, with about half of this respiration attributed to the

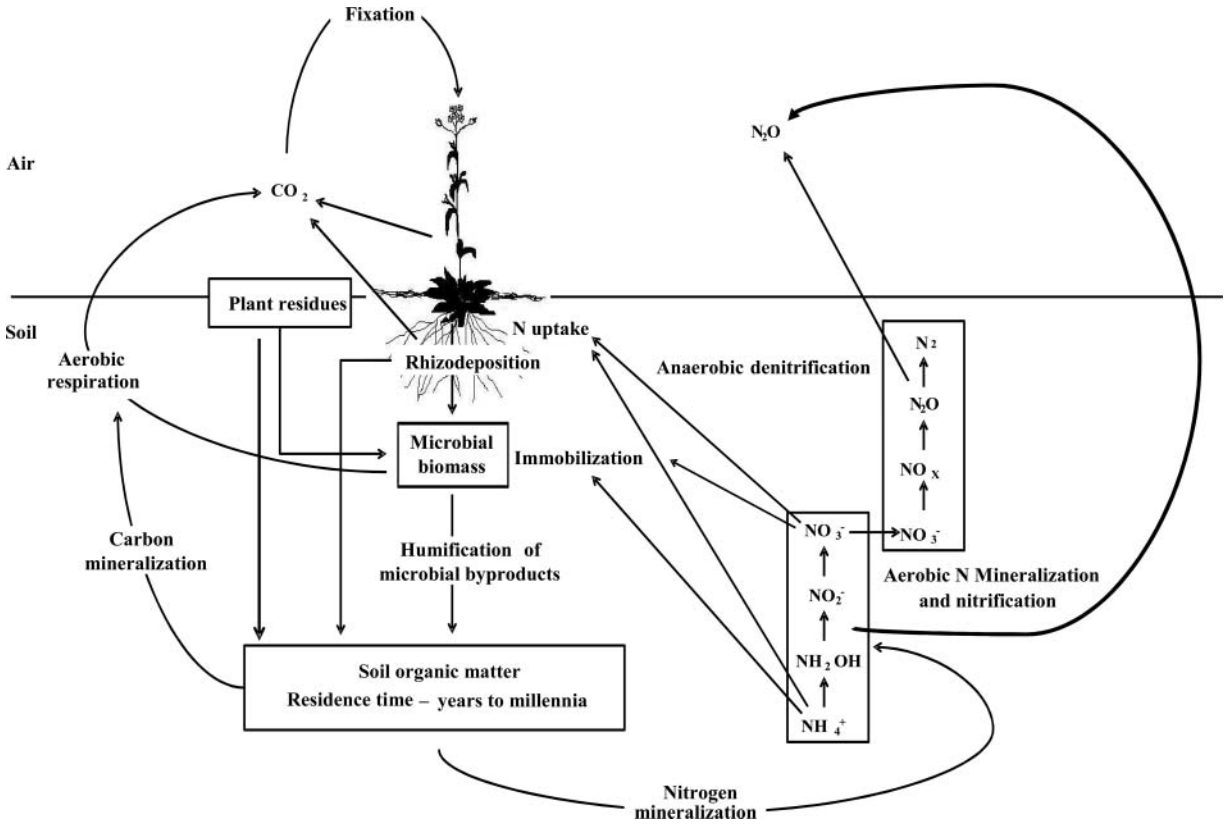


FIG. 1. Hypothetical model illustrating factors affecting $CO_2$ and $N_2O$ emission from soil and the role of plants in controlling emissions of these gases through their influence on microbial biomass increment in soil by organic matter input (plant residues and rhizodeposits.)

metabolic activities of roots and root-associated microorganisms (Atwell *et al.*, 1999). Root-associated microorganisms are fueled by rhizodeposits such as sloughed root cells, sugars, proteins and other compounds that are released into the soil surrounding roots. Based on studies with different plant species, Hutsch *et al.* (2002) demonstrated that about 20% of the $CO_2$ fixed during the plant life cycle is transferred to soil through rhizodeposition, while literature reviewed by Lynch and Whipps (1990) reveals that root exudates account for up to 40% (or more) dry matter production by plants. Rhizodeposits may be metabolized completely to $CO_2$, or transformed by microorganisms into soil organic matter (SOM). The SOM pool undergoes slow mineralization to $CO_2$ as well (Figure 1).

Fixed $CO_2$-C retained in the plant during its life span is allocated to cellular components (e.g., cell walls), tissues and organs. After death of the plant or plant organs (i.e., senesced leaves and fine roots, broken twigs, etc.), the residue is mineralized by soil microorganisms to produce $CO_2$-C or transformed into SOM. Some slowly decomposable compounds to biodegradation in the residues (e.g., lignin) remain undecomposed for a decade or longer due to their complex chemical structure (Marschner *et al.*, 2008). Carbon mineralization from the SOM pool is accompanied by N mineralization, which releases mineral N compounds (primarily ammonium, $NH_4^+$ and nitrate, $NO_3^-$) from organic N compounds. Nitrogen mineralization is a source of $NH_4^+$ for plant uptake and immobilization in microbial biomass. This reaction produces $N_2O$ as a byproduct of ammonia oxidation (Figure 1), also known as nitrifier denitrification, in well aerated soils (Wrage *et al.*, 2001; Bernard *et al.*, 2005). When the soil $NO_3^-$ concentration exceeds plant uptake and immobilization, and there is labile organic C (e.g., from rhizodeposition or dead residues) and anaerobic soil conditions, the denitrification process contributes to $N_2O$ emission from soil (Canfield *et al.*, 2010), as illustrated in Figure 1. The contribution of each process (nitrifier denitrification vs. denitrification) to $N_2O$ emissions from soil depends on factors such as oxygen ($O_2$) concentration (Khalil *et al.*, 2004), mineral N fertilizer inputs (Rochette *et al.*, 2008) and the concentration of labile organic C, which supplies energy for the denitrification reaction (Miller *et al.*, 2008). Nitrate is the preferred as a terminal electron acceptor in the reaction, so the $N_2O$ emission is proportional to soil $NO_3^-$ concentration under anaerobic conditions (Huang *et al.*, 2004; Miller *et al.*, 2008; Richardson *et al.*, 2009).

Given that $CO_2$ and $N_2O$ production in soils are largely driven by microbially-mediated reactions, how do plants interact with soil microorganisms to influence the emissions of these GHG? Rhizodeposition is one way that plants introduce substrates into the soil environment that stimulate respiration

by root-associated microorganisms. As the quantity and chemical composition of rhizodeposits varies during the plant life span, temporal variation in the response of root-associated microorganisms is expected. Roots consume $O_2$ and emit $CO_2$, which can create a redox gradient that favors facultative anaerobic microorganisms such as denitrifiers in root-associated soil. Transpiration affects the soil water content and the concentration of nutrients moving by mass flow (e.g., $NO_3^-$), another example of how plants create micro-environments around their roots. If transpiration is impeded and the soil $NO^3_-$ concentration remains high, this could facilitate denitrification and possibly lead to greater $N_2O$ emissions from root-associated soil.

Dead plant residues play an important role in influencing $CO_2$ emission from soil. The rate of C mineralization depends on plant residue chemistry, namely the concentration of lignin, concentration of acid unhydrolyzable fraction (AUF) and C:N ratio (Kirk, 1975; Johnson *et al.*, 2007; Blanco-Canqui and Lal, 2009). AUF is the product of gravimetric method for separation of various components of cell wall (Van Soest et al., 1991). In many published articles the AUF was cited as lignin but because it contains insoluble lipids (suberin for bark and roots, cutins and waxes for leaves and fruits), soluble polyphenolics and condensed tannins along with lignin, Preston *et al*., (1997, 2006, 2009) and Lorenz *et al.* (2007) called it as AUF or acid insoluble residue (AIR). AUF is relatively recalcitrant to biodegradation compared to other C-rich substances in plants (Melillo *et al.*, 1982; Cadish and Giller, 1997). The soil residence time of lignin was estimated at 14 to 22 years for agricultural crops, whereas hemicellulose and cellulose were largely degraded within a year (Marschner *et al.*, 2008). Moreover, as lignin is the second most abundant plant derived organic compound after polysaccharides (Boerjan *et al.*, 2003), it physically limits microbial access to labile organic compounds within a plant cell (Austin and Ballare, 2010). Microbial breakdown of complex biomolecules provides energy and substrates for microbial growth, and the C:N ratio of plant residues is an indicator of whether microorganisms can obtain enough N from residue biodegradation to meet their protein requirements. Therefore, concentration of lignin (and AUF) and C:N ratio in plant residues are important factors influencing $CO_2$ emissions from soil (Yanni *et al.*, 2011). Plant residue chemistry also affects N mineralization (Vandat *et al.*, 2011), nitrification and denitrification reactions (Millar and Baggs, 2004; Frimpong and Baggs, 2010) that lead to $N_2O$ emissions from soil. The direct and indirect interactions between plants and microorganisms that affect these reactions will be discussed in more detail in this review.

Modifying lignin biosynthesis in plants is of great interest to plant scientists because it can improve the characteristics of commercially important crops. Efforts have focused on reducing the lignin concentration or changing lignin chemistry to make the plant more readily biodegradable when it is eaten by an animal (e.g., improved forages) or in a feedstock destined for biofuel production (e.g., second generation lignocelullosic biofuel crops). Lignin biosynthesis takes place in two main pathways: (1) the formation of coenzyme A-thioesters of ferulic, 4-coumari, and sinapic acid from phenylpropanoid pathway, and (2) their reduction to coniferyl, 4-coumaryl and sinapyl alcohol (Boerjan *et al.*, 2003; Petersen *et al.*, 2010). These monolignols (coniferyl, 4-coumaryl, and sinapyl alcohol) act as building blocks of lignin monomers, the syringyl, vanillyl/guaiacyl and cinnamyl phenols, and their derivatives (Otto and Simpson 2006). There are a number of candidate genes for modifying plant lignin concentration (Zhong *et al.* 2008; see Table 1 for enzymes involved in the biosynthesis of lignin and their abbreviations). Down-regulation of Cinnamyl Alcohol Dehydrogenase (CAD), Caffeoyl CoA 3-O-Methyl Transferase (*CCOMT*), coniferaldehyde 5-hydroxylase (*CAld5H*), Cinnamyl CoA-Reductase (*CCR1*), Early Arabidopsis Aluminum-Induced Gene 1 (*EARLI1*), 4-coumarate: CoA Ligase (4CL) reduces lignin concentration and/or lignin chemistry in terms of G:S ratio, commonly in stem tissues (see Table 2 for references). In contrast, the Production of Anthocyanin Pigment1 (*PAP1*/*MYB75*) and Knotted *Arabidopsis Thaliana 7* (*KNAT7*) knockout mutations increase secondary cell wall thickness and give greater lignin concentration, particularly in stems (see Table 2 for references).

TABLE 1
Enzymes controlling biosynthesis of lignin and their abbreviations

| Enzyme | Abbreviation |
|---|---|
| 4-coumarate: CoA ligase1 | 4CL |
| Cinnamyl alcohol dehydrogenase | CAD |
| Coniferaldehyde 5-hydroxylase | CAld5H |
| Caffeoyl CoA 3-O-methyl transferase | CCOMT |
| Cinnamyl CoA-reductase 1 | CCR1 |
| Corngrass 1 | Cg1 |
| Caffeic acid O-methyl transferase | COMT |
| Early Arabidopsis aluminum-induced gene 1 | EARLI1 |
| Shikimate hydroxycinnamoyl transferase | HCT |
| Knotted Arabidopsis thaliana 7 | KNAT7 |
| Production of anthocyanin pigment 1/ myeloblast 75 | PAP1/MYB75 |

Most of the work to date on modifying lignin biosynthesis in plants has focused on genetic and physiological responses such as gene expression, biochemistry of lignin monomers and histochemical analysis of lignin in tissues. There is evidence that mutations associated with lignin biosynthesis change plant phenological and morphological traits, as well as the residue chemistry (see Table 2 for references), all of which can potentially influence the emissions of $CO_2$ and $N_2O$ from soil. This article aims to show how modifying lignin biosynthesis in plants can affect the plant-microbial interactions affecting C and N mineralization, leading to feedbacks on GHG emissions from soil.

TABLE 2
Cell wall phenotype and plant morphological and phenological traits of various down-regulated (k/o) and over expression (o/x) cell wall mutants

| Plant species | mutant gene | Lignin or AUF concentration (mg $g^{-1}$ of plant material) | G:S ratio | Plant morphology and biomass | Plant Fertility | Plant phenology | References |
|---|---|---|---|---|---|---|---|
| *Populus tremuloides* | *4CL* k/o | Low | nd[*1] | Nd | ..[*2] | – | Roque-Rivera *et al.* (2011) |
| Rice | *4CL* k/o | Low | High | Dwarf | Low | – | Gui *et al.* (2011) |
| *A. thaliana* | *CAD, CCR1* k/o double mutant | Low | – | Dwarf | Low | Delayed senescence | Thevenin *et al.* (2011) |
| *Medicago sativa* | *CAD* k/o | Low | – | Reduced biomass in severely down-regulated lines | – | No difference | Jackson *et al.* (2008) |
| *Nicotiana tabacum* | *CAD* k/o | Low | High | Nd | nd | – | Sirisha *et al.* (2012) |
| *Populus tremuloides* | *CAld5H* o/x | nd | Low | Dwarf, low leaf area | – | – | Hencock *et al.* (2007) |
| *Populus tremuloides* | *CAld5H* o/x | nd | Low | Nd | – | – | Roque-Rivera *et al.* (2011) |
| *Populus tremuloides* | *4CL* k/o + *CAld5H* o/x | Low | Low | Dwarf, lower leaf, stem and root biomass | – | – | Roque-Rivera *et al.* (2011) |
| *Panicum virgatum* | *Cg1* expression | Low | – | Dwarf, moderate expression cause many leaves, thicker stems, many branches | – | No flowering | Chuck *et al.* (2011) |
| *A. thaliana* | *CCOMT* k/o | Low | Low | Dwarf | – | – | Do *et al.* (2007) |
| Poplar | *CCOMT* k/o | Low | – | – | – | – | Zhong *et al.* (2000) |
| Tobacco | *CCOMT* k/o | Low | – | Dwarf | – | – | Pincon *et al.* (2001) |
| *A. thaliana* | *COMT* k/o | nd | High | nd | nd | Early flowering | Goujon *et al.* (2003), Gul (data unpublished) |
| *Nicotiana tabacum* | *COMT* k/o | nd | High | Nd | – | – | Pincon *et al.* (2001), Atanassova *et al.* (1995) |
| Poplar | *COMT* k/o | nd | – | Nd | – | – | Halpin *et al.* (2007) |
| Rye grass | *COMT* k/o | Low | Low | – | nd | – | Tu *et al.* (2010) |
| *A. thaliana* | *CCR* k/o | Low | – | Dwarf | Low | Delayed senescence | Jones *et al.* (2001), Gul (2012a) |
| *Medicago sativa* | *CCR* k/o | Low | – | Reduced biomass in most down-regulate lines | – | nd | Jackson *et al.* (2008) |
| *Nicotiana tabacum* | *CCR* k/o | Low | Low | Dwarf | – | – | Piquemal *et al.*, (1998) |
| Poplar | *CCR* k/o | Low | High | Dwarf in field conditions | – | – | Leple *et al.* (2010) |
| Rye grass | *CCR* k/o | Low | Low | – | nd | – | Tu *et al.* (2010) |
| *A. thaliana* | *EARLI1* k/o | Low | – | smaller leaves | Low | Early flowering | Shi *et al.* (2011) |
| *Medicago sativa* | *HCT* (k/o) | Low | – | Dwarf and reduced biomass in severely down-regulated lines | Low in severely down-regulated lines | Delayed flowering in severely down-regulated lines | Shadle *et al.* (2007) |
| *A. thaliana* | *KNAT7* k/o | High | High | Nd | nd | nd | Gul (2012a) |
| *A. thaliana* | *MYB75* k/o | High | High | nd[1] | nd | nd | Gul (2012a) |

1 nd abbreviate for "not different" than their wild ecotype
2 – Represents no published data

The objectives of this review are 1) to describe how plants influence $CO_2$ and $N_2O$ emissions from soil during their life cycle, 2) to explain how plant residue chemistry affects its mineralization, contributing to $CO_2$ and $N_2O$ emissions from soil, and 3) to show how modification of plant lignin biosynthesis could influence $CO_2$ and $N_2O$ emissions from soil, based on experimental data from genetically modified cell wall mutants of *Arabidopsis thaliana*. Conceptual models and experimental evidence from studies with cell wall mutants demonstrate how modified lignin biosynthesis can influence upon $CO_2$ and $N_2O$ emissions from soil during the plant life cycle and through mineralization of plant residues.

## II. PLANT LIFE HISTORY INFLUENCES $CO_2$ AND $N_2O$ EMISSIONS

Living plants induce $CO_2$ emissions from the plant-soil system directly from root respiration and indirectly through their interactions with soil microorganisms. Direct root respiration is related to root biomass and metabolic activity, which varies among plant species and during a plant's life span. Indirect $CO_2$ emissions are the result of microbial respiration induced by plant activities, primarily rhizodeposition, but also alteration of the soil conditions in the rhizosphere (e.g., water relations, soluble nutrient concentration; Henry *et al*., 2005). Temporal fluctuations in the indirect $CO_2$ emissions are related to factors such as the amount and chemical composition of rhizodeposits produced at different growth stages during the plant life span, soil moisture regimes and soil nutrient availability. Factors affecting $N_2O$ emissions from the plant-soil system are complex, but generally peak when conditions favor denitrification due to sufficient soluble C, $NO_3^-$ and temporary water-logging (anaerobic) in microsites or in the bulk soil. Activities of denitrification enhance when the water filled pore space of soil exceeds 70% (Baruah *et al.,* 2010) due to paucity of oxygen ($O_2$) in soil by its consumption in aerobic respiration and restriction of $O_2$ penetration into soil by high water contents. During their growth and development, plants influence $CO_2$ and $N_2O$ emissions from soil through their phenology, morphological traits and plant fertility as outlined in Figure 2 and explained in the following sections.

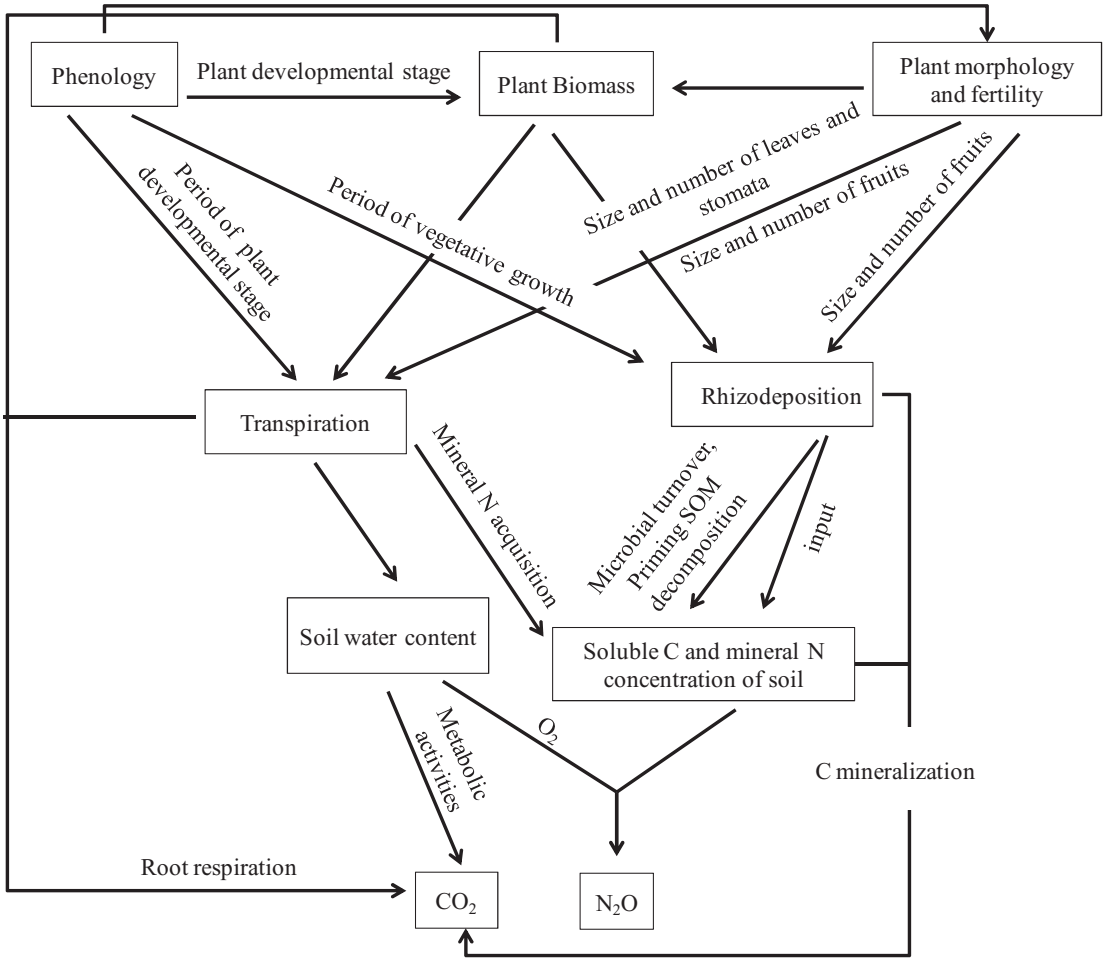


FIG. 2. Hypothetical model illustrating the role of morphological and phenological traits of *A. thaliana* cell wall mutants upon $CO_2$ and $N_2O$ emission from soil. Plant phenology, morphology and plant fertility influence emissions of $CO_2$ and $N_2O$ via water contents, amount of mineral N and rhizodeposits of soil.

## A. Plant Phenology

The term phenology refers to the development, differentiation, and initiation of plant organs (Hodges, 1991). Plant phenology is divided into two main phases: 1) vegetative growth phase that is related to the development and growth of the vegetative plant body, i.e., leaves, stems, and roots, and 2) reproductive growth phase when a plant develops flowers and fruits. Plant phenology is an important controller of resource acquisition from soil (Nord and Lynch, 2009) and it has a differential influence on 1) amount and chemical composition of rhizodeposits, on a per unit dry weight of roots basis 2), rate of transpiration and 3) uptake of mineral N. All these factors also influence $CO_2$ and $N_2O$ emissions from soil, as illustrated in Figure 2 and is further discussed in following sections.

### *1. Root-derived rhizodeposition*

Growth of the vegetative organs is rapid during vegetative stage and slows down during reproductive stage when most of energy and nutrients are translocated to flower and seed development. Thus the degree of resource allocation (photosynthates) to a given plant organ varies with developmental stages. The vegetative growth phase is characterized by a higher resource allocation to roots (Warembourg and Estelrich, 2001). After 21 d, *A. thaliana* roots comprised 15–20% of the total plant biomass (Cambui et al., 2011). Root growth is important for water acquisition, to increase the surface area of roots for the absorption of mineral nutrients from soil, and to anchor plants in soil (Peng *et al*., 2012).

Roots deposit organic substances in soil. Root exudates can account for up to 40% or more of the dry matter produced by plants (review by Lynch and Whipps 1990; Hutsch et al., 2002). Warembourg and Estelrich (2000) found that in three months old bromegrass (*Bromus erectus*) grown in fertile and nutrient poor soils had net $^{14}C$ assimilation of 31% and 36% in roots, respectively, of which 24% and 23% was respired by roots and soil microorganisms, and 21% and 12% was found in soil matrix. Likewise, in two species of bromegrass; *Bromus madritensis* and *B. erectus* respectively, the annual net assimilated $^{14}C$ in roots was 37% and 49%, of which 34% and 31% respired by roots and microorganisms, 22% and 17% was found in soil matrix (Warembourg and Estelrich 2001).

Plant derived rhizodeposits comprise 1) sloughed-off cells and tissues at the root cap, 2) high-molecular-weight compounds such as extracellular enzymes and mucilage that contain polysaccharides (Waisel *et al.*, 2003, Shukla *et al.*, 2011), phospholipids (Read *et al.*, 2003) and unidentified substances (Shukla *et al.*, 2011) and 3) low-molecular-weight compounds such as sugars, amino acids, phenolics, nucleotides and vitamins. (Waisel *et al.*, 2003, Jones *et al.*, 2009; Shukla *et al.*, 2011). The secretion of high-molecular and low-molecular-weight organic compounds takes place via exocytosis and diffusion, respectively (Waisel *et al.*, 2003; Neumann 2007). The concentration of root exudates varies along the root, with higher concentrations found at the root apices and very near of root cap of primary and secondary roots (Curl and Truelove, 1986; Waisel *et al.*, 2003). Paterson (2003) found that soluble C accounts for 1–10% of total C in root exudates whereas, Hutsch *et al.* (2002) reported 79% soluble C in the root exudates of maize. Consequently, microbial activity and respiration are elevated in the rhizosphere relative to bulk soil, particularly in zones where soluble C is excreted.

Amount of rhizodeposition varies among plant species (Grayston *et al.*, 1997; Haynes and Beare, 1997; Van der Krift *et al.*, 2001; Hutsch *et al.*, 2002; Weisskopf *et al.*, 2008; Zhang *et al.*, 2011). For instance, in a study with 12 mediterranean species of grasses, legumes and non-leguminous forbs at vegetative growth stage using $^{14}C$ tracers, Warembourg *et al.* (2003) found that rhizosphere respiration was significantly lower in non-legume forbs (42% of total $^{14}C$ assimilated) than grasses (46%) and legumes (51%). Rhizosphere respiration was positively correlated with the concentration of root N and $^{14}C$ in solution used for washing roots. Kuzyakov and Domanski (2000) reported that wheat and barley translocated respectively 20%-30% of total assimilated C belowground. Of this, about 50% was found in root biomass, around 1/3 was respired as $CO_2$ by roots and microorganisms in rhizosphere, and the rest of the assimilate was incorporated into microbial biomass, whereas pastures translocated 30%–50% of assimilated C belowground whereas the pattern of translocation was almost similar to crop plants.

Environmental conditions also influence rhizodeposition (Carvalhais *et al.*, 2011; Lopez-Bellido *et al.*, 2011; Wittenmayer and Merbach, 2005; Yao *et al.*, 2012). For example in *Lolium multiflorum*, N fertilization (180 $\mu$moles N $d^{-1}$ in a microcosom) promoted the root growth, with an increase of up to 35% in root surface area and as much as 28% more root exudation compared to control (Henry *et al.*, 2005). Bengough *et al.* (2011) found marked negative influence of mechanical impedance and water stress on root elongation, which in turn is expected to reduce root growth and root exudation. Biotic factors such as competition and the soil microbial community structure (symbionts, pathogens) also influence the amount and quality of root exudation. A detailed review explaining how biotic and abiotic factors influence root exudation is provided by Jones *et al.* (2004) and Wichern *et al.* (2008). How root exudates influence emissions of $CO_2$ and $N_2O$ at different developmental stages of plant (i.e. vegetative vs reproductive phase) is explained in section I. and is further described in section II. A. 1a and 4.

*a. Influence of rhizodeposition on $CO_2$ emission from soil in perspective of plant phenology.* The $CO_2$ production from the rhizosphere comes from root respiration, mineralization of root exudates (Billes and Bottner, 1981; Sparling *et al.*, 1982), faunal grazing on rhizosphere microorganisms (Griffiths, 1994) and SOM decomposition (Kuzyakov, 2002; Kuzyakov *et al.*, 2007; Graaff *et al.*, 2009; Bird *et al.*, 2011; Marianne *et al.*, 2011). In fact, the "priming" effect (Kuzyakov, 2002) of rhizodeposition on soil microbial activity is important for SOM turnover and dynamics. In a greenhouse study, Bird *et al.* (2011) observed a

20% reduction in the SOM of a grassland soil after two cycles of *Avena barbata* plantation, compared to unplanted soil.

Root derived rhizodeposits are a readily metabolizable C substrate for microorganisms (Kuzyakov, 2002). Consequently, the rhizosphere, considered to be soil under the influence of roots has a higher microbial abundance than bulk soil and is a zone of intense microbial activities (Hiltner, 1904; Vale *et al.*, 2005; Richard *et al.* 2011). Bodelier *et al.* (1997) reported 19 to 32 times greater number of *Pseudomonas chlororaphis* in the rhizosphere of *Glyceria maxima* than the bulk soil.

Phenology, which refers to the development, differentiation, and initiation of plant organs (Hodges, 1991), clearly influences root growth and root exudation (i.e., amount and chemical composition of rhizodeposits). The amount of root exudates varies with plant age (Gransee and Wittenmayer 2000; Warembourg and Esterlich 2001; Hutsch *et al.*, 2002; Kuzyakov, 2002). The rhizodeposition per unit dry mass of roots is higher at the vegetative growth stage than the reproductive growth stage (Gransee and Wittenmayer 2000; Warembourg and Esterlich 2001; Hutsch *et al.*, 2002; Kuzyakov, 2002; Mougel *et al.*, 2006) due to greater below ground resource allocation (Warembourg and Estelrich 2001; Sey *et al.*, 2010) and greater root growth rate (Peng *et al.*, 2012). Likewise, the chemical composition of plant derived rhizodeposits varies with plant age (Hutsch *et al.*, 2002; Shaw and Burns, 2003; Mougel *et al.*, 2006). Gransee and Wittenmayer (2000) reported that in root exudates of pea and maize plants, the amount of sugars decreased relative to hot water soluble substances (e.g., carboxylic acids) with increasing plant age. Therefore the microbial $CO_2$ respiration from the rhizosphere per unit dry weight of roots under optimal plant growth conditions is expected to be higher at the vegetative growth phase due to higher root derived rhizodeposits per unit dry weight of roots (as root development is rapid during vegetative growth stage) and secretion of easily biodegradable organic compounds in greater amount as compared to reproductive stage.

### 2. *Rate of transpiration*

Plant biomass and rate of transpiration are positively related (Xu *et al.*, 2006; Novak and van Genuchten, 2008; Kanemoto *et al.*, 2009; Li *et al.*, 2010; Lai *et al.*, 2011; Matsunami *et al.*, 2012). In a study with 35 wetland plants, Lai *et al.* (2011) found that the plant species with higher biomass had higher transpiration rate and greater N uptake. Likewise in a study with 70 rice cultivars, Matsunami *et al.* (2012) found a positive correlation between plant dry weight and water uptake ability.

### 3. *Nitrogen uptake by plants*

The biomass of vascular plants increases as plant grows with the uptake of water and nutrients from soil. Barbanti *et al.* (2011) reported that the mineral N concentration after 20 days of seedling emergence of sorghum was 53 mg $kg^{-1}$ in compost-amended soil and 38 mg $kg^{-1}$ in the control soil, which dropped to $< 5$ mg N $kg^{-1}$ soil by the end of the growing season. Likewise, Gul (2012a) found that the concentration of mineral N in soil planted with *Arabidopsis thaliana* was 16 mg $kg^{-1}$ during the vegetative stage whereas at the fruit developing stage, the concentration dropped to $\sim$5 mg N $kg^{-1}$ soil.

Plant biomass and uptake of mineral N are positively related (Singh and Arora, 2001; Tian *et al.*, 2006: Richard-Molard *et al.*, 2008; Shahzad *et al.*, 2012). For example, in a study with twenty wheat varieties of different heights, Singh and Arora (2001) found a strong positive correlation between N uptake and dry matter production under both normal and nutrient limited conditions. In another study, Richard-Molard *et al.* (2008) found a variation in N acquisition and growth rate in two genotypes of *Arabidopsis thaliana*. The *A. thaliana* line that had higher biomass acquired more mineral N from soil. Tian *et al.* (2006) reported a positive relation for N uptake with leaf area and root growth in two varieties of wheat. Similar results were reported by Peng *et al.* (2010) for two other varieties of wheat in which the N acquisition was found positively related with shoot growth potential and root growth. However, exceptions exist. For example, Bertholdsson and Stoy (1995) observed variation in N uptake for two varieties of wheat for N uptake. The genotype with higher protein content had also higher N contents instead of lower biomass.

### 4. *Influence of phenology on $N_2O$ emission*

Phenology should also influence $N_2O$ emissions from soil. Because of the higher amount of rhizodeposition at the vegetative growth phase of plants, the mineralization of organic N (whether it comes from rhizodeposition or from the residual SOM), should be higher at this growth phase of plants. For example, Jensen (1996) found that in barley, about 50% of rhizodeposited N was mineralized at an early stage of plant development while only 23% was mineralized at maturity.

In unfertilized soils, the source of N in the rhizosphere comes from residual mineral N and microbially mineralized N. Rhizosphere microbes immobilize N from the surrounding soil, root exudates and from mineralized SOM (Kuzyakov, 2002; Paterson, 2003). Rhizodeposits have high C:N ratio (Kuzyakov, 2002; Paterson, 2003). The C:N ratio of rhizodeposits is much higher than that of bacteria; bacterial C:N ratio range from 5:1 to 6:1 (literature review by kuzyakov, 2002). This high C:N ratio increases the competition between plant and microbes for mineral N in the surrounding environment. This factor creates a priming effect on mineralization of residual SOM (Kuzyakov, 2002). The rapid turnover of microorganisms in the rhizosphere makes the N available for plants (Paterson, 2003). The degree of competition between microbes and plants for mineral N however, depends on N demand of plants. In addition, the mineral N pool in soil is expected to be greater in the vegetative than reproductive growth stage of annual plants due to less uptake of mineral N because of lower biomass at vegetative stage (Fig. 3).

Microbial community structure as influenced by chemical composition of root exudates may also influence the degree of $N_2O$ emission from soil. The shift in the chemical composition

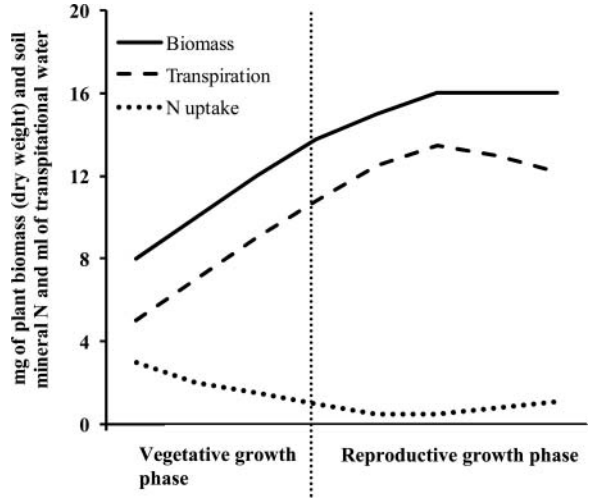


FIG. 3. Hypothetical graph illustrating the pattern of transpiration (ml) and concentration of mineral N from soil (mg $kg^{-1}$ of dry soil) with increasing plant biomass (mg of dry weight) under controlled conditions. Rate of transpiration increases with increasing plant biomass and therefore is higher at reproductive growth phase. The concentration of mineral N of soil decreases with increasing plant biomass and therefore, it's concentration is higher in soil at the vegetative growth phase of plant.

of root exudates with plant age causes a shift in microbial community structure (Shaw and Burns 2003). For example, Mougel *et al.* (2006) found that during the vegetative stage, the rhizosphere of *Medicago truncatula* was dominated by bacteria while at the reproductive stage, microbial community structure shifted to fungal dominance over bacteria. Due to the higher metabolic efficiency and respiration rate of bacteria compared to fungi, it is expected that microbial respiration would be greater during vegetative than reproductive growth of *M. truncatula*, but this remains to be determined. Bacteria are so far known to be the dominant denitrifiers (literature review by Shoun *et al.*, 2012), the production of readily available source of C from roots at vegetative growth stage may also contribute into $N_2O$ emission from soil by promoting bacterial growth. However this phenomenon merits future research.

Water content of soil influences rhizodeposition and $N_2O$ production. Depending on soil texture and vegetation type (trees versus herbaceous plants), after water logging due to rain fall or irrigation, the water content of soil reaches to field capacity in one to three days (Brady and Weil, 2008). At higher soil water content, the rhizodeposition is expected to be lower due to lower oxygen concentration that reduces the metabolic activities of roots, whereas; the emission of $N_2O$ from anaerobic denitrification is expected to be higher under such conditions. However, the amount of $N_2O$ production at those environmental conditions depends on concentration of soluble C (e.g., root exudates) before water logging and the concentration of mineral N.

As mentioned previously (Section I), $N_2O$ emission from soil through denitrification requires anaerobic soil conditions (e.g., temporary waterlogging), concentration of soluble C and $NO_3$ as substrates for the reaction. Consequently, production of $N_2O$ is expected to be higher at the vegetative than reproductive growth stage. This is because of of the occurrence of higher root exudation per unit mass of roots, secretion of greater amount of readily available source of C, higher bacterial abundance, less water depletion due to lower transpiration rate, and less N depletion from soil by plants due to lower biomass at vegetative growth stage as compared to reproductive growth stage (Section I., Section II. A. 1–3) (Figures 3 and 4). Sey *et al.* (2010) reported that in sandy loam soil in pots planted with corn and soybean respectively, the production of $N_2O$ ($\mu$g $N_2O$-N $pot^{-1}$ $h^{-1}$) was 98% and 78% at vegetative growth stage of the total $N_2O$ production sampled at three growth stages (i.e., vegetative, tasseling and milk stages).

## B. Plant Morphology

Size of plant, size of leaf and the size and abundance of stomata have an impact on rate of transpiration and uptake of mineral N, which we know are important controllers of the microbially-mediated reactions leading to $CO_2$ and $N_2O$ emissions from soil (Figure 2).

### *1. Influence of plant size on rate of transpiration and nitrogen uptake*

Plant size is positively correlated to plant biomass (i.e., larger plants are heavier) and therefore positively related to the rate of transpiration and uptake of mineral N. These phenomena were described in section II. A. 2 and II. A. 3.

### *2. Influence of leaf area and stomatal abundance on rate of transpiration and nitrogen uptake*

As the center for photosynthesis and transpiration in a vascular plant, leaves influence the uptake of water and minerals especially mineral N through transpiration-driven bulk flow from the soil solution (Salisbury and Ross, 1992; Barber, 1995; Farooq *et al.*, 2010; Matsunami; Victoria *et al.*, 2010). There are many published reports that demonstrate strong positive relation between transpiration and nutrient uptake (Novak and Vidovic, 2003) in particular uptake of N (Reddy *et al.*, 1996; Szlovak and Szlovak, 1999; Novak and Vidovic, 2003; Kanemoto et al 2009), transpiration and leaf area index (Wang *et al.*, 2012), and transpiration and leaf biomass (Nilson, 1995). However, stomatal morphology (i.e. size; Tanaka *et al.*, 2010) and stomatal number (Franks *et al.*, 2009; Yan *et al.*, 2012) also play an important part in controlling the rate of transpiration and N uptake (Yan *et al.*, 2012). For instance, Orsini *et al.* (2012) reported that in strawberry, Elsanta cultivar had 26% lower stomatal abundance per $mm^{-2}$ of leaf area and had a 17% reduction in transpiration rate as compared to Elsinore cultivar.

### *3. Influence of plant morphology on $CO_2$ emission*

The effect of plant morphology on emission of $CO_2$ production depends on respiration of root and amount of rhizodeposition, which in return is affected by phenology via biomass and

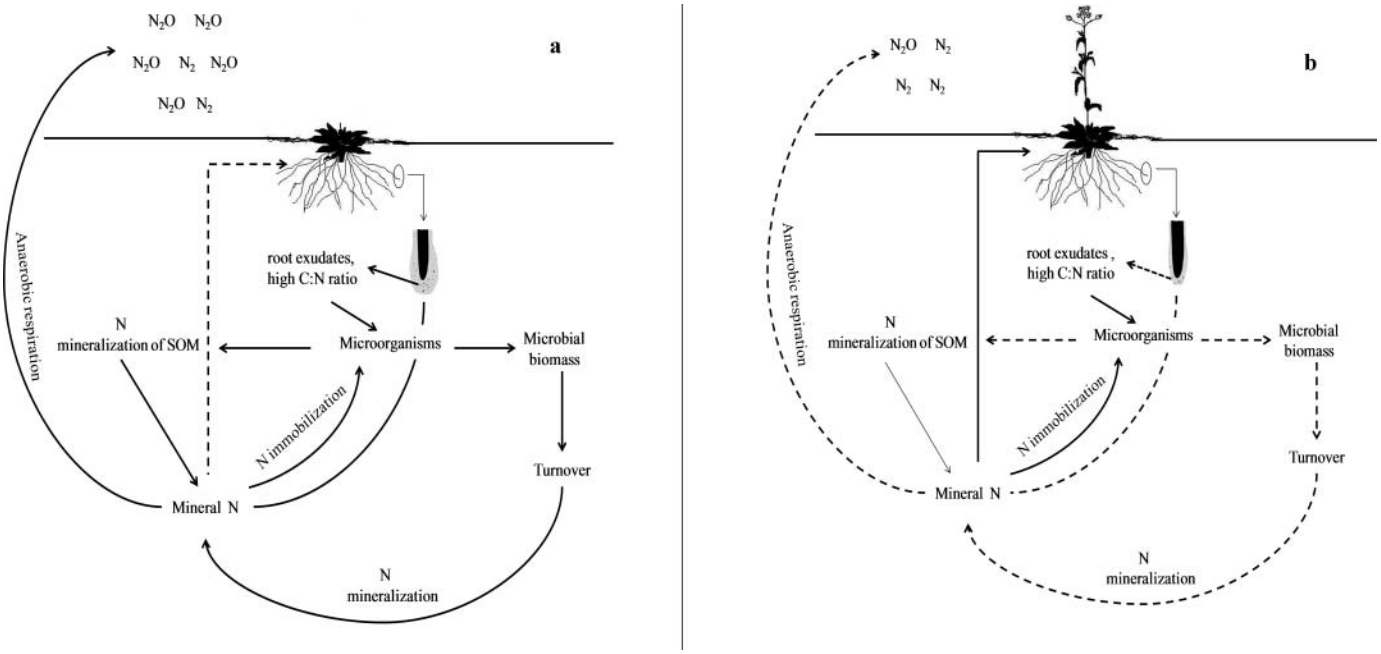


FIG. 4. Hypothetical model illustrating the influence of rhizodeposition at vegetative (a) and reproductive (b) phase on processes leading to emission of $N_2O$ from soil. Plain and dashed lines indicate respectively the strong and weak intensities of related processes. At the vegetative growth phase, the greater amount of rhizodeposits in soil enhances microbial mediated mineralization of N via rhizodeposit-driven higher microbial biomass. In return, the higher microbial biomass and higher amount of mineral N in concert with organic C source (rhizodeposition) in soil causes higher emission of $N_2O$ in anaerobic conditions.



fertility of plants via fruit load. This phenomenon is described in section II. A. and section II. C. Larger plant biomass causes greater respiration from soil (from roots and from soil organisms in the close vicinity of roots) (Gray *et al.*, 2012; Emran *et al.*, 2012; Luan *et al.*, 2012; Shahzad *et al.*, 2012), results in higher exudation from roots (Shahzad *et al.*, 2012) and promotes aeration by depleting more water through transpiration. Therefore, higher plant biomass is positively related to the amount of $CO_2$ emission from soil. In a study with *Lolium perenne* in controlled environmental conditions, Shazad *et al.* (2012) found that clipping reduced above ground biomass by ∼40% and soil respiration by ∼66% after 30 days of clipping.

*4. Influence of plant morphology on $N_2O$ emission*

Size of plant as biomass, area of leaf and abundance of stomata positively influence the rate of transpiration (section II. A. 2). Biomass of plant also influences uptake of mineral N (section II. A. 3). Moreover, the rate of transpiration and the uptake of N by plants are positively related (Matsunami *et al.*, 2010). Greater biomass of plants promotes aeration by depleting more water from soil via transpiration, causes higher absorption of mineral N (Section II. A. 3) (Shahzad *et al.*, 2012), and therefore, reduces emission of $N_2O$. In a study with *Arabidopsis thaliana* mutant lines Gul *et al.* (2012) found that the *A. thaliana* line, down-regulated for *CCR1* gene had ∼28% reduced above ground biomass and ∼25% lower crown cover of rosette leaves as compared to its wild ecotype. The mineral N of soil planted with *CCR1* line was ∼50% ∼25% higher at flowering and fruit developing stages respectively. The $N_2O$ production was also higher from the soil planted with *CCR1* line than wild ecotype. Likewise, Agner and Schenk, (2006) found that reduction in transpiration in two ornamental plant species i.e. *Euphorbia pulcherrima* and *Pelargonium zonale*, at a certain level of vapour pressure deficit of air, also promoted $N_2O$ emission from soil when the water contents of soil was higher than 60% water filled pore space. The influence of plant biomass on water contents and concentration of mineral N of soil and how these factors in return influence the emission of $N_2O$ is explained in sections I., II. A. 2, II. A. 3 and II. A. 4.

## C. Plant Fertility

Plant fertility influences root growth, fine root production, rate of transpiration and uptake of nitrogen from soil, which should affect $CO_2$ and $N_2O$ emissions from soil (Figure 2). Root growth (Kuzyakov, 2002) and fine root production is associated with rhizodeposition as root exudates protect root tips from damage during their growth (Waisel *et al.*, 2003). This rhizodeposition can in return promotes mineralization of organic matter and release mineral N in the rhizosphere (section II. A.4). Moreover, the readily available source of C promotes $N_2O$ emission when soils are anaerobic (section I. and section II. A. 5). The effects of transpiration and N uptake on $CO_2$ and $N_2O$ emissions from soil were already discussed in section II. A. 2 and 3.

*1. Influence of plant fertility on root growth and fine root production*

Root growth and fine root production depend upon fruit load. Root growth (Elkeblawy and LovettDoust, 1996; Morinaga *et al.*, 1998; Morinaga *et al.*, 2003; Lopez *et al.*, 2008; Sadras and Denison, 2009; Alves *et al.*, 2011) and fine root production declines with increasing fruit load (Morinaga *et al.*, 1998). For example, Morinaga *et al.* (2003) observed that grapevines with no fruit load had 29% higher dry mass of fine roots than the grapevines with heavy fruit load. Moreover, the $^{13}C$ and $^{15}N$ allocation to roots was also higher for the plants with no fruit load as compared to plants with heavy fruit load (Table 3). Likewise, Yao *et al.* (2006) reported an average of 31 new roots $dm^{-2}$ in apple trees during the growing season when they were in their vegetative phase, while in the next growing season when fruits were produced, the average number of new roots was 12 $dm^{-2}$. The rhizodeposition associated with root growth and fine root production provide readily available C in soil, which can stimulate microbial activities both in aerobic (i.e., $CO_2$ production) and anaerobic respiration (e.g., $N_2O$ production).

*2. Influence of plant fertility on rate of transpiration*

Plant yield and rate of transpiration are positively related (Salisbury and Ross, 1992; Masarovicova and Navara, 1994; Naor, 2004; Fasinmirin *et al.*, 2009; Martin-Vertedor *et al.*, 2011). Martin-Vertedor *et al.* (2011) found a strong positive relation ($y = 1.2302\ x - 21.15$; $R^2 = 0.8864$) between yield (fruit load) and transpiration in olive trees. Likewise, Fasinmirin *et al.* (2009) found a positive correlation between fruit load and transpiration in *Amaranthus cruentus* grown under drip ($r = 0.78$) and sprinkler ($r = 0.74$) irrigation. Therefore, plants with higher yields should promote water loss from the rhizosphere, which could stimulate aerobic processes (e.g., $CO_2$ production) and limit anaerobic processes (e.g., $N_2O$ production from denitrification).

*3. Influence of plant fertility on nitrogen uptake*

The degree of resource allocation to grain production and N uptake of plants are positively related to fruit load (Sanches *et al.*, 1991; Elkeblawy and LovettDoust, 1996; Morinaga *et al.*, 1998; Lea-Cox *et al.*, 2001; Morinaga *et al.*, 2003; Alva *et al.*, 2006; Sadras and Denison, 2009). Alva *et al.* (2006) found a strong positive correlation between fruit load and total N in fruits of *Citrus sinensis* (L.). They found that at all four N fertilizer treatments, the $R^2$ values between total N contents in fruits and fruit load were $\geq 0.85$ respectively. Therefore, plants with higher yields should have higher uptake of mineral N from soil, leaving lesser substrate N for microorganisms to produce $N_2O$.

*4. Influence of plant fertility on $CO_2$ emission*

The $CO_2$ production may not be different between plants of higher fertility versus plants with lower fertility if the biomass of later one has same shoot, root and leaf biomass. This is due to the reason that $CO_2$ production from rhizosphere is the outcome of root as well as of microbial respiration, while microbial respiration depends on the amount of rhizodeposits and other substrates. This phenomenon is explained in Figure 2 and Figure 4. The expected lower $CO_2$ production from the rhizosphere microbial respiration of a high fertility plant can be offset by its greater root respiration. Likewise, the expected higher $CO_2$ production from rhizosphere microbial respiration of a low fertility plant due to higher rhizodeposits can be compensated with comparatively lower $CO_2$ production from roots. Reduced fertility is therefore expected to cause reduced transpiration and deposition of more exudates from roots. All these factors collectively can contribute to a higher emission of $CO_2$ and $N_2O$ from microbial activities from the rhizosphere of plants with lower fertility.

*5. Influence of plant fertility on $N_2O$ emission*

Plants with higher fertility in terms of fruit load are expected to have lower $N_2O$ emission from rhizosphere than crops with

TABLE 3
Distribution of $^{13}C$ and $^{15}N$ as percentages in large, medium and fine roots of heavy fruit load and no fruit load grapevine plants during fruit developing stage and preharvest stage

| | Root size | | | | | |
|---|---|---|---|---|---|---|
| | ....Fruit developing stage.... | | | ....Preharvest stage.... | | |
| | Large | Medium | Fine | Large | Medium | Fine |
| | Percentage of $^{13}C$ | | | | | |
| Heavy fruit load | 1 | 4 | 7.8 | 2 | 4 | 4 |
| No fruit load | 1.2 | 4 | 14 | 2.5 | 10 | 14 |
| | Percentage of $^{15}N$ | | | | | |
| Heavy fruit load | 2.5 | 11 | 16 | 2.5 | 4 | 16 |
| No fruit load | 2.5 | 6 | 34 | 4 | 14 | 41 |

(Morinaga *et al.*, 2003)

lower grain size and lower fertility. This is because higher fertility plants invest higher resource allocation for fruit production (Morinaga *et al.*, 1998; Sadras and Denison, 2009), have less root growth and less fine root production (section II. C. 1), possess higher rate of transpiration, and deplete soil mineral N in greater amounts (Katterer *et al.*, 1993; Baruah *et al.*, 2010) than plants with lower fruit load at reproductive stage. All these factors lead to lower substrate availability and aerobic conditions, which inhibits $N_2O$ production by denitrifying bacteria in the rhizosphere of these plants at reproductive stage (Haider *et al.*, 1987; Hu *et al.*, 2001).

## III. MODIFYING LIGNIN BIOSYNTHESIS AFFECTS PLANT LIFE HISTORY TRAITS

### A. Evidence from Cell Wall Mutants

Interaction of genes is a natural phenomenon and a single trait can be controlled by many genes, therefore mutation in one gene can influence more than one trait. Although GM cell wall mutants can be engineered to have altered cell wall biosynthesis for alteration in concentration of cell wall components such as lignin, such mutations can cause physiological alterations in plants. For instance, delayed senescence (Derikvand *et al.*, 2008) and delayed development (Patten *et al.*, 2005; Gul *et al.*, 2012a) is reported for *Arabidopsis CCR1* knockout mutant, whereas early flowering was noted in the *Arabidopsis EARLI1* knockout mutant (see Table 2 for references). Down-regulation of *EARLI1* in *A. thaliana* also caused reduction in number of rosette leaves and fecundity, lower fecundity was observed in *A. thaliana* down-regulated *CCR1* (Gul *et al.*, 2012a) and *A. thaliana* double mutant with down-regulated *CAD* and *CCR1* genes (Thevenin *et al.*, 2011). Dwarfness has been observed in various species down-regulated for *CCOMT*, and *CCR1* and in over-expressing *Populus tremuloides* mutant for coniferaldehyde 5-hydoxylase (*CAld5H*) (see Table 2 for references). However, no difference in morphological traits was observed for *KNAT7* and *MYB75 A. thaliana* knockout mutants (Li *et al.*, 2009; Bhargava *et al.*, 2010; Gul *et al.*, 2012a).

The influence of mutations on a given trait also depends on the degree of expression of a mutation. For instance, severe down-regulation of shikimate hydroxycinnamoyl transferase (*HCT*) resulted in reduction in biomass and delay in flowering in alfalfa while moderate level of expression of this mutation caused no change in these traits (Shadle *et al.*, 2007). Likewise, in alfalfa reduction in lignin to less than 60% by down-regulating *CCR* and to less than 35% by down-regulating *CAD* resulted in reduced biomass and fertility (Jackson *et al.*, 2008).

The maize corngrass1 (*Cg1*) is an interesting gene that encodes a microRNA, This RNA belongs to miR156 class and promotes juvenile cell wall morphology (Jackson *et al.*, 2008). The overexpression of *Cg1* mutation caused reduction in lignin, increased biomass and repressed flowering stage initiation in switchgrass (Jackson *et al.*, 2008). These findings were similar with overexpression of miR156 in *Arabidopsis* (Schwab *et al.*, 2005) and rice (Luo *et al.*, 2006) however; in these species, miR156 overexpression did not cause complete repression of reproductive traits.

A trend exists that cell wall mutations that decrease the concentration of lignin or AUF, also alter phenology, biomass, leaf morphology and plant fertility (Table 2). Lignin provides mechanical strength to the inflorescence stem. Zhao *et al.* (2012) found a strong correlation of mechanical strength of the inflorescence stem in herbaceous peony (*Paeonia lactiflora*), which is provided by lignin, with the diameter ($r = 0.96$) and fresh weight ($r = 0.96$) of flower. This study provides an insight into the importance of lignin in influencing reproductive traits in plants. However exceptions exist, for instance; knockout mutation in *MYB75* and *KNAT7* increase the concentration of lignin and AUF respectively in inflorescence stems of *A. thaliana.* Despite of that, no alteration in the phenology, morphology and fertility was observed in *A. thaliana* (Gul *et al.*, 2012a).

### B. Feedback on Greenhouse Gas Emissions

As evident from Table 2, mutations related to reduction in lignin concentration tend to influence phenology, biomass and fertility of plants. In such mutant plants, the net $CO_2$ production (root plus microbial derived $CO_2$ production) from soil at the reproductive stage however, is not expected to be different than the $CO_2$ production from soil planted with wild type as explained in section II.C.4. Prolonged vegetative growth phase and reduced fertility if coupled with lower leaf biomass (e.g., *CCR1* k/o, *CAD* k/o mutations in various plant species), can result in higher net $N_2O$ emission from rhizosphere. This is because of the reduced uptake of water and N by such kind of plants from soil and higher root-derived rhizodeposition per gram root dry weight of these plants as compared to their wild ecotypes, as illustrated in Figure 5.

## IV. PLANT RESIDUES INFLUENCE $CO_2$ AND $N_2O$ EMISSIONS FROM SOIL

Chemical composition of plant residues influences its rate of biodegradation and it has a priming effect on SOM decomposition. Therefore it can have an influence on SOM quantity per unit time. Plant residues contain fiber contents, soluble polyphenolics, non-structural carbohydrates etc. The amount of these organic substances depends on plant organ (i.e., leaves, stem, roots), plant species, and on the time of crop harvest (Hendricks and Boring, 1992; Webster and Stone, 1994; Johnson *et al.*, 2007; Abiven *et al.*, 2011; Yanni *et al.*, 2011). For instance, in general, the amount of AUF or true lignin in a plant is in the order of leaves < stems < roots (Hendricks and Boring, 1992; Johnson *et al.*, 2007; Abiven *et al.*, 2011; Yanni *et al.*, 2011) and its concentration increases with the growth of plant (Abiven *et al.*, 2011). For example, Abiven *et al.* (2011) reported that the lignin concentration in mg C-lignin g C-plant$^{-1}$ in maize after 175 days of sowing was 53 in leaves, 162 in stems and 210 in roots (approximate values) while in wheat after 290 days of sowing, the approximate lignin concentration in mg C-lignin

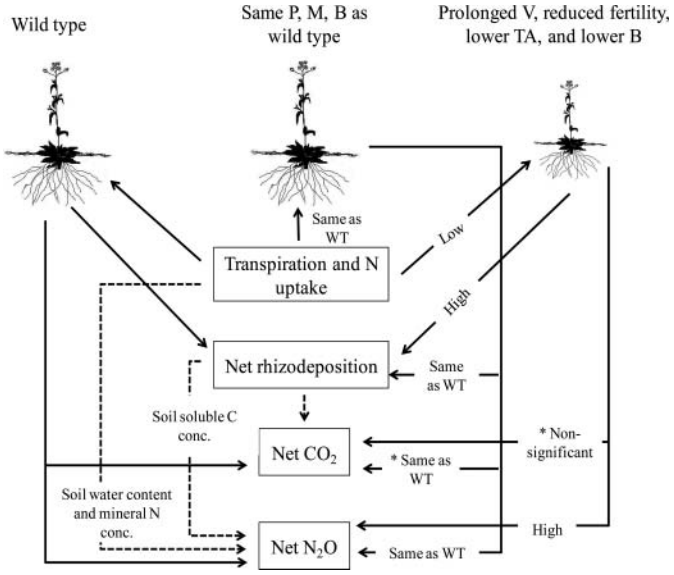


FIG. 5. Hypothetical model illustrating the role of GM cell wall mutants in influencing $CO_2$ and $N_2O$ emission via their phenological and morphological traits. P is phenology, M morphology, B biomass, V vegetative growth period, TA transpiration apparatus (leaf number and leaf area). Dashed lines represent relationship of factors. * $CO_2$ emission from soil is the function of root and microbial respiration, which can be influenced by plant biomass, fertility, and rhizodeposition.

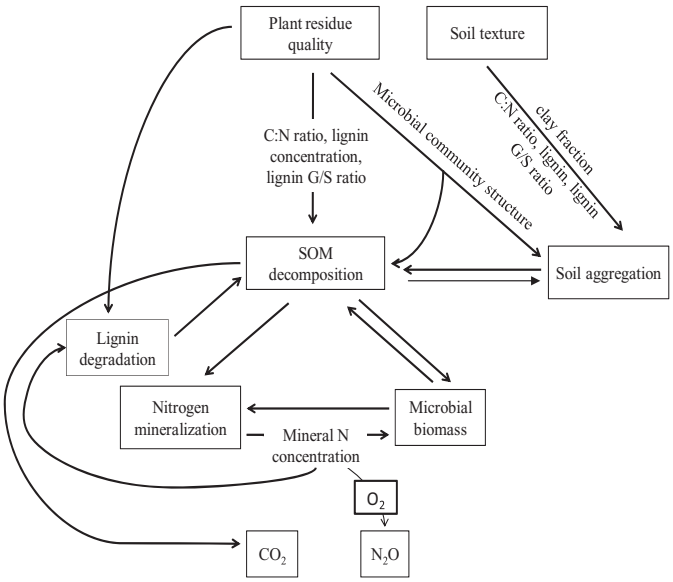


FIG. 6. Hypothetical model illustrating the role of lignin concentration and C:N ratio of plant residue upon soil processes i.e. soil aggregation, SOM decomposition, emission of $CO_2$ and $N_2O$, nitrogen mineralization, degradation of lignin and microbial biomass.

g C-plant$^{-1}$ was 20 in leaves, 100 in stems and 140 in roots (approximate values). The C:N ratio also varies with plant age and between plant organs. In general, lower C:N ratio is found in leaves than stem and roots (Hendricks and Boring, 1992; Johnson *et al.*, 2007; Yanni *et al.*, 2011).

Concentration of AUF and lignin and C:N ratio of plant residues influence their biodegradation in soil. Lignin is relatively resistant to decomposition among other plant derived organic substances (e.g., non-structural carbohydrates) because only a few microorganisms (i.e., brown and white rot fungi; Hedges *et al.*, 1988; Boerjan *et al.*, 2003) can decompose them. Carbon is the major component of cellular organic substances whereas N is the component of nucleic acids, their precursors, proteins, hormones, chlorophylls, and coenzymes. N ranks fourth in amount among other nutrients for the requirement of growth and development of an organism. Residues with higher C:N ratios provide a more N-limited environment for microorganisms to grow and reproduce than residues with lower C:N ratios. There are a number of studies, which demonstrate that plant residues with higher AUF and higher C:N ratio mineralize slower than plant residues with lower AUF and lower C:N ratio and produce less $CO_2$ from soil during their biodegradation (Williams and Gray, 1974; Sun *et al.*, 2009; Galicia *et al.*, 2011; Puttaso *et al.*, 2011; Yanni *et al.*, 2011). In anaerobic conditions, such residue types also reduce the emission of $N_2O$ from soil (Millar and Baggs, 2004).

The influence of plant residue chemistry on emissions of $CO_2$ (aerobic conditions) and $N_2O$ (in anaerobic conditions) is conceptualized in Figure 6. Since C:N ratio and concentration of AUF and true lignin are the important determinants for the rate of decomposition of plant residues, this article will focus on these parameters in following sections.

### A. Influence of Lignin Concentration on Mineralization of Plant Residues

Concentration of lignin influences the decomposition of plant residues. Frouz *et al.* (2011) found that ∼27% reduction in the concentration of lignin due to photooxidation increased the C mineralization of *Calamagrostis epigeios* by 25% in soil (Figure 7a). Likewise, Yanni *et al.* (2011) found that mixing of indulin lignin by 0.5% (0.1 g 50 g$^{-1}$ soil) with stem residues of corn, reduced $CO_2$-C production by ∼9% in a sandy-loam soil (Figure 7b). These studies show that how lignin influences mineralization of plant residues.

### B. Influence of Lignin Chemistry on Mineralization of Plant Residues

Lignin is a heterogeneous molecule that contains Guaiacyl (G), syringyle (S), and p- hydroxyphenyl (H) (also known as cinnamyl) phenols with acid, aldehyde and ketone substitutions (Thevenot *et al.*, 2010). The amount of a given monomer varies between plant organ (Abiven *et al.*, 2011) and species (Boerjan *et al.*, 2003: Thevenot *et al.*, 2010). Lignin chemistry is another factor that influences litter biodegradation. Brown and white rot fungi degrade S lignin monomers preferentially over G monomers (Hedges *et al.*, 1985; Boergan, 2003; Thevenot *et al.*, 2010) and lignin with higher G/S ratio degrade slower than lignin with lower G/S ratio (Thevenot *et al.*, 2010; Talbot

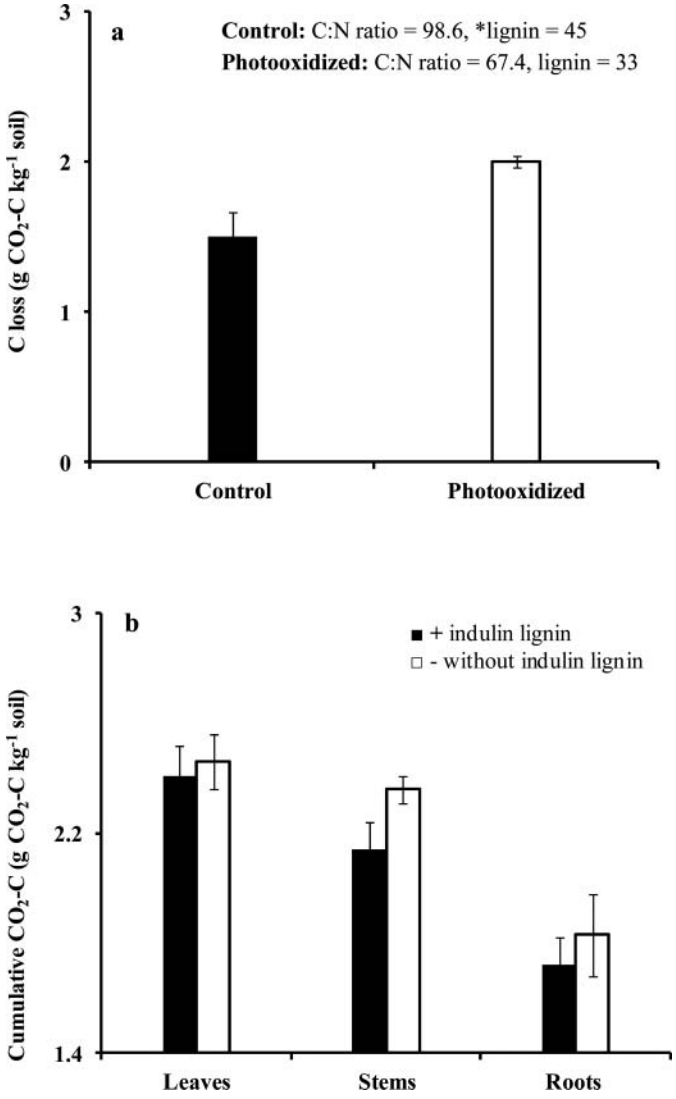


FIG. 7. (**a**) Influence of photooxidized residue of *Calamagrostis epigios* on C loss (measured as $CO_2$-C loss $g^{-1}$ soil) * lignin as cumulative of 2 methoxi 4 vinilphenol and 3,4-dimethoxibenzaldehide (Frouz *et al.*, 2011). Significant ∼27% reduction in concentration of lignin from photooxidation resulted in ∼25% increase in C loss from soil (**b**) influence of indulin lignin mixed with plant residue type on $CO_2$-C production from soil (Yanni *et al.*, 2011) indulin lignin significantly reduced emission of $CO_2$ from soil amended with stem residue.

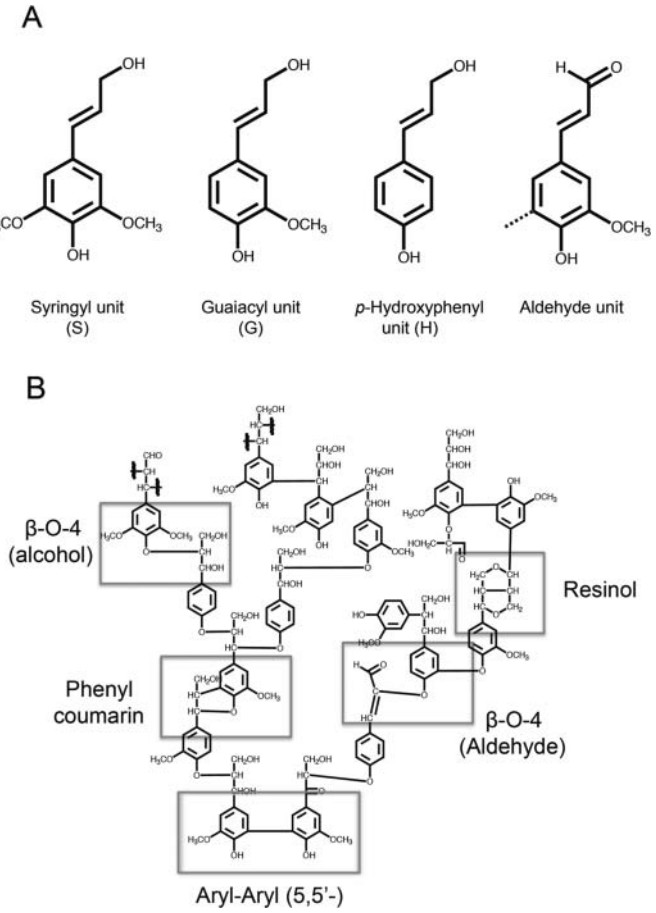


FIG. 8. **(a)** Phenolic alcohols (syringyl, guaiacyl and hydroxyphenyl alcohol) and phenolic aldehyde precursor units (monolignols) of lignin polymer and **(b)** and linkages between units; a phenylcoumaran linkage between guaiacyl alcohol units, a $\beta$-O-4 linkage between normal alcohol units, $\beta$-O-4 linkage between aldehyde units and a resinol linkage found in *P*-hydroxyphenyl lignin (Talbot *et al.*, 2012).

*et al.*, 2012). This can be explained by the molecular structure of lignin monomers, which differ in the number of methyl groups (Thevenot *et al.*, 2010). This difference in molecular structure of lignin monomers explains the difference in lignin structure, which in turn exerts an influence on susceptibility of lignin to biodegradation (Hedges *et al.*, 1985). For instance, G units form condensed arly-arly linkages and therefore lignin molecule with more G units are condensed and difficult to biodegradation whereas, lignin with high S units have more $\beta$-O-4 linkages (Figure 8; Talbot *et al.*, 2012). Moreover, it is observed that aryl-aryl linkages persist longer than other linkages in soil (Bahri *et al.*, 2006; Dignac and Rumpel, 2006; Opsahl and Benner, 1995).

Lignin chemistry not only influences rate of biodegradation of lignin in soil, it also influence the biodegradation of plant residue. For example, lignin with higher G units is found to have high levels of cross linking with cell wall associated polysaccharides (hemicelluloses and cellulose) and therefore offer more protection to these cell wall components than the lignin with higher concentration of *p*-hydroxyphenyl monomers (Talbot *et al.*, 2012). However, there are mixed results in this regard for instance, Bertrand *et al.* (2006) found that the internodes of wheat instead of having significantly higher C:N ratio but similar lignin concentration as roots decomposed faster than root residues. They attributed their findings to the reason that root residues had more condensed lignin and higher G/S ratio than internode residues. However, in another study, Talbot *et al.* (2012) found no difference in residue mass loss by decomposition between wild type and mutant *A. thaliana* residues that had higher G/S ratios and the same lignin

concentration as the wild types. The mutant residues had lower lignin:N ratio, which to some extant explained the non-significant difference in litter decay rate between mutant and wild type residues. These findings suggest that not only lignin chemistry but other factors such as N contents of plant residues also play role in influencing the rate of residue decay.

### C. Influence of Plant Residue Chemistry on Concentration of Mineral Nitrogen and Microbial Biomass of Soil

The biodegradation of SOM (residual SOM and/or fresh residue) is positively related to the concentration of mineral nitrogen of soil (Neff *et al.*, 2002; Guillou *et al.*, 2011) while litter with lower C:N ratio mineralizes faster and increases the concentration of mineral N of soil (Nourbakhsh and Dick, 2006; Yanni *et al.*, 2011). Moreover, the residues with lower C:N ratio and lower AUF concentration promote microbial biomass (Saggar *et al.*, 1999; Sun *et al.*, 2009; Hoyle and Murphy, 2011). Therefore, plant residues with lower C:N ratios and lower concentration of AUF is expected to decompose faster, cause higher soil mineral N concentration and higher microbial biomass than plant residues with higher C:N ratios and higher concentration of AUF (Sun *et al.*, 2009; Potthast *et al.*, 2010; Hoyle and Murphy, 2011). The higher mineral N concentration and microbial biomass in turn can have a positive priming effect on biodegradation of residual SOM (Guenet *et al.*, 2010). This factor in return causes higher emissions of $CO_2$ from aerobic respiration and $N_2O$ from anaerobic and aerobic respiration (Figure 6). Moreover, mineral N can also have a positive influence on degradation of lignin. This phenomenon is explained in the section IV. D and is illustrated in Figure 6.

### D. Influence of Plant Residue Chemistry on Degradation of Lignin and AUF of Soil and Their Feedback on Soil Organic Matter Decomposition

Plant residue chemistry has an influence on degradation of lignin and AUF (Sanaullah *et al.*, 2010; Yanni *et al.*, 2011; Gul *et al.*, 2012c). Sanaullah *et al.* (2010) found differential influence of young versus senesced leaf litter of *Festuca arundinacea* on lignin degradation. Young leaves that had lower C:N ratio and lower lignin concentration caused greater loss of lignin than senesced leaves after 44 weeks of their burial in soil (Figure 9a). Likewise, Yanni *et al.* (2011) observed higher lignin degradation of the soil amended with leaf, which had lower concentration of AUF than root residues of corn (Figure 9b). As lignin provides physical protection to organic matter against microbial attack, the degree of its degradation consequently influences the residence time of SOM and ultimately the magnitude of $CO_2$ and $N_2O$ emissions from soil and this phenomenon is illustrated in Figure 6 and is described in section IV. C. and section F.

#### *1. Influence of concentration of mineral nitrogen*

Degradation of lignin of soil can be promoted by mineral N, because as it can act as a direct N source to lignin degrading organisms (i.e., white rot fungi). This mineral N comes from either the mineralization of OM (fresh plant residue and/or residual SOM) and/or N fertilizer. But the level of lignin degradation also depends on the other sources of C such as cellulose concentration, lignin:cellulose ratio etc. (Talbot and Treseder, 2012). Some studies demonstrated that N fertilization inhibits lignin degradation (Fog, 1988; Frey *et al.*, 2004; Liu *et al.*, 2010). One hypothesis is that microbes degrade lignin to release cell-wall-bound N (Craine *et al.*, 2007); therefore, if N is present in mineral form, microbes will avoid investing resources in producing lignolytic enzymes (Talbot and Treseder, 2012). One possibility is that N fertilization results in a shift of microbial community structure and promotes microorganisms with high cellulase activity and they outcompete lignin decomposers (Couteaux *et al.*, 1995). The other explanation is N fertilization may induce browning of plant residues, which may be toxic to lignin degrading microbes (Fog 1988). In a litter bag based study in field, Talbot and Treseder (2012) found that N fertilizer application tended to reduce lignin degradation of *A. thaliana* residues. However there are some studies, which demonstrate positive or neutral effect of fertilizer N on lignin degradation. For instance, over 6 years field study, Majdi *et al.* (2007) reported that N fertilization (100 kg N and 114 kg S $ha^{-1}$) had a positive effect on lignin degradation of spruce root litter. However, over five years field study, Hobbie (2008) found no

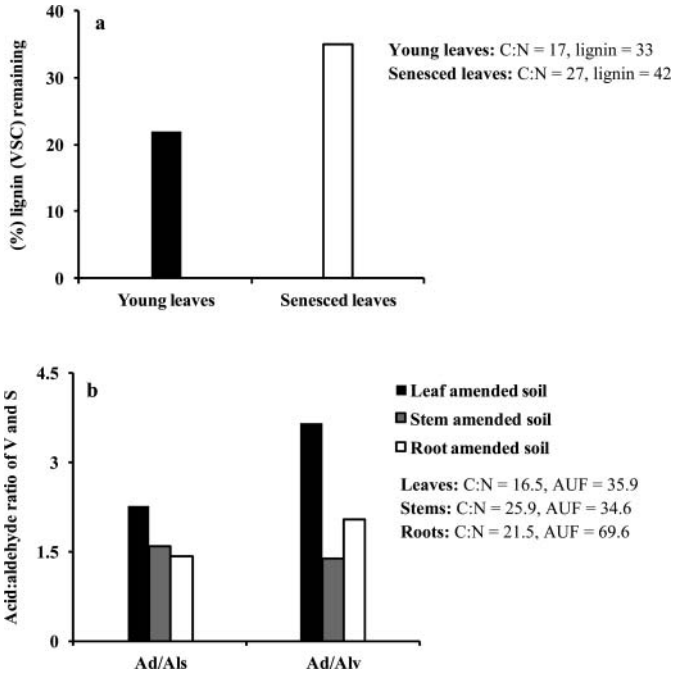


FIG. 9. (**a**) Influence of C:N ratio and lignin concentration (total of VSC) of young and senesced leaves of *Festuca arundinacea* on lignin degradation after 44 weeks of burial in soil in litter bags (Sanaullah *et al.*, 2010) young leaves that had lower C:N ratio and lower concentration of lignin resulted in higher degradation of lignin in soil (**b**) influence of residue type of corn on lignin degradation of soil (Yanni *et al.*, 2011) leaves that had a lower C:N ratio and lower concentration of lignin resulted in higher degradation of lignin in soil.

influence of N fertilizer on AUF degradation of seven substrates varying in AUF concentration.

*2. Influence of soil microorganisms*

Microorganisms are diverse regarding their preferences for utilizing a given substrate. Chemistry of plant residues influences microbial community structure (Nicolardot *et al.*, 2007; Potthast *et al.*, 2010). Nutrient poor organic matter such as residues with higher AUF concentration and higher C:N ratio, favor fungal colonization over bacteria resulting in higher fungal:bacterial ratio in soil than plant residues with lower AUF concentration and lower C:N ratios (Bossuyt *et al.*, 2001; Cerli *et al.*, 2006; Fioretto *et al.*, 2007; Hogberg *et al.*, 2007; Arenz and Blanchette, 2011). Fresh organic substrate with high nutrient availability increases the abundance of gram negative bacteria (Marschner *et al.*, 2003; Bastian *et al.*, 2009), whereas gram positive bacteria (Fierer *et al.*, 2003) actinomycetes (Potthast *et al.*, 2010) and fungi (Cerli *et al.*, 2006; Fioretto *et al.*, 2007; Eskelinen *et al.*, 2009) are adapted to nutrient poor conditions. Garcia-Pausas and Paterson (2011) showed that the application of readily degradable organic substrate (glucose) caused a priming effect on the degradation of residual SOM and mostly through the activity of actinomycetes and fungi. Likewise, Bell *et al.* (2003) found a priming effect on residual SOM decomposition mainly by fungi in response to $^{14}C$ labeled wheat straw addition. These findings and reviews (Blagodatskaya and Kuzyakov, 2008) suggest that residues with higher concentration of readily available C also cause an increase in activity of fungi to decompose native or residual SOM fractions that also contain lignin and/or AUF. Therefore addition of residues with low lignin and AUF concentration are expected to cause higher $CO_2$ production from decomposing residue as well as from decomposing residual SOM and can cause degradation of lignin. These factors collectively result in reduction of soil aggregation that in turn has a positive influence on mineralization of SOM.

## E. Soil Aggregation as a Mechanism for Protecting Plant Residues from Decomposition

Microbes need space for their activities. Kilbertus (1980) reported that active bacteria need pores in soil at least three times larger than their size. Soil aggregation is therefore, important in terms of protecting OM from microbial attack, hence reducing the emission of $CO_2$ in aerobic conditions and $N_2O$ in mostly anaerobic conditions from soil by slowing down decomposition and N mineralization of OM (Jimenez and Lal, 2006).

Soil aggregation is determined by the quantity and quality of SOM (including fresh plant residue) and the associated microbial activities (Blanco-Canqui and Lal, 2004; Jimenez and Lal, 2006; Guillou *et al.*, 2011) whereas SOM decomposition is concomitant with soil structure degradation (Six *et al.*, 2000; Guillou *et al.*, 2011). Plant residues act as a primary skeleton for the formation of aggregates in soil (Blanco-Canqui and Lal, 2004) and their chemistry influences soil aggregation (Blanco-Canqui and Lal, 2004; Chivenge *et al.*, 2011). For example, N contents of plant residues have high affinity to bind with mineral particles (Kleber *et al.*, 2007). Plant residues with moderate level of C:N ratio promote soil aggregate formation at the initial stages of their decomposition while the influence of plant residues of high C:N ratio and high AUF concentration on soil aggregation can be low at initial stages in conditions of low soil mineral N contents (Guillou *et al.*, 2011), however; such kind of plant residues can have a positive influence at later stages of their biodegradation via influencing microbial community structure (Blanco-Canqui and Lal, 2004; Jimenez and Lal, 2006; see Section IV. F) and their slow mineralization. Therefore, plant residues with higher C:N ratio and higher concentration of AUF and/or lignin are expected to play greater part in formation and stabilization of aggregates than plant residues with lower C:N ratio and lower concentration of AUF and/or lignin.

Soil aggregation also depends on soil texture (Blanco-Canqui and Lal, 2004; Jimenez and Lal, 2006). Due to higher binding affinity of clay particles to organic matter as compare to silt and sand particles, soils with higher clay fraction have higher impact on soil aggregate formation than soils with higher sand fraction (Blanco-Canqui and Lal, 2004).

*1. Soil aggregation via microbial community structure as influenced by plant residue chemistry*

Microbes secrete organic compounds such as polysaccharides and extracellular enzymes that aid soil aggregate formation (Tang *et al.*, 2011) by interacting with wide range of organic matter and mineral particles (Rillig *et al.*, 2005). Plants provide primary skeleton to soil aggregate formation while microbes play role in aggregate formation and its stability by cementing plant debris within aggregates (Jimenez and Lal, 2006; Blanco-Canqui and Lal, 2004). Polysaccharides of microbial origin are more important for aggregate stability than plant derived polysaccharides (Cheshire *et al.*, 1984). Both bacterial and fungal communities play a significant role in formation and stabilization of macroaggregates (Tang *et al.*, 2011), however; fungi have the dominant role over bacteria in this regard (Chantigny *et al.*, 1997; Bossuyt *et al.*, 2001; Tang *et al.*, 2011) and in the reduction of $CO_2$ and $N_2O$ emissions from soil. This is because the growth of fungal hyphae and associated release of extracellular organic compounds contribute to macroaggregate formation and its stabilization (Jimenez and Lal, 2006; Rillig and Mummey, 2006). Moreover, fungal cell walls contain substantial amount of chitin, which is also a slowly decomposable organic substance to biodegradation (Langley and Hungate, 2003). Therefore, the importance of fungi in reducing $CO_2$ emission via its dominant contribution in macroaggregate formation, greater biomass production and chitin production is expected to be greater than bacteria (Six *et al.*, 2006).

## F. Influence of Soil Texture on Soil Processes in Perspective of Plant Residue Chemistry

Soil texture is another factor that influences the biodegradation of organic matter and therefore emission of $CO_2$ in aerobic

and $N_2O$ in anaerobic conditions. Clay particles due to high surface area per unit mass have higher binding affinity for organic matter. Generally soils with high clay contents better protect organic C (Chivenge *et al.*, 2011), organic N (Strong *et al.*, 1999; McInerney and Bolger, 2000; Chivenge *et al.*, 2011), support larger microbial biomass (Six *et al.*, 2006) and retain more nutrients (Knops and Tilman, 2000) than soils with high sand fraction. The extent of biodegradation of residue in different soil textural classes is expected to depend on its C:N ratio and the concentration of AUF and pure lignin (Gul *et al.*, 2012b).

The influence of C:N ratios and the concentration of AUF of plant residues on soil aggregation vary in different soil textural classes (Blanco-Canqui and Lal, 2004). The associated processes such as microbial biomass of soil can also vary in this regard. The influence of plant residue chemistry on N mineralization, microbial biomass, microbial community structure is conceptualized in Figure 10. Plant residues with higher C:N ratio and higher concentration of AUF can mineralize relatively faster in soils with higher clay contents during early stages of biodegradation and increase microbial biomass than soils with higher sand contents (Gul *et al.*, 2012c). This is because of the lower binding affinity of such kind of plant residues to mineral particles (Kleber *et al.*, 2007) and organo-mineral particles (Sylvia *et al.*, 2005) due to lower N contents. Therefore, such types of residues are more exposed to microbial attach in clayey soils that have higher microbial biomass and higher nutrients than sandy soils. The greater microbial biomass may in turn favor protection of such type of plant residues at later stages of their biodegradation by increasing the aggregate formation and stability via dead cells of microbes and secretion of organic compounds from living cells of microbes. Moreover, the low N content of plant residues itself could reduce its biodegradation at later stages in soils with higher clay particles. Gul *et al.* (2012b, c) found that over 63 days of incubation study, the stem residues of *A. thaliana MYB75* k/o with ~2 fold higher C:N ratio than wild type but had same AUF concentration caused no reduction in $CO_2$ production in clay loam soil in response to its degradation while in sandy loam soil, $CO_2$ production was significantly lower than wild type residue. In clay loam soil *A. thaliana MYB75* k/o stem residues caused numerically greater microbial biomass than wild type whereas there was no difference in $CO_2$ production as compared to wild type.

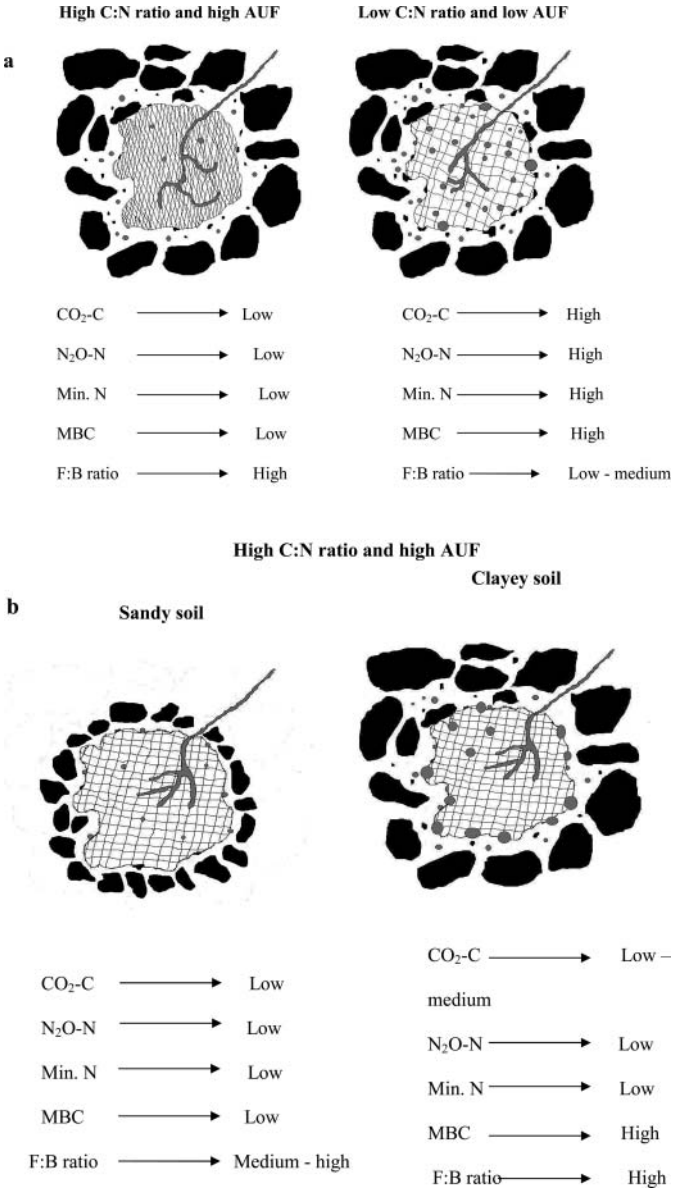


FIG. 10. Conceptual model illustrates (a) the influence of plant residue chemistry (C:N ratio and concentration of acid unhydrolyzable fraction (AUF)) on emission of $CO_2$-C, $N_2O$-N, concentration of mineral N (min. N), microbial biomass C (MBC), and fungal:bacterial (F:B) ratio within a macro-aggregate (cross section) after incubation period of 63 d, and (b) the interactive effect of texture of soil and chemistry of plant residue on emission of $CO_2$-C, $N_2O$-N, concentration of mineral N, microbial biomass C (MBC), and fungal:bacterial (F:B) ratio within macro-aggregates (cross section) after incubation period of 63 d. Microaggregate, ; fungal hypha, ; plant residue debris, ; small organo-mineral complex, ; microbial colony, (Gul *et al.*, 2012c with some modifications).

## G. Biomass Partitioning

Root to shoot ratio for biomass of plants may play significant role in influencing $CO_2$ and $N_2O$ (mostly in anaerobic conditions) emissions from soil in response to decomposition of their residues when they die. As root residues decompose slower than stem residues in soil, plants with higher root:shoot ratio contribute more in reucing the emission of $CO_2$ an $N_2O$ from soil as compare to the plants that have lower root:shoot ratio. It also makes differentiation between plant species in contributing to soil C sequestration.

# V. MODIFYING LIGNIN BIOSYNTHESIS AFFECTS PLANT RESIDUE CHEMISTRY

## A. Evidence From Cell Wall Mutants

As evident from Table 4, modifications associated with lignin biosynthesis tend to alter plant residue chemistry regarding C:N

TABLE 4
Influence of genetically modified plants on $CO_2$-C production from soil

| Species | Mutated gene | C:N ratio | AUF or lignin (mg $g^{-1}$ plant material or in ppm in NMR spectroscopy) | $CO_2$-C production | Reference |
|---|---|---|---|---|---|
| *A. thaliana* | Wild type | 52.5 | 104 | | |
| | CCR1 | 37.3 | 121 | High | |
| | KNAT7 | 58.2 | 65.4 | Low | Gul (2012a) |
| | Wild type | 46.9 | 95.4 | | |
| | MYB75 | 81.4 | 99.0 | Low | |
| *Nicotiana tabacum* | Wild type | 106 | | | Hopkins et al. (2001) |
| | CAD | 113 | nd*1 | High | |
| | COMT | 73.3 | Nd | High | |
| | CCR | 61.1 | Low | High | |
| *Nicotiana tabacum* | Wild type | 57 | 192 | | Webster et al. (2005) |
| | CAD | 74 | 194 | High | |
| | COMT | 61 | 197 | High | |
| | CCR | 53 | 175 | High | |
| *Nicotiana tabacum* | Wild type | –*2 | – | | Henault et al. (2006) |
| | CAD | – | – | High | |
| | COMT | – | – | High | |
| *Popular* | Wild type | 465 | | | Tilston et al. (2004) |
| | CAD | 352 | – | nd | |
| | COMT | 472 | – | nd | |

*1 represents not different than wild type.
*2 represents no data.



ratio and concentration of AUF. Many genes associated with cell wall biosynthesis are members of multigene families (Zhong and Ye, 2007). Moreover, genes interact with each other to control a given trait. Given that, targeting one gene for mutation may result in influencing the other traits. Little data is available that demonstrates the influence of mutated gene related to secondary cell wall formation on other biochemical traits such as concentration of proteins, non-structural and structural carbohydrates. Donaldson and Knox (2012) observed that the concentration of various cell wall bound non-cellulosic polysaccharides in normal and compressed wood of *radiata* pine depends on cell type and concentration of lignin. Xylan and mannan were absent in parenchyma cells, $\beta$ (1,4)-galactan had positive strong correlation with concentration of lignin in compressed wood, whereas galactoglucomannan had negative correlations in both normal and compressed wood. Gul (2012c) found a higher C:N ratio, lower hemicelluloses and higher AUF in inflorescence stem of *A. thaliana* down-regulated for *KNAT7,* however, results were not consistent for C:N ratio and concentration of hemicelluloses when the same line was grown in different environmental condition. Leple *et al.* (2010) observed a reduction in concentration of hemicelluloses in the stem of poplar tree, down-regulated for *CCR1* while no such reduction was observed in other species, which were down-regulated for the same gene (e.g,. Gul, 2012b). Gul *et al.* (2012b, c) found a lower C:N ratio and lower concentration of AUF in the stem tissues of down-regulated *CCR1 A. thaliana* mutants, while *A. thaliana MYB75* k/o mutant exhibited higher C:N ratio in stems. In another study, lower C:N ratio and lower concentration of lignin has been reported for stem tissues of *Nicotiana tabaccum* down-regulated for *CCR* (Hopkins *et al.*, 2001; Webster *et al.*, 2006). Likewise, lower C:N ratio was also observed in *Nicotiana tabacum* down-regulated for *COMT* (Hopkins *et al.*, 2001).

Little data is available that demonstrates the influence of mutations associated with lignin biosynthesis on root:shoot ratio. In a study with *A. thaliana* knockout mutants of *KNAT7* and *MYB75*, Gul (data unpublished) found no difference in root:shoot ratio between mutant lines and their wild type at fruit ripening stage. Hancock *et al.* (2007) found a 15–17% reduction in root C in transgenic *Populus tremuloides* having lower concentration of lignin however they did not assess root:shoot ratio of these lines.

## B. Feedback on Soil Greenhouse Gas Emissions

Residues of GM cell wall mutants that differ in chemistry in terms of C:N ratio, concentration of AUF or lignin concentration and/or lignin chemistry can alter the $CO_2$ emission from soil as compared to their wild ecotypes (Table 4). For instance, higher

residue biodegradation for stem tissues has reported for down-regulated mutants of *CAD*, *COMT* (Henault *et al.*, 2006), *CAD, CCR1,* and *COMT* (Hopkins *et al.*, 2001; 2006) that have lower AUF concentration or lower G:S ratio in stem tissues.

These results and previous findings regarding the influence of plant residue chemistry on $CO_2$ and $N_2O$ emissions, suggest that GM residues with lower lignin and C:N ratio are expected to mineralize faster than their wild types and will cause higher $CO_2$ and $N_2O$ emissions from soil as compared to their wild ecotypes. This phenomenon is illustrated in Figure 10. The higher mineral N concentration and higher soil microbial biomass resulted from the biodegradation of such plant residues may cause substantial SOM loss as $CO_2$ from soil and reduce the aggregate size of soil (Blanco-Canqui and Lal, 2004). Moreover, the potentially higher nitrogen mineralization of soil amended with such residue types in turn can lead to higher $N_2O$ emission from soil.

In contrast, GM plant residues with higher lignin and C:N ratio may cause reduced $CO_2$ emission from their biodegradation and lower $N_2O$ emission due to less N mineralization from biodegradation of such residues, as compared to their wild ecotypes. Such residues may also promote a higher fungal:bacterial ratio of soil, which in turn could reduce soil $CO_2$ emission as fungal cell wall itself is more resistant to biodegradation than bacterial cell wall and expected higher macroaggregate formation and stability caused by fungi. It is reported that *MYB75/PAP1* down-regulation results in an increase in lignin concentration and G/S ratio in inflorescence stems of *Arabidopsis thaliana* (Bhargava *et al.*, 2010). Higher lignin deposition in inflorescence stems relative to wild type plants has also been observed in *KNAT7* down-regulated *Arabidopsis thaliana* (Douglas, 2011). Such mutations could potentially be useful in reducing atmospheric $CO_2$ and $N_2O$ concentration by playing a role in reducing C and N mineralization of SOM if incorporated in the non-harvested plant organs of food crops, ornamental plants and cotton.

## VI. CONCLUSIONS AND FUTURE DIRECTIONS

Phenological and morphological characteristics of plants influence $CO_2$ and $N_2O$ emission from soil via period of vegetative growth phase, plant biomass, morphology such as size of plant and leaf, and fertility. Such characteristics of plants impact $CO_2$ and $N_2O$ emission by influencing water contents and mineral N concentration of soil and by the amount of rhizodeposition. Production of roots is associated with phenology and fruit load. The root tips are hot spots of root exudates. Moreover, the exudates at these sites of roots contain less slowly decomposable compounds than older or more mature parts. Transpiration has a positive relation with plant biomass and fruit load. Prolonged vegetative growth phase and reduced fertility may result in more fine root production and associated more secretion of readily available organic C in soil and less water depletion from soil. Higher rhizodeposition leads to higher $CO_2$ production from microbial activities. In anaerobic conditions, the concentration of soluble organic C and mineral N will be higher in the soil planted with plants in their vegetative growth phase or in the microcites around plant that has reduced fertility. These environmental conditions can result in more $N_2O$ emission from soil than when plants are in their reproductive growth phase and the plants that have high fertility.

Genetic modification of cell wall biosynthesis can alter substantially the emissions of these two GHGs from soil as compared to their wild ecotypes. Genetic modifications with respect to reduce the concentration of lignin in non-harvested residues tend to influence plant phenology, biomass and fertility. For instance, *Cg1* over-expression leads to reduced lignin concentration in leaves, cause profound leaf production and also results in delayed flowering stage initiation. Likewise, down-regulation of *CCR1* and *CAD* also has the tendency to reduce biomass and fertility and/or delay flowering stage initiation. Further research is needed to know the influence of these mutations on soil processes such as fine root production, rhizodeposition, concentration of mineral N and transpiration to get an insight their potential contribution in emission of $CO_2$ and $N_2O$ and to adapt proper management practices for reduction of these greenhouse gases.

Plant residues with lower C:N ratio, lignin concentration, and/or higher S/G ratio of lignin monomers decompose faster, cause higher mineral N concentration and microbial biomass in soil, and consequently result in higher $CO_2$ in aerobic and $N_2O$ emissions in anaerobic conditions than the residues with higher C:N ratio and lignin concentration and/or higher G/S ratio of lignin monomer. Such plant residues therefore degrade faster and also results in greater SOM degradation and cause lower macroaggregate formation and its stability as compared to the later type of plant residue. Genetic modifications that reduce lignin concentration and/or reduce the G/S ratio in plants to enhance production of biofuel or high quality paper, the residues of those plants when are left in field, can negatively influence soil aggregation and result in higher emissions of $CO_2$ and $N_2O$ from soil.

In contrast, crops that are genetically modified for higher lignin concentration, and/or higher G/S ratio of lignin monomers those plants can reduce the net emission of $CO_2$ and $N_2O$ from soil as compared to their wild ecotypes due to higher lignin concentration and/or higher lignin G/S ratio. This assumes that their phenological and morphological traits are not affected due to such mutations. Knocking out *KNAT7* and *MYB75/PAP1* could be potential candidate mutations that can hold promise to reduce the emission of $CO_2$ and $N_2O$ from soil.

Further studies are needed to evaluate the influence of application of environmentally friendly agricultural practices such as biochar application or tree-based intercropping as a mitigation purpose while cropping GM plants with lower cell-wall lignin concentration or lower G/S ratio of lignin monomers. Moreover, induction of mutations that can increase concentration of lignin and/or G/S ratio of lignin monomers in non-harvested

plant7break; tissues (e.g. knockout of *KNAT7* and *MYB75*) in plant species that are less or not important for biofuel purpose such as ornamental plants, cotton, wheat needs to be rendered to help reduce emissions of $CO_2$ and $N_2O$ from soil. Furthermore, the influence of such mutations on phonological and morphological traits as well as fertility, and on concentration and chemistry of lignin in different environmental conditions merits further study. Future research is also needed to investigate the influence of mutations that increase concentration of lignin and G/S ratio on soil processes.

Biomass partitioning (i.e., root:shoot ratio) can play in important role in overall contribution of plant in influencing emission of $CO_2$ and $N_2O$ from soil. The plants with higher root:shoot ratio may contribute greater part in reduction of their biodegradation and in return emission of $CO_2$ and $N_2O$ (when environmental conditions met for $N_2O$ emission from anaerobic means) than the plants with lower root:shoot ratio. It is important to study the biomass partitioning in transgenic plants for secondary cell wall regarding lignin and cellulose biosynthesis to make better understanding in their role in reducing or stimulating $CO_2$ and $N_2O$ emissions in response to their biodegradation when they die.

## ACKNOWLEDGMENTS

Financial support was from Green Crop Network funded by the Natural Sciences and Engineering Research Council of Canada (NSERC). Many thanks to Dr. Caroline Preston and Dr. Sandra Yanni for their critical review of this manuscript, which improved it substantially.

## REFERENCES

Abiven, S., Heim, A., and Schmidt, M. W. I. 2011. Lignin content and chemical characteristics in maize and wheat vary between plant organs and growth stages: consequences for assessing lignin dynamics in soil. *Plant Soil* **343**: 369–378.

Agner, H., and Schenk, M. K. 2006. Plant effects on variability of denitrification N emissions in cultures of potted ornamental plants. *Eur. J. Horticul. Sci.* **71**: 15–20.

Alva, A. K., Paramasivam, S., Fares, A., Obreza, T. A., and Schumann, A. W. 2006. Nitrogen best management practice for citrus trees:11. Nitrogen fate, transport, and components of N budget. *Scientia Horticul.* **109**: 223–233.

Alves, J. D., Paglis, C. M., Livramento, D. E., Linhares, S.S.D., Becker, F. B., and Mesquita, A. C. 2011. Source-sink manipulations in *Coffea Arabica* and its effect on growth of shoots and root systems. *Cienc. Agrotec. Lavras.* **35**: 956–964.

Arenz, B.E., and Blanchette, R.A. 2011. Distribution and abundance of soil fungi in Antarctica at sites on the Peninsula, Ross sea region and McMurdo dry valleys. *Soil Biol. Biochem.* **43**: 308–315.

Atanassova, R., Favet, N., Martz, F., Chabbert, B., Tollier, M.T., Monties, B., Fritig, B., and Legrand, M. 1995. Altered lignin composition in transgenic tobacco expressing O-Methyl transferase sequences in sense and antisense orientation. *Plant J.* **8**: 465–477.

Atwell, B. J., Kriedemann, P. E., and Turnbull, C.G.N., Eds. 1999. *Plants in Action: Adaptation in Nature, Performance in Cultivation*. MacMillian Publishers, South Yarra, Australia, 664 p.

Austin, A.T., and Ballare, C. L. 2010. Dual role of lignin in plant litter decomposition in terrestrial ecosystems. *Proc. Nat. Acad. Sci. USA* **107**: 4618–4622.

Bahri, H., Dignac, M. F., Rumpel, C., Rasse, D. P., Chenu, C., and Mariotti, A. 2006. Lignin turnover kinetics in an agricultural soil is monomer specific. *Soil Biol. Biochem.* **38**: 1977–1988.

Barber, S. A. 1995. *Soil Nutrient Biodiversity: A Mechanistic Approach*. John Wiley and Sons Inc, New York.

Barnes, A. D. 2002. Effects of phenology, water availability and seed source on loblolly pine biomass partitioning and transpiration. *Tree Physiol.* **22**: 733–740.

Barbanti, L., Marco, G., and Claudio, C. 2011. Nitrogen release from a N-15-labeled compost in a sorghum growth experiment. *J. Plant Nutr. Soil Sci.* **174**: 240–248.

Baruah, K. K., Gogoi, B., Gogoi, P., and Gupta, P. K. 2010. $N_2O$ emission in relation to plant and soil properties and yield of rice varieties. *Agron. Sustain. Develop.* **30**: 733–742.

Bastian, F., Bouziri, L., Nicolardot, B., and Ranjard, L. 2009. Impact of wheat straw decomposition on successional patterns of soil microbial community structure. *Soil Biol. Biochem.* **41**: 262–275.

Bell, J. M., Smith, J. L., Bailey, V. L., and Bolton, H. 2003. Priming effect and storage in semi- arid no-till spring crop rotations. *Biol. Fertil. Soils* **37**: 237–244.

Bengough, A. G., Mckenzie, B. M., Hallette, P. D., and Valentine, T. A. 2011. Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. *J. Exp. Bot.* **62**: 59–68.

Bernard, R., Leadley, P., and Hungate, B. A. 2005. Global change, nitrification, and denitrification: a review. *Global Biogeochem Cycl* **19**: GB1007, doi:10.1029/2004GB002282.

Bertholdsson, N. O., and Stoy, V. 1995. Accumulation of biomass and nitrogen during plant growth in highly diverging genotypes of winter wheat. *J. Agr. Crop Sci.* **175**: 167–182.

Bertrand, I., Chabbert, B., Kurek, B., and Recous, S. 2006. Can the biochemical features and histology of wheat residues explain their decomposition in soil? *Plant Soil* **281**: 291–307.

Bhargava, A., Mansfield, S. D., Hall, H. C., Douglas, C. J., and Ellis, B. E. 2010. *MYB75* functions in regulation of secondary cell wall formation in the *Arabidopsis* inflorescence stem. *Plant Physiol.* **154**: 1428–1438.

Billes, G., and Bottner, P. 1981. Living roots effect on $^{14}C$-labelled root litter decomposition. *Plant Soil* **62**: 193–208.

Bird, J. A., Herman, D. J., and Firestone, M. K. 2011. Rhizosphere priming of soil organic matter by bacterial groups in a grassland soil. *Soil BViol. Biochem.* **43**: 718–725.

Blagodatskaya, E., and Kuzyakov, Y. 2008. Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review. *Biol. Fertil. Soils* **45**: 115–131.

Blanco-Canqui, H., and Lal, R. 2004. Mechanisms of carbon sequestration in soil aggregates. *Critic. Rev. Plant Sci.* **23**: 481–504.

Bodelier, P. L. E., Wijlhuizen, A. G., Blom, C. W. P. M., and Laanbroek, H. J. 1997. Effects of photoperiod on growth of and denitrification by *Pseudomonas chlororaphis* in the root zone of *Glyceria maxima*, studied in a gnotobiotic microcosm. *Plant Soil* **190**: 91–103.

Boerjan, W., Ralph, J., and Baucher, M. 2003. Lignin biosynthesis. *Ann. Rev. Plant Biol.* **54**: 519–546.

Bossuyt, H., Denef, K., Six, J., Frey, S. D., Merckx, R., and Paustian, K. 2001. Influence of microbial populations and residue quality on aggregate stability. *Appl. Soil Ecol.* **16**: 195–208.

Brady, N. C., and Weil, R. R. 2008. *The Nature and Properties of Soils. Fourth edition*, pp. 204–205. Pearson Prentice Hall, Upper Saddle River, New Jersey.

Cadish, G., and Giller, K. E. 1997. *Driven by Nature: Plant Residue Quality and Decomposition*. CAB International, Wallingford, Oxon, UK.

Cambui, C. A., Svennerstam, H., Gruffman, L., Nordin, A., Ganeteg, U., and Nasholm, T. 2011. Patterns of plant biomass partitioning depend on nitrogen source. *Plos One* **6**: DOI: 10.1371/journal.pone.0019211.

Canfield, D. E., Glazer, A. N., and Falkowski, P. G. 2010. The evolution and future of earth's nitrogen cycle. *Science* **330**: 192–196.

Carvalhais, L. C., Dennis, P. G., Fedoseyenko, D., Hajirezaei, M. R., Borriss, R., and von Wiren, N. 2011. Root exudation of sugars, amino acids, and

organic acids by maize as affected by nitrogen, phosphorus, potassium, and iron deficiency. *J. Plant Nutr. Soil Sci.* **174**: 3–11.

Cerli, C., Johansson, M.B., Kogel-Knabner, I., Rosenqvist, L., and Zanini, E. 2006. Soil organic matter changes in a spruce chronosequence on Swedish former agricultural soil 1. Carbon and lignin dynamics. *Soil Sci.* **171**: 837–849.

Chantigny, M. H., Angers, D. A., Prevost, D., Vezina, L. P., and Chalifour, F. P. 1997. Soil aggregation and fungal and bacterial biomass under annual and perennial cropping systems. *Soil Sci. Soc. Am. J.* **61**: 262–267.

Cheshire, M. V., Sparling, G. P., and Mundie, C. M. 1984. Influence of soil type, crop and air drying on residual carbohydrate content and aggregate stability after treatment with periodate and tetraborate. *Plant Soil* **76**: 339–347.

Chivenge, P., Vanlauwe, B., Gentile, R., and Six, J. 2011. Comparison of organic versus mineral resource effects on short-term aggregate carbon and nitrogen dynamics in a sandy soil versus a fine textured soil. *Agri. Ecosyst. Environ.* **140**: 361–371.

Chuck, G. S., Tobias, C., Sun, L., Kraemer, F., Li, C., Dibble, D., Arora, R., Bragg, J. N., Vogel, J. P., Singh, S., Simmons, B. A., Pauly, M., and Hake, S. 2011. Overexpression of the maize Corngrass1 microRNA prevents flowering, improves digestibility, and increases starch content of switchgrass. *Proc. Nat. Acad. Sci.* **108**: 17550–17555.

Couteaux, M. M., Bottner, P., and Berg, B. 1995. Litter decomposition, climate and litter quality. *Trend. Ecol. Evol.* **10**: 63–66.

Craine, J. M., C. Morrow, and N. Fierer. 2007. Microbial nitrogen limitation increases ecomposition. *Ecology* **88**: 2105–2113.

Curl, E. A., and Truelove, B. (Eds.). (1986). *The Rhizosphere*. Springer, New York.

Dalal, R. C., and Allen, D. E. 2008. Greenhouse gas fluxes from natural ecosystem. *Aust. J. Bot.* **56**: 369–407.

Derikvand, M. M., Sierra, J. B., Ruel, K., Pollet, B., Do, C. T., Thevenin, J., Buffard, D., Jouanin, L., and Lapierre, C. 2008. Redirection of the phenylpropanoid pathway to feruloyl malate in *Arabidopsis* mutants deficient for cinnamoyl-CoA reductase 1. *Planta* **227**: 943–956.

Dignac, M. F., and Rumpel, C. 2006. relative distributions of phenol dimmers and hydroxyl acids in a cultivated soil and above ground maize tissue. *Org. Geochem.* **37**: 1634–1638.

Do, C-T., Pollet, B., Thevenin, J., Sibout, R., Denoue, D., Barriere, Y., Lapierre, C., and Jouanin, L. 2007. Both caffeoyl coenzyme A 3-O-methyltransferase 1 and caffeic acid O-methyltransferase 1 are involved in redundant functions for lignin, flavonoids and sinapyl malate biosynthesis in *Arabidopsis*. *Planta* **226**: 1117–1129.

Donaldson, L. A., and Paul, K. J. 2012. Localization of cell wall polysaccharides in normal and compression wood of Radiata pine: relationships with lignifications and microfibril orientation. *Plant Physiol.* **158**: 642–653.

Douglas, C. J. 2011. *Transcription Factors and Transcription Factor Complexes Governing Secondary Wall Biosynthesis in Arabidopsis: Potential Tools for Manipulating Carbon Flux into Plant Cell Walls*. Green Crop Network Forum May 2011.

Elkeblawy, A., and LovettDoust, J. 1996. Resource re-allocation following fruit removal in cucurbits: patterns in cantaloupe melons. *New Phytol.* **134**: 413–422.

Emran, M., Gispert, M., and Pardini, G. 2012. Comparing measurements methods of carbon dioxide fluxes in a soil sequence under land use and cover change in North Eastern Spain. *Geoderma* **70**: 176–185.

Eskelinen, A., Sari, S., and Minna, M. 2009. Links between plant community composition, soil organic matter quality and microbial communities in contrasting tundra habitats. *Oecologia* **161**: 113–123.

Farooq, M., Kobayashi, N., Ito, O., Wahid, A., and Serraj, R. 2010. Broader leaves result in better performance of indica rice under drought stress. *J. Plant Physiol.* **167**: 1066–1075.

Fasinmirin, J. T., Olufayo, A. A., Oguntunde, P. G., and Oguntuase, A. M. 2009. Parametrizing simple model between yield and evapotranspiration for *Amaranthus cruentus* under drip and sprinkler irrigations. *Int. J. Plant Prod.* **3**: 75–90.

Fierer, N., Schimel, J. P., and Holden, P. A. 2003. Variations in microbial community composition through two soil depth profiles. *Soil Biol. Biochem.* **35**: 167–176.

Fioretto, A., Papa, S., Pellegrino, A., and Fuggi, A. 2007. Decomposition dynamics of *Myrtus communis* and *Quercus ilex* leaf litter: mass loss, microbial activity and quality change. *Appl. Soil Ecol.* **36**: 32–40.

Fog, K. 1988. The effect of added nitrogen on the rate of decomposition of organic matter. *Biolog. Rev.* **63**: 433–462.

Franks, P. J., Drake, P. L., and Beerling, D. J. 2009. Plasticity in maximum stomatal conductance constrained by negative correlation between stomatal size and density: an analysis using Eucalyptus globules. *Plant Cell Environ.* **32**: 1737–1748.

Frey, S. D., Knorr, M., Parrent, J., and Simpson, R. T. 2004. Chronic nitrogen enrichment affects the structure and function of the soil microbial community in a forest ecosystem. *Forest Ecol. Manage.* **196**: 159–171.

Frimpong, K. A., and Baggs, E. M. 2010. Do combined application of crop residues and inorganic fertilizer lower emission of N(2)O from soil? *Soil Use Manage.* **26**:412–424.

Frouz, J., Cajthaml, T., and Mudrak, O. 2011. The effect of lignin photodegradation on decomposability of *Calamagrostis epigeios* grass litter. *Biodegrad.* **22**: 1247–1254.

Galicia, L., and Felipe, G. O. 2011. Litter quality of two remnant tree species affects soil microbial activity in tropical seasonal pastures in Western Mexico. *Arid Land Res. Manag.* **25**: 75–86.

Garcia-Pausas, J., and Paterson, E. 2011. Microbial community abundance and structure are determinants of soil organic matter mineralization in the presence of labile carbon. *Soil Biol. Biochem.* **43**: 1705–1713.

Goujon, T., Ferret, V., Mila, I., Pollet, B., Ruel, K., Burlat, V., Joseleau, J. P., Barriere, Y., Lapierre, C., and Jouanin, L. 2003. Down-regulation of the AtCCR1 gene in *Arabidopsis thaliana*: effects on phenotype, lignins and cell wall degradability. *Planta* **217**: 218–228.

Graaff, M. A., Kessel, C. V., and Six, J. 2009. Rhizodeposition-induced decomposition increases N availability to wild and cultivated wheat genotypes under elevated $CO_2$. *Soil Biol. Biochem.* **41**: 1094–1103.

Gransee, A., and Wittenmayer, L. 2000. Qualitative and quantitative analysis of water-soluble exudates in relation to plant species and development. *J. Plant Nutr. Soil Sci.* **163**: 381–385.

Gray, D. M., Swanson, J., and Dighton, J. 2012. The influence of contrasting ground cover vegetation on soil properties in the NJ pine barrens. *Appl. Soil Ecol.* **60**: 41–48.

Grayston, S. J., Vaughan, D., and Jones, D. 1997. Rhizosphere carbon flow in trees, in comparison with annual plants: The importance of root exudation and its impact on microbial activity and nutrient availability. *Appl. Soil Ecol.* **5**: 29–56.

Griffiths, B. S. 1994. Microbial-feeding nematodes and protozoa in soil- Their effects on microbial activity and nitrogen mineralization in decomposition hotspots and the rhizosphere. *Plant Soil* **164**: 25–33.

Guenet, B., Neill, C., Bardoux, G., and Abbadie, L. 2010. Is there a linear relationship between priming effect intensity and the amount of organic matter input? *Appl. Soil Ecol.* **46**: 436–442.

Gui, J., Junhui, S., and Laigeng, L. 2011. Functional characterization of evolutionary divergent 4-coumarate: Coenzyme A ligases in rice. *Plant Physiol.* **157**: 574–586.

Guillou, L., Angers, D. A., Leterme, P., and Menasseri-Aubry, S. 2011. Differential and successive effects of residue quality and soil mineral N on water-stable aggregation during crop residue decomposition. *Soil Biol. Biochem.* **43**: 1955–1960.

Gul, S., and Whalen, J. K. 2012a. Phenology, morphology, aboveground biomass and root-associated soil respiration of *Arabidopsis thaliana* down-regulated cell wall mutants of MYB75, KNAT7, and CCR1. *Pedobiologia* DOI, http://dx.doi.org/10.1016/j.pedobi.2012.11.001

Gul, S., Whalen, J. K, Ellis, B. E., and Mustafa, A. 2012b. Influence of plant residue chemistry on soil $CO_2$–C production: A study with *Arabidopsis thaliana* cell wall mutants of KNAT7, MYB75 and CCR1. *Pedobiologia* **55**: 349–356.

Gul, S., Whalen, J. K., Ellis, B., and Grayston, S. J. 2012c. Plant residue chemistry impacts soil processes and microbial community structure: A study with *Arabidopsis thaliana* cell wall mutants. *Appl. Soil Ecol.* DOI:10.1016/j.apsoil.2012.03.006.

Haider, K., Mosier, A., and Heinemeyer, O. 1987. The effect of growing plants on denitrification at high soil nitrate concentration. *Soil Sci. Soc. Am. J.* **51**: 97–102.

Halpin, C., Thain, S. C., Tilson, E. L., Guiney, E., Lapierre, C., and Hopkins, D. W. 2007. Ecological impacts of trees with modified lignin. *Tree Gen. Genome.* **3**: 101–110.

Hancock, J. E., Loya, W. M., Giardina, C. P., Li, L., Chiang V. L., and Pregitzer, K. S. 2007. Plant growth, biomass partitioning and soil carbon formation in response to altered lignin biosynthesis in *Populus tremuloides*. *New Phytologist* **173**: 732–742.

Haynes, R. J., and Beare, M. H. 1997. Influence of six crop species on aggregate stability and some labile organic matter fractions. *Soil Biol. Biochem.* **29**: 1647–1653.

Hedges, J. I., Blanchette, R. A., Weliky, K., and Devol, A. H. 1988. Effects of fungal degradation on the CuO oxidation products of lignin: a controlled laboratory study. *Geochim Cosmochim Acta* **52**: 2717–2726.

Henault, C., English, L. C., Halpin, C., Andreux, F., and Hopkins, D. W. 2006. Microbial community structure in soils with decomposing residues from plants with genetic modifications to lignin biosynthesis. *FEMS Microbiol. Lett.* **263**: 68–75.

Hendricks, J. J., and Boring, L. R. 1992. Litter quality of native herbaceous legumes in a burned pine forest of the Georgia piedmont. *Can. J. For. Res.* **22**: 2007–2010.

Henry, F., Nguyen, C., Paterson, E., Sim, A., and Robin, C. 2005. How does nitrogen availability alter rhizodeposition in *Lolium multiflorum* Lam. During vegetative growth? *Plant Soil* **269**: 181–191.

Hiltner, L. 1904. Uber neuere Erfahrungen und problem auf dem Gebiet der Bodenbakteriologie und unter besonderer Berucksichtigung der Grunddungung und Brache. *Arb. Deutsch. Landw. Gesell.* **98**: 59–78.

Hobbie, S. E. 2008. Nitrogen effects on decomposition: a five-year experiment in eight temperate sites. *Ecology* **89**: 2633–2644.

Hodges, T. 1991. *Predicting Crop Phenology* CRC Press, Boston.

Hogberg, M. N., Yu, C., and Hogberg, P. 2007. Gross nitrogen mineralization and fungi-to-bacteria ratios are negatively correlated in boreal forests. *Biol. Fertil. Soil* **44**: 363–366.

Hopkins, D. W., Webster, E. A., Chudek, J. A., and Halpin, C. 2001. Decomposition of tobacco plants with genetic modifications to lignin biosynthesis. *Soil Biol. Biochem.* **33**: 1455–1462.

Hopkins, D. W., Webster, E. A., Tilson, E. L., and Halpin, C. 2006. Influence of available substrates on the decompositions to lignin biosynthesis. *Eur. J. Soil Sci.* **57**: 495–503.

Hoyle, F. C., and Murphy, D. V. 2011. Influence of organic residues and soil incorporation on temporal measures of microbial biomass and plant available nitrogen. *Plant Soil* **347**: 53–64.

Hu, S., Chapin, III, F. S., Firestone, M. K., Field, C. B., and Chiariello, N. R. 2001. Nitrogen limitation of microbial decomposition in a grassland under elevated $CO_2$. *Nature* **409**: 188–190.

Huang, Y., Zou, J., Zheng, X., Wang, Y., and Xu, X. 2004. Nitrous oxide emissions as influences by amendment of plant residues with different C:N ratios. *Soil Biol. Biochem.* **36**: 973–981.

Hutsch, B. W., Augustin, J., and Merbach, W. 2002. Plant rhizodeposition – an important source for carbon turnover in soils. *J. Plant Nut. Soil Sci.* **165**: 397–407.

IPCC 2007. *Climate Change 2007: The Physical Science Bases*. Cambridge University Press, Cambridge, UK.

Jackson, L. A., Shadle, G. L., Zhou, R., Nakashima, J., Chen, F., and Dixon, R. A. 2008. Improving saccharification efficiency of alfalfa stems through modification of the terminal stages of monolignol biosynthesis. *Bioenerg. Res.* **1**: 180–192.

Jensen, B., and Christensen, B. T. 2004. Interactions between elevated $CO_2$ and added N: effects on water use, biomass, and soil N-15 uptake in wheat. *Acta Agric. Scand. Sect B- Soil Plant Sci.* **54**: 175–184.

Jensen, E. S. 1996. Rhizodeposition of N by pea and barley and its effecton soil N dynamics. *Soil Biol. Biochem.* **28**: 65–71.

Jimenez, J. J., and Lal, R. 2006. Mechanisms of C sequestration in soils of Latin America. *Crit. Rev. Plant Sci.* **25**: 337–365.

Jones, D. L., Hodge, A., and Kuzyakov, Y. 2004. Plant and mycorrhizal regulation of rhizodeposition. *New Phytol.* **163**: 459–480.

Jones, D. L., Nguyen, C., and Finlay, R. D. 2009. Carbon flow in the rhizosphere: carbon trading at the soil–root interface. *Plant Soil* **321**: 5–33.

Jones, L., Ennos, A. R., and Turner, S. R. 2001. Cloning and characterization of irregular xylem4 (irx4): a severely lignin-deficient mutant of Arabidopsis. *Plant J.* **26**: 205–216.

Johnson, J. M. F., Barbour, N. W., and Weyers, S. L. 2007. Chemical composition of crop biomass impacts its decomposition. *Soil Sci. Soc. Am. J.* **71**: 155–162.

Kanemoto, K., Yamashita, Y., Ozawa, T., Imanishi, N., Nguyen, N. T., Suwa, R., Mohapatra, P. K., Kanai, S., Moghaieb, R. E., Ito, J., El-Shemy, H., and Fujita, K. 2009. Photosynthetic acclimation to elevated $CO_2$ is dependent on N partitioning and transpiration in soybean. *Plant Sci.* **177**: 398–403.

Katterer, T., Hansson, A. C., and Andren, O. 1993. Wheat root biomass and nitrogen dynamics – effects of daily irrigation and fertilization. *Plant Soil* **151**: 21–30.

Khalil, K., Mary, B., and Renault, P. 2004. Nitrous oxide production by nitrification and denitrification in soil aggregates as affected by O-2 concentration. *Soil Biol. Biochem.* **36**: 687–699.

Kilbertus, G. 1980. Study of microhabitates in soil aggregates - relation to bacterial biomass and size of prokaryotes. *Revue d'Ecologie et de Biologie du Sol* **17**: 543–557.

Kirk, T. K. 1975. Lignin-degrading enzyme-system. *Biotech. Bioeng.* **5**: 139–150.

Kleber, M., Sollins, P., and Sutton, R. 2007. A conceptual model of organo-mineral interactions in soils: self-assembly of organic molecular fragments into zonal structures on mineral surfaces. *Biogeochem.* **85**: 9–24.

Knops, J. H., and Tilman, D. 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology* **81**: 88–98.

Kuzyakov, Y. 2002. Review: factors affecting rhizosphere priming effects. *J. Plant Nutr. Soil Sci.* **165**: 382–396.

Kuzyakov, Y., and Domanski, G. 2000. Carbon input by plants into the soil. Review. *J. Plant Nutr. Soil Sci.* **163**: 421–431.

Kuzyakov, Y., Hill, P. W., and Jones, D. L. 2007. Root exudate components change litter decomposition in a simulated rhizosphere depending on temperature. *Plant Soil* **290**: 293–305.

Langley, J. A., and Hungate, B. A. 2003. Mycorrhizal controls on belowground liter quality. *Ecology* **84**: 2302–2312.

Lai, W. L., Wang, S. Q., Peng, C. L., and Chen, Z. H. 2011. Root features related to plant growth and nutrient removal of 35 wetland plants. *Water Res* **45**: 3941–3950.

Lea-Cox, J. D., Syvertsen, J. P., and Graetz, D. A. 2001. Springtime (15) nitrogen uptake, partitioning, and leaching losses from young bearing citrus trees of differing nitrogen status. *J. Am. Soc. Horticul. Sci.* **126**: 242–251.

Leple, J-C., Dauwe, R., Moreel, K., Storme, V., Lapierre, C., Pollet, B., Naumann, A., Kang, K-Y., Kim, H., Ruel, K., *et al*. 2007. Downregulation of Cinnamoyl-Coenzyme A reductase in poplar: Multiple level phenotyping reveals effects on cell wall polymer metabolism and structure. *Plant Cell* **19**: 3669–3691.

Li, E. 2009. Identification and characterization of regulatory genes associated with secondary wall formation in Populus and Arabidopsis thaliana. PhD thesis, University of British Columbia, Vancouver, Canada, p. 79.

Li, Y., Zhong-ming, H., Li-min, Y., and Mei, H. 2010. Effects of water stress on photosynthesis, biomass and medicinal material quality of *Tribulus terrestri*. *J. Appl. Ecol.* **21**: 2523–2528.

Liu, N., He, H., Xie, H., Bai, Z., Zhang, X., Peng, C., Zhu, P., Ren, J., and Wang, L. 2010. Impacts of long-term inorganic and organic fertilization on lignin in a Mollisol. *J. Soil Sediment* **10**: 1466–1474.

Lopez-Bellido, L., Benitez-Vega, J., Garcia, P., Redondo, R., and Lopez-Bellido, R. J. 2011. Tillage system effect on nitrogen rhizodeposited by faba bean and chickpea. *Field Crop. Res.* **120**: 189–195.

Lopez, G., Arbones, A., Mata, M., Paris, C., Girona, J., and Marsal, J. 2008. Root growth following defruiting improves peach tree water status. *J. Horticul. Sci. Biotec.* **83**: 804–808.

Lorenz, K., Lal, R., Preston, C. M. and Nierop, K. G. J. 2007. Strengthening the soil organic carbon pool by increasing contributions from recalcitrant aliphatic bio(macro)molecules. *Geoderma* **142**: 1–10.

Luan, J., Liu, S., Zhu, X., Wang, J., and Liu, K. 2012. Roles of biotic and abiotic variables in determining spatial variation of soil respiration in secondary oak and planted pine forests. *Soil Biol. Biochem.* **44**: 143–150.

Luo, Y. C., Zhou, H., Li, Y., Chen, J. Y., Yang, J. H., Chen, Y. Q., Qu, L. H. 2006. Rice embryogenetic calli express a unique set of microRNAs, suggesting regulatory roles of microRNAs in plant post-embyogenetic development. *FEBS Lett.* **580**: 5111–5116.

Lynch, J. M., and Whipps, J. M. 1990. Substrate flow in the rhizosphere. *Plant soil.* **129**: 1–10.

Majdi, H. 2007. Root and root-lignin degradation in a Norway spruce stand: effects of long-term nitrogen addition. *Plant Biosyst.* **141**: 214–221.

Marianne, K., Schnecker, J., Kaiser, C., Fuchslueger, L., Kitzler, B., Stange, C. F., Sessitsch, A., Zechmeister-Boltenstern, S., and Richter, A. 2011. Microbial processes and community composition in the rhizosphere of European beech – the influence of plant C exudates. *Soil Biol. Biochem.* **43**: 551–558.

Marschner, B., Brodowski, S., Dreves, A., Gleixner, G., Gude, A., Grootes, P. M., Hamer, U., Hein, A., Jandl, G., Ji, R., Kaiser, K., Kalbitz, K., Kramer, C., Leinweber, P., Rethemeyer, J., Schäffer, A., Schmidt, M. W. I., Schwark, L. and Wiesenberg, G. L. B. 2008. How relevant is recalcitrance for the stabilization of organic matter in soils? *J. Plant Nutr. Soil Sci.* **171**: 91–110.

Martin-Vertedor, A. I., Rodriguez, J. M. P., Losada, H. P., and Castiel, E. F. 2011. Interactive responses to water deficits and crop load in olive (*Olea europaea* L., cv. Morisca).II: water use, fruit and oil yield. *Agric. Water Manag.* **98**: 950–958.

Masarovicova, E., and Navara, J. 1994. Influence of fruit load on $CO_2$ exchange, water-uptake, and biomass of apple-trees. *Gartenbauwissenschaft* **59**: 132–138.

Matsunami, M., Matsunami, T., and Kokubun, M. 2010. Comparison of nitrogen uptake, transpiration rate and exudation rate between upland NERICAs and Japanese cultivars. *Plant Prod. Sci.* **13**: 347–350.

Matsunami, M., Matsunami, T., Ogawa, A., Toyofuku, K., Kodama, I., and Kokubun, M. 2012. Genotypic variation in biomass production at the early vegetative stage among rice cultivars subjected to deficient soil moisture regimes and its association with water uptake capacity. *Plant Prod. Sci.* **15**: 82–91.

Mclnerney, M., and Bolger, T. 2000. Temperature, wetting cycles and soil texture effects on carbon and nitrogen dynamics in stabilized earthworm casts. *Soil. Biol. Biochem.* **32**: 335–349.

Melillo, J. M., Aber, J. D., and Muratore, J. F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* **63**: 621–626.

Millar, N., and Baggs, E. M. 2004. Chemical composition, or quality, of agroforestry residues influences $N_2O$ emissions after their addition to soil. *Soil Biol. Biochem.* **36**: 935–943.

Miller, M. N., Zebarth, B. J., Dandie, C. E., Burton, D. L., Goyer, C., and Trevor, J. T. 2008. Crop residue influence on denitrification, $N_2O$ emissions and denitrifier community abundance in soil. *Soil Biol. Biochem.* **40**: 2553–2562.

Morinaga, K., Yakushiji, H., and Koshita, Y. 1998. Effect of fruit load levels on root activity, vegetative growth and sugar accumulation in berries of grapevine. *ISHS Acta Horticulturae* **512**: 121–128.

Morinaga, K., Imai, S., Yakushiji, H., and Koshita, Y. 2003. Effects of fruit load on partitioning of $^{15}N$ and $^{13}C$, respiration, and growth of grapevine roots at different fruit stages. *Sci. Horticul.* **97**: 239–253.

Mougel, C., Offire, P., Ranjard, L., Corberand, T., Gamalero, E., Robin, C., and Lemanceau, P. 2006. Dynamic of the genetic structure of bacterial and fungal communities at different developmental stages of Medicago truncatula Gaertn. cv. Jemalong line J5. *New Phytologist* **170**: 165–175.

Naor, A. 2004. The interactions of soil- and stem-water potentials with crop level, fruit size and stomatal conductance of field-grown 'Black Amber' Japanese plum. *J. Horticul. Sci. Biotech.* **79**: 273–280.

Neff, J. C., Townsend, A. R., Gleixner, G., Lehman, S. J., Turnbull, J., and Bowman, W. D. 2002. Variable effects of nitrogen additions on the stability and turnover of soil carbon. *Nature* **419**: 195–197.

Neumann, G. 2007. Root exudates and nutrient cycling. *Nutr. Cycling Terr. Ecosyst.* **10**: 123–157.

Nicolardot, B., Bouziri, L., Bastian, F., and Ranjard, L., 2007. A microcosm experiment to evaluate the influence of location and quality of plant residues on residue decomposition and genetic structure of soil microbial communities. *Soil Biol. Biochem.* **39**: 1631–1644.

Nilson, P. 1995. Effect of nitrogen on drought strain and nutrient uptake in Norway spruce *Picea abies* (L.) Karst.) trees. *Plant Soil* **172**: 73–85.

Nord, E. A., and Lynch, J. P. 2009. Plant phenology: a critical controller of soil resource acquisition. *J. Exp. Bot.* **60**: 1927–1937.

Nourbakhsh, F., and Dick, R. P. 2006. Net nitrogen mineralization or immobilization potential in a residue-amended calcareous soil. *Arid land res. Manag.* **19**: 299–306.

Novak, V., and van Genuchten, M. T. 2008. Using the transpiration regime to estimate biomass production. *Soil Sci.* **173**: 401–407.

Novak, V., and Vidovic, J. 2003. Transpiration and nutrient uptake dynamics in maize (*Zea mays* L.). *Ecol. Mod.* **166**: 99–107.

Opsahl, S., and Benner, R. 1995. Early diagenesis of vascular plant tissues: lignin and cutin decomposition and biogeochemical implications. *Geochim. Cosmochim. Acta* **59**: 4889–4904.

Orsini, F., Alnayef, M., Bona, S., Maggio, A., and Gianquinto, G. 2012. Low stomatal density and reduced transpiration facilitate strawberry adaptation to salinity. *Environ. Exp. Bot.* **81**: 1–10.

Otto, A., and Simpson, M. J. 2006. Evaluation of CuO oxidation parameters for determining the source and stage of lignin degradation in soil. *Biogeochem.* **80**: 121–142.

Patten, A. M., Cardenas, C. L., Chrane, F. C., Laskar, D. D., Bedgar, D. L., Davin, L. B., and Lewis, N. G. 2005. Reassessment of effects of ligninfication and vascular development in the *irx4 Arabidopsis* mutant. *Phytochem.* **66**: 2092–2107.

Peng, Y., Niu, J., Peng, Z., Zhang, F., and Li, C. 2010. Shoot growth potential drives N uptake in maize plants and correlates with root growth in the soil. *Field Crop. Res.* **115**: 85–93.

Peng, Y. F., Yu, P., Zhang, Y., Sun, G., Nig, P., Li, X. X., and Li, C. J. 2012. Temporal and spatial dynamics in root length density of field-grown maize and NPK in the soil profile. *Field Crop. Res.* **131**: 9–16.

Paterson, E. 2003. Importance of rhizodeposition in the coupling of plant and microbial productivity. *Eur. J. Soil Sci.* **54**: 741–750.

Petersen, M., Hans, J., and Matern, U. 2010. Biosynthesis of phenylpropanoids and related compounds. *Annu. Plant Rev.* **40**: 182–257.

Piquemal, J., Lapierre, C., Myton, K., O'Connell, A., Schuch, W., Grima-Pettenati, J., and Boudet, A-M. 1998. Down-regulation of Cinnamoyle-CoA reductase induces significant changes of lignin profiles in transgenic tobacco plants. *Plant J.* **13**: 71–83.

Pincon, G., Maury, S., Hoffman, L., Geoffroy, P., Lapierre, C., Pollet, B., and Legrand, M. 2001. Repression of O-methyltransferase genes in transgenic tobacco affects lignin synthesis and plant growth. *Phytochem.* **57**: 1167–1176.

Potthast, K., Hamer, U., and Makeschin, F. 2010. Impact of litter quality on mineralization processes in managed and abandoned pasture soils in Southern Ecuador. *Soil Biol. Biochem.* **42**: 56–64.

Preston, C. M., Trofymow, J. A., Sayer, B. G., and Niu, J. 1997. $^{13}C$ nuclear magnetic resonance spectroscopy with cross-polarization and magic-angle spinning investigation of the proximate-analysis fractions used to assess litter quality in decomposition studies. *Can. J. Bot.* **75**:1601–1613.

Preston, C. M., Trofymow, J. A., and Flanagan, L. B. 2006. Decomposition, $\delta^{13}C$, and the "lignin paradox". *Can. J. Soil Sci.* **86**: 235–245.

Preston, C. M., Nault, J. R., and Trofymow, J. A. 2009. Chemical changes during 6 years of decomposition of 11 litters in some Canadian forest sites. Part 2. $^{13}C$ abundance, solid-state $^{13}C$ NMR spectroscopy and the meaning of "lignin". *Ecosyst*. **12**: 1078–1102.

Puttaso, A., Vityakon, P., Saenjan, P., Trelo-ges, V., and Cadisch, G. 2011. Relationship between residue quality, decomposition patterns, and soil organic matter accumulation in a tropical sandy soil after 13 years. *Nutr. Cycl. Agroecosys.* **89**: 159–174.

Ravishankara, A. R., Daniel, J. S., and Portmann, R. W. 2009. Nitrous oxide ($N_2O$): The dominant ozone-depleting substance emitted in the 21st century. *Science* **326**: 123–125.

Read, D. B., Bengough, A. G., Gregory, P. J., Crawford, J. W., Robinson, D., Scrimgeour, C. M., Young, I. M., Zhang, K., and Zhang, X. 2003. Plant roots release phospholipid surfactants that modify the physical and chemical properties of soil. *New Phyto.l* **157**:315–321.

Reddy, A. R., Reddy, K. R., Padjung, R., and Hodges, H. F. 1996. Nitrogen nutrition and photosynthesis in leaves of Pima cotton. *J. Plant Nutri.* **19**: 755–770.

Richard, P. P., Adrien, F. C., and Emily, B. S. 2011. Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term $CO_2$ fumigation. *Ecol. Lett.* **14**: 187–194.

Richardson, D., Felgate, H., Watmough, N., Thomson, A., and Baggs, E. 2009. Mitigating release of the potent greenhouse gas $N_2O$ from the nitrogen cycle – could enzymatic regulation hold the key? *Trends Biotechnol.* **27**: 388–396.

Richard-Molard, C., Krapp, A., Brun, F., Ney, B., Daniel-Vedele, F., and Chaillou, S. 2008. Plant response to nitrate starvation is determined by N storage capacity matched by nitrate uptake capacity in two *Arabidopsis* genotypes. *J. Exp. Bot.* **59**: 779–791.

Rillig, M. C., Lutgen, E. R., Ramsey, P. W., Klironomos, J. N., and Gannon, J. E. 2005. Microbiota accompanying different arbuscular mycorrhizal fungal isolates influence soil aggregation. *Pedobiologia* **49**: 251–259.

Rillig, M. C., and Mummey, D. L. 2006. Mycorrhizas and soil structure. *New. Phytol.* **171**: 41–53.

Rochette, P., Angers, D. A., Chantigny, M. H., Gagnon, B., and Bertrand, N. 2008. $N_2O$ fluxes in soils of contrasting textures fertilized with liquid and solid dairy cattle manures. *Can. J. Soil. Sci.* **88**: 175–187.

Roque-Rivera, R., Talhelm, A. F., Johnson, D. W., Chiang, V. L., and Pregitzer, K. S. 2011. Effects of lignin-modified *Populus tremuloides* on soil organic carbon. *J. Plant Nutr. Soil Sci.* **174**: 818–826.

Sadras, V. O., and Denison, R. F. 2009. Do plant parts compete for resources? An evolutionary viewpoint. *New Phytol.* **183**: 565–574.

Saggar, S., Mclntosh, P. D., Hedley, C. B., and Knicker, H. 1999. Changes in microbial biomass, metabolic quotient, and organic matter turnover under *Hieracium* (H – *pilosella* L.). *Biol. Fert. Soil.* **30**: 232–238.

Salisbury, F. B., and Ross, C. W. 1992. *Plant Physiology*. Wadsworth Publishing Company, Belmont, CA, pp. 160.

Sanaullah, M., Abad, S., Lemaire, G., Charrier, X., and Rumpel, C. 2010. How does plant leaf senescence of grassland species influence decomposition kinetics and litter compounds dynamics? *Nutr. Cycl. Agroecosyst.* **88**: 159–171.

Sanches, E. E., Righetti, T. L., Sugar, D., and Lambard, P. B. 1991. Nitrogen variability between comice pear fruits from trees having high and low nitrogen status. *J. Horticul. Sci.* **66**: 43–50.

Schwab, P. M., Lamb, F. S., Sheaffer, C. C., and Barnes, D. K. 2005. Germplasm variability and environmental effects on stem cellulose and lignin concentrations in alfalfa. *J. Agron. Crop Sci.* **191**: 386–392.

Sey, B. K., Manceur, A. M., Whalen, J. K., and Gregorich, P. R. 2010. Root-derived respiration and nitrous oxide production as affected by crop phenology and nitrogen fertilization. *Plant Soil* **326**: 369–379.

Shadle, G., Chen, F., Reddy, M. S. S., Jackson, L., Nakashima, J., and Dixon, R. A. 2007. Down-regulation of hydroxycinnamoyl CoA: Shikimate hydroxycinnamoyl transferase in transgenic alfalfa affects lignification, development and forage quality. *Phytochem.* **68**: 1521–1529.

Shazad, T., Chenu, C., Repincay, C., Mougin, C., and Ollier, J-L. 2012. Plant clipping decelerates the mineralization of recalcitrant soil organic matter under multiple grassland species. *Soil Biol. Biochem.* **51**: 73–80.

Shaw, L. J., and Burns, R. C. 2003. Biodegradation of organic pollutants in the rhizosphere. *Adv. Appl. Microbiol.* **53**: 1–59.

Shi, Y., Zhang, X., Xu, Z. Y., Li, L., Zhang, C., Schlappi, M., and Xu, Z. Q. 2011. Influence of EARLI1-like genes on flowering time and lignin synthesis of *Arabidopsis thaliana*. *Plant Biol.* **13**: 731–739.

Shoun, H., Shinya, F., Li, J., Kim, S-W., and Wakagi, T. 2012. Fungal denitrification and nitric oxide reductase cytochrome P450nor. *Phil. Trans. R. Soc. B.* **367**: 1186–1194.

Shukla, K. P., Sharma, S., Singh, N. K., Singh, V., Tiwari, K., and Singh, S. 2011. Nature and role of root exudates: efficacy in bioremediation. *Afr. J. Biotech.* **10**: 9717–9724.

Singh, V. P., and Arora, A. 2001. Intraspecific variation in nitrogen uptake and nitrogen utilization efficiency in wheat (*Triticum aestivum* L.). *J. Agr. Crop Sci.* **186**: 239–244.

Sirisha, V. L., Prashant, S., Kumar, D. R., Pramod, S., Jalaja, N., Kumari, P. H., Rao, P. M., Rao, S. N., Mishra, P., Karumanchi, S. R., Khan, B. M., and Kishor, P. B. K. 2012. cloning, characterization and impact of up- and down-regulating subabul cinnamoyl alcohol dehydrogenase (*CAD*) gene on plant growth and lignin profiles in transgenic tobacco. *Plant Growth Regul.* **66**: 239–253.

Six, J., Frey, S. D., Thiet, R. K., and Batten, K. M. 2006. Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil. Sci. Soc. Am. J.* **70**: 555–569.

Sparling, G. S., Cheshire, M. V. and Mundie, C. M. 1982. Effect of barley plants on the decomposition of $^{14}C$-labelled soil organic matter. *J. Soil Sci.* **33**: 89–100.

Strong, D. T., Sale, P. W. G., and Helyar, K. R. 1999. The influence of the soil matrix on nitrogen mineralization and nitrification. *IV. Texture. Aus. J. Soil. Res.* **37**: 329–344.

Sun, G., Luo, P., Qiu, P. F., Gao, Y. H., Chen, H., and Shi, F. S. 2009. *Stellera chamaejasme* L. increases soil N availability, turnover rates and microbial biomass in an alpine meadow ecosystem on the eastern Tibetan Plateau of China. *Soil Biol.Biochem.***41**: 86–91.

Sylvia, D. M., Fuhrmann, J. J., Hartel, P. G., and Zuberer, D. A. 2005. *Principles and Applications of Soil Microbiology*. Prentice Hall, Upper Saddle River, New Jersey.

Szlovak, S., and Szlovak, S. 1999. Dry matter yield and nitrogen uptake of maize at various nitrogen - and two soil moisture levels. *Cereal Res. Comm.* **27**: 189–196.

Talbot, J. M., and Treseder, K. K. 2012. Interactions among lignin, cellulose, and nitrogen drive litter chemistry–decay relationships. *Ecol.* **93**: 345–354.

Talbot, J. M., Yelle, D. J., Nowick, J., and Treseder, K. K. 2012. Liter decay rates are determined by lignin chemistry. *Biogeochem.* DOI 10.1007/s 10533-011-9599-6.

Tang, J., Mo, Y. H., Zhang, J. Y., and Zhang, R. D. 2011. Influence of biological aggregating agents associated with microbial population on soil aggregate stability. *Appl. Soil Ecol.* **47**: 153–159.

Tanaka, Y., Fujii, K., and Shiryaiwa, T. 2010. Variability of leaf morphology and stomatal conductance in soybean (Glycine max (L.) Merr.) cultivars. *Crop Sci.* **50**: 2525–2532.

Tans, P. 2012. Trends in atmospheric carbon dioxide: Recent Mauna Loa $CO_2$. Available at www.esrl.noaa.gov/gmd/ccgg/trends/.

Thevenin, J., Pollet, B., Letarnec, B., Saulnier, L., Gissot, L., Maia-Grondard, A., Lapierre, C., and Jouanin, L. 2011. The simultaneous repression of CCR and CAD, two enzymes of the lignin biosynthetic pathway: results in sterility and dwarfism in *Arabidopsis thaliana*. *Mol. Plant* **4**: 70–82.

Thevenot, M., Dignac, M. F., and Rumpel, C. 2010. Fate of lignins in soils: a review. *Soil Biol. Biochem.* **42**: 1200–1211.

Tian, Q., Chen, F., Zhang, F., and Mi, G. 2006. Genotypic difference in nitrogen acquisition ability in maize plants is related to the coordination of leaf and root growth. *J. Plant Nutr.* **29**: 317–330.

Tilston, E. L., Halpin, C., and Hopkins, D. W. 2004. Genetic modifications to lignin biosynthesis in field-grown poplar trees have inconsistent effects on the rate of woody trunk decomposition. *Soil Biol. Biochem.* **36**: 1903–1906.

Tu, Y., Rochfort, S., Liu, Z., Ran, Y., Griffith, M., Badenhorst, P., Gordon, V., Louie, M. E., Kevin, B. F., Joseph S. P., Mouradov, N. A., and Spangenberga, G. 2010. Functional Analyses of caffeic acid O-methyltransferase and Cinnamoyl-CoA-Reductase genes from perennial ryegrass (Lolium perenne). *Plant Cell* **22**: 3357–3373.

Vale, M., Nguyen, C., Dambrine, E., and Dupouey, J. L. 2005. Microbial activity in the rhizosphere soil of six herbaceous species cultivated in a greenhouse is correlated with shoot biomass and root C concentration. *Soil Biol. Biochem.* **37**: 2329–2333.

Vandat, E., Nourbakhsh, F., and Basiri, M. 2011. Lignin content of range plant residues controls N mineralization in soil. *Eur. J. Soil Biol.* **47**: 243–246.

Van der Krift, T. A. J., Kuikman, P. J., Moller, F., and Berendse, F. 2001. Plant species and nutritional-mediated control over rhizodeposition and root decomposition. *Plant Soil* **228**:191–200.

Vega-Sanchez, M. E., and Ronald, P. C. 2010. Genetic and biotechnological approaches for biofuel crop improvement. *Curr. Opin. Biotechnol.* **21**: 218–224.

Victoria, G. D., Durand, J. L., and Gastal, F. 2010. Water deficit and nitrogen nutrition of crops: a review. *Agron. Sustain. Dev.* **30**: 529–544.

Waisel, Y., Eshel, A., and Kafkafi, U. 2003. *Plant Roots the Hidden Half*. pp 627–628 Marcel Dekker, New York.

Wang, L., Liu, H., Horn, R., and Bernhofer, C. 2012. Effect of grazing intensity on evapotranspiration in the semiarid grasslands of Inner Mongolia, China. *J. Arid. Environ.* **83**: 15–24.

Warembourg, F. R., and Estelrich, H. D. 2000. Towards a better understanding of carbon flow in the rhizosphere a time-dependent approach using carbon-14. *Biol. Fertile. Soils* **30**: 528–534.

Warembourg, F. R., and Estelrich, H. D. 2001. Plant phenology and soil fertility effects on below-ground carbon allocation for an annual (*Bromus madritensis*) and a perennial (*Bromus erectus*) grass species. *Soil Biol. Biochem.* **33**: 1291–1303.

Warembourg, F. R., Roumet, C., and Lafont, F. 2003. Differences in rhizosphere carbon partitioning among plant species of different families. *Plant Soil* **256**: 347–357.

Webster, E. A., Halpin, C., Chudek, J. A., Tilson, E. L., and Hopkins, D. W. 2005. Decomposition in soil of soluble, insoluble and lignin-rich fractions of plant material from tobacco with genetic modifications to lignin biosynthesis. *Soil Biol. Biochem.* **37**: 751–760.

Webster, J., and Stone, B. A. 1994. Isolation, structure and monosaccharide composition of the walls of vegetative parts of Heterozostera tasmanica (Martens ex Aschers.) den Hartog. *Aqua. Bot.* **47**: 39–52.

Weisskopf, L., Bayon, R-C. L., Kohler, F., Page, V., Jossi, M., Gobat, J-M., Martinoia, E., and Aragno, M. 2008. Spatio-temporal dynamics of bacterial communities associated with two plant species differing in organic acid secretion: A one-year microcosm study on lupin and wheat. *Soil Biol. Biochem.* **40**: 1772–1780.

Wichern, F., Eberhardt, E., Mayer, J., Joergensen, R. G., and Muller, T. 2008. Nitrogen rhizodeposition in agricultural crops: Methods, estimates and future prospects. *Soil Biol. Biochem.* **40**: 30–48.

Williams, S. T., and Gray, T. R. G. 1974. Decomposition of litter on the soil surface. **In:** *Biology of Plant Litter Decomposition*, pp. 611–632. Dickinson, C. H., Pugh, G. J. F. Eds., Academic Press, New York.

Wittenmayer, L., and Merbach, W. 2005. Plant responses to drought and phosphorus deficiency: Contribution of phytohormones in root-related processes. *J. Plant Nutr. Soil Sci.* **168**: 531–540.

Wrage, K., Velthof, G. L., van Beusichem, M. L., and Oenema, O. 2001. Role of nitrifier denitrification in the production of nitrous oxide. *Soil Biol. Biochem.* **33**: 1723–1732.

Xu, B. C., Gichuki, P., Shan, L., and Li, F. M. 2006. Aboveground biomass production and soil water dynamics of four leguminous forages in semiarid region, northwest China. *South Afr. J. Bot.* **72**: 507–516.

Yan, F., Sun, Y. Q., Song, F. B., and Liu, F. 2012. Differential responses of stomatal morphology to partial root-zone drying and deficit irrigation in potato leaves under varied nitrogen rates. *Scientia Horticul*. **145**: 76–83.

Yanni, S. F., Whalen, J. K., Simpson, M. J., and Janzen, H. H. 2011. Plant lignin and nitrogen contents control carbon dioxide production and nitrogen mineralization in soils I incubated with Bt and non-Bt corn residues. *Soil Biol. Biochem.* **43**: 63–69.

Yao, S., Merwin, I. A., and Brown, M. G. 2006. Root dynamics of apple rootstocks in a replanted orchard. *Hortscience* **41**: 1149–1155.

Yao, H., Thornton, B., and Paterson, E. 2012. Incorporation of 13C-labelled rice rhizodeposition carbon into soil microbial communities under different water status. *Soil Biol. Biochem.* **53**: 72–77.

Zhang, C., Liu, G., Xue, S., and Song, Z. 2011. Rhizosphere soil microbial activity under different vegetation types on the Loess Plateau, China. *Geoderma* **161**: 115–125.

Zhao, D., Han, C., Tao, J., Wang, J., Hao, Z., Geng, Q., and Du, B. 2012. Effects of inflorescence stem structure and cell wall components on the mechanical strength of inflorescence stem in herbaceous peony. *Int. J. Mol. Sci.* **13**: 4993–5009.

Zhong, R., Morrison, W. H., Himmelsbach, D. S., Poole, F. L., and Ye, Z. H. 2000. Essential role of caffeoyl coenzyme A O-methyltransferase in lignin biosynthesis in woody poplar plants. *Plant Physiol*. **124**: 563–578.

Zhong, R. Q., Lee, C. H., Zhou, J. L., McCarthy, R. L., and Ye, Z. H. 2008. A battery of transcription factors involved in the regulation of secondary cell well biosynthesis in *Arabidopsis*. *Plant Cell* **20**: 2763–2782.

Zhong, R., and Ye, Z. H. 2007. Regulation of cell wall biosynthesis. *Curr. Opin. Plant Biol.* **10**: 564–572.