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Plant Life History and Residue Chemistry Influences Emissions of CO₂ and N₂O 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

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Plant Life History and Residue Chemistry Influences Emissions of CO$_2$ and N$_2$O 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 (CO₂) through photosynthesis. Some of the fixed CO₂ is respired by the plant directly, with additional CO₂ 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 (N₂O). In anaerobic soils, reduction of nitrate by microbial denitrifiers also produces N₂O. The plant-microbial interactions that result in CO₂ and N₂O 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-pulp 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 CO₂ and N₂O emissions from soil. The objective of this review are the following: 1) to describe how plants influence CO₂ and N₂O emissions from soil during their life cycle; 2) to explain how plant residue chemistry affects its mineralization, contributing to CO₂ and N₂O emissions from soil; and 3) to show how modification of plant lignin biosynthesis could influence CO₂ and N₂O 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 CO₂ and N₂O 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 CO₂ and N₂O 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 CO₂ and N₂O 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 CO₂ and N₂O is of environmental concern. The contribution of CO₂ and N₂O to global warming is 60% and 6%, respectively (Dalal and Allen, 2008). The CO₂ 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 N₂O 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 N₂O is 298 times greater than CO₂ and it also contributes to destruction of the stratospheric ozone layer (Ravishankara et al., 2009). Increasing CO₂ concentration is mainly from human activities such as fossil fuel combustion, cement production, land use change and agricultural practices whereas the increased N₂O emission is predominantly due to greater use of N fertilizer in agriculture (Dalal and Allen, 2008).

Vascular plants influence emissions of CO₂ and N₂O from soil during their growth and when their dead residues are incorporated in soil (Figure 1). Considering the CO₂ emissions first, we begin with photosynthesis, a chemical reaction that fixes CO₂ into organic compounds in green plants. About 30 to 50% of the fixed CO₂ is respired daily and returns to the atmosphere, with about half of this respiration attributed to the
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$_2$O 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$_2$O emission from soil (Canfield et al., 2010), as illustrated in Figure 1. The contribution of each process (nitrifier denitrification vs. denitrification) to N$_2$O 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$_2$O 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$_2$O 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 lignocellulosic biofuel crops). Lignin biosynthesis takes place in two main pathways: (1) the formation of coenzyme A-thioesters of ferulic, 4-coumaric, 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 Pigment 1 (PAP1/MBY75) 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).

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 1
Enzymes controlling biosynthesis of lignin and their abbreviations

<table>
<thead>
<tr>
<th>Enzyme</th>
<th>Abbreviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>4-coumarate: CoA ligase 1</td>
<td>4CL</td>
</tr>
<tr>
<td>Cinnamyl alcohol dehydrogenase</td>
<td>CAD</td>
</tr>
<tr>
<td>Coniferaldehyde 5-hydroxylase</td>
<td>CALD5H</td>
</tr>
<tr>
<td>Caffeoyl CoA 3-O-methyl transferase</td>
<td>CCOMT</td>
</tr>
<tr>
<td>Cinnamyl CoA-reductase 1</td>
<td>CCR1</td>
</tr>
<tr>
<td>Cormgrass 1</td>
<td>Cg1</td>
</tr>
<tr>
<td>Caffeic acid O-methyl transferase</td>
<td>COMT</td>
</tr>
<tr>
<td>Early Arabidopsis aluminum-induced gene 1</td>
<td>EARLI1</td>
</tr>
<tr>
<td>Shikimate hydroxycinnamoyl transferase</td>
<td>HCT</td>
</tr>
<tr>
<td>Knotted Arabidopsis thaliana 7</td>
<td>KNAT7</td>
</tr>
<tr>
<td>Production of anthocyanin pigment 1/myeloblast 75</td>
<td>PAP1/MBY75</td>
</tr>
<tr>
<td>Plant species</td>
<td>mutant gene</td>
</tr>
<tr>
<td>-----------------------</td>
<td>-------------</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Populus tremuloides</em></td>
<td>4CL k/o</td>
</tr>
<tr>
<td>Rice</td>
<td>4CL k/o</td>
</tr>
<tr>
<td><em>A. thaliana</em></td>
<td><em>CAD, CCR1</em> k/o, double mutant</td>
</tr>
<tr>
<td><em>Medicago sativa</em></td>
<td><em>CAD</em> k/o</td>
</tr>
<tr>
<td><em>Nicotiana tabacum</em></td>
<td><em>CAD</em> k/o</td>
</tr>
<tr>
<td><em>Populus tremuloides</em></td>
<td><em>CAD</em> k/o</td>
</tr>
<tr>
<td><em>Populus tremuloides</em></td>
<td><em>CAD</em> k/o</td>
</tr>
<tr>
<td><em>Populus tremuloides</em></td>
<td>4CL k/o + <em>CAD</em> k/o</td>
</tr>
<tr>
<td><em>Panicum virgatum</em></td>
<td><em>Cg1</em> expression</td>
</tr>
<tr>
<td><em>A. thaliana</em></td>
<td><em>CCOMT</em> k/o</td>
</tr>
<tr>
<td><em>Poplar</em></td>
<td><em>CCOMT</em> k/o</td>
</tr>
<tr>
<td><em>Rye grass</em></td>
<td><em>CCOMT</em> k/o</td>
</tr>
<tr>
<td><em>A. thaliana</em></td>
<td><em>COMT</em> k/o</td>
</tr>
<tr>
<td><em>Nicotiana tabacum</em></td>
<td><em>COMT</em> k/o</td>
</tr>
<tr>
<td><em>Rye grass</em></td>
<td><em>COMT</em> k/o</td>
</tr>
<tr>
<td><em>A. thaliana</em></td>
<td><em>CCR</em> k/o</td>
</tr>
<tr>
<td><em>Medicago sativa</em></td>
<td><em>CCR</em> k/o</td>
</tr>
<tr>
<td><em>Nicotiana tabacum</em></td>
<td><em>CCR</em> k/o</td>
</tr>
<tr>
<td><em>Poplar</em></td>
<td><em>CCR</em> k/o</td>
</tr>
<tr>
<td><em>Rye grass</em></td>
<td><em>CCR</em> k/o</td>
</tr>
<tr>
<td><em>A. thaliana</em></td>
<td><em>EARLI1</em> k/o</td>
</tr>
<tr>
<td><em>Medicago sativa</em></td>
<td><em>HCT</em> (k/o)</td>
</tr>
<tr>
<td><em>A. thaliana</em></td>
<td><em>KNAT7</em> k/o</td>
</tr>
<tr>
<td><em>A. thaliana</em></td>
<td><em>MYB75</em> k/o</td>
</tr>
</tbody>
</table>

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$_2$O emissions from soil during their life cycle, 2) to explain how plant residue chemistry affects its mineralization, contributing to CO$_2$ and N$_2$O emissions from soil, and 3) to show how modification of plant lignin biosynthesis could influence CO$_2$ and N$_2$O 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$_2$O emissions from soil during the plant life cycle and through mineralization of plant residues.

II. PLANT LIFE HISTORY INFLUENCES CO$_2$ AND N$_2$O 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$_2$O 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$_2$O emissions from soil through their phenology, morphological traits and plant fertility as outlined in Figure 2 and explained in the following sections.

![Hypothetical model illustrating the role of morphological and phenological traits of A. thaliana cell wall mutants upon CO$_2$ and N$_2$O emission from soil.](image-url)
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\textsubscript{2} and N\textsubscript{2}O 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 Whipp 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\textsuperscript{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 madriensis and B. erectus respectively, the annual net assimilated 14\textsuperscript{C} in roots was 37% and 49%, of which 34% and 31% respired by roots and soil 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 Knift 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\textsuperscript{C} tracers, Warembourg et al. (2003) found that rhizosphere respiration was significantly lower in non-legume forbs (42% of total 14\textsuperscript{C} assimilated) than grasses (46%) and legumes (51%). Rhizosphere respiration was positively correlated with the concentration of root N and 14\textsuperscript{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\textsubscript{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; Wittmayer and Merbach, 2005; Yao et al., 2012). For example in Lolium multiflorum, N fertilization (180 µmoles N d\textsuperscript{-1} in a microcosm) 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\textsubscript{2} and N\textsubscript{2}O 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\textsubscript{2} emission from soil in perspective of plant phenology. The CO\textsubscript{2} production from the rhizosphere comes from root respiration, mineralization of root exudates (Billes and Bottnner, 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 Estelrich 2001; Hutsh 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 Estelrich 2001; Hutsh 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 (Hutsh 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 CO₂ 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 ~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 N₂O emission

Phenology should also influence N₂O 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 N₂O emission from soil. The shift in the chemical composition
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$_2$O emission from soil by promoting bacterial growth. However this phenomenon merits future research.

Water content of soil influences rhizodeposition and N$_2$O 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$_2$O from anaerobic denitrification is expected to be higher under such conditions. However, the amount of N$_2$O 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$_2$O 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$_2$O is expected to be higher at the vegetative than reproductive growth stage. This is because 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$_2$O ($\mu$g N$_2$O-N pot$^{-1}$ h$^{-1}$) was 98% and 78% at vegetative growth stage of the total N$_2$O 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$_2$O 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; Matsuami; 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
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\textsubscript{2} emission from soil. In a study with Lolium perenne in controlled environmental conditions, Shahzad et al. (2012) found that clipping reduced above ground biomass by \sim 40\% and soil respiration by \sim 66\% after 30 days of clipping.

4. Influence of plant morphology on N\textsubscript{2}O 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\textsubscript{2}O. In a study with Arabidopsis thaliana mutant lines Gul et al. (2012) found that the A. thaliana line, down-regulated for CCR1 gene had \sim 28\% reduced above ground biomass and \sim 25\% lower crown cover of rosette leaves as compared to its wild ecotype. The mineral N of soil planted with CCR1 line was \sim 50\% \sim 25\% higher at flowering and fruit developing stages respectively. The N\textsubscript{2}O 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\textsubscript{2}O 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\textsubscript{2}O 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\textsubscript{2} and N\textsubscript{2}O 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\textsubscript{2}O emission when soils are anaerobic (section I. and section II. A. 5). The effects of transpiration and N uptake on CO\textsubscript{2} and N\textsubscript{2}O 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 Lovett-Doust, 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$_2$O 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$_2$O production).

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 Lovett-Doust, 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$_2$O.

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$_2$O from microbial activities from the rhizosphere of plants with lower fertility.

5. Influence of plant fertility on N$_2$O emission

Plants with higher fertility in terms of fruit load are expected to have lower N$_2$O emission from rhizosphere than crops with

<table>
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<th>TABLE 3</th>
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<tr>
<td>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</td>
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<table>
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<tr>
<th>Root size</th>
<th>Fruit developing stage</th>
<th>Preharvest stage</th>
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<tr>
<td>Large</td>
<td>Medium</td>
<td>Fine</td>
</tr>
<tr>
<td>Heavy fruit load</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>No fruit load</td>
<td>1.2</td>
<td>4</td>
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<tr>
<td>Heavy fruit load</td>
<td>2.5</td>
<td>11</td>
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<tr>
<td>No fruit load</td>
<td>2.5</td>
<td>6</td>
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(Morinaga et al., 2003)

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.
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$_2$O 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-hydroxylase (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 (Cgl) 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 Cgl 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$_2$O 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$_2$O 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 pheynolics, 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 CO₂ and N₂O 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.

* CO₂ emission from soil is the function of root and microbial respiration, which can be influenced by plant biomass, fertility, and rhizodeposition.

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 CO₂ 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 N₂O from soil (Millar and Baggs, 2004).

The influence of plant residue chemistry on emissions of CO₂ (aerobic conditions) and N₂O (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 CO₂-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 cinamyl) 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
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 aryl-aryl linkages and therefore lignin molecule with more G units are condensed and difficult to biodegradation whereas, lignin with high S units have more β-O-4 linkages (Figure 8; Talbot et al., 2012). Moreover, it is observed that aryl-aryl linkages persist longer than other linkages in soil.
concentration as the wild types. The mutant residues had lower lignin:N ratio, which to some extent 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 (Saggur 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$_2$O 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$_2$O 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
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 14C 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 CO2 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 CO2 in aerobic conditions and N2O 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; Chivengue 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 CO2 and N2O 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 CO2 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 CO2 in aerobic
and N2O 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 CO2 production in clay loam soil in response to its degradation while in sandy loam soil, CO2 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 CO2 production as compared to wild type.

G. Biomass Partitioning

Root to shoot ratio for biomass of plants may play significant role in influencing CO2 and N2O (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 CO2 an N2O 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.

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 CO2-C, N2O-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 CO2-C, N2O-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).

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Mutated gene</th>
<th>C:N ratio</th>
<th>AUF or lignin (mg g$^{-1}$ plant material or in ppm in NMR spectroscopy)</th>
<th>CO$_2$-C production</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. thaliana</td>
<td>Wild type</td>
<td>52.5</td>
<td>104</td>
<td>High</td>
<td>Gul (2012a)</td>
</tr>
<tr>
<td></td>
<td>CCR1</td>
<td>37.3</td>
<td>121</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KNAT7</td>
<td>58.2</td>
<td>65.4</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Wild type</td>
<td>46.9</td>
<td>95.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>MYB75</td>
<td>81.4</td>
<td>99.0</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>Nicotiana tabacum</td>
<td>Wild type</td>
<td>106</td>
<td></td>
<td>High</td>
<td>Hopkins et al. (2001)</td>
</tr>
<tr>
<td></td>
<td>CAD</td>
<td>113</td>
<td>nd$^1$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>COMT</td>
<td>73.3</td>
<td>Nd</td>
<td>High</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CCR</td>
<td>61.1</td>
<td></td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>Nicotiana tabacum</td>
<td>Wild type</td>
<td>57</td>
<td>192</td>
<td></td>
<td>Webster et al. (2005)</td>
</tr>
<tr>
<td></td>
<td>CAD</td>
<td>74</td>
<td>194</td>
<td>High</td>
<td></td>
</tr>
<tr>
<td></td>
<td>COMT</td>
<td>61</td>
<td>197</td>
<td>High</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CCR</td>
<td>53</td>
<td>175</td>
<td>High</td>
<td></td>
</tr>
<tr>
<td>Nicotiana tabacum</td>
<td>Wild type</td>
<td>–$^2$</td>
<td></td>
<td></td>
<td>Henault et al. (2006)</td>
</tr>
<tr>
<td></td>
<td>CAD</td>
<td>–</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>COMT</td>
<td>–</td>
<td></td>
<td>High</td>
<td></td>
</tr>
<tr>
<td>Popular</td>
<td>Wild type</td>
<td>465</td>
<td></td>
<td></td>
<td>Tilston et al. (2004)</td>
</tr>
<tr>
<td></td>
<td>CAD</td>
<td>352</td>
<td></td>
<td>nd</td>
<td></td>
</tr>
<tr>
<td></td>
<td>COMT</td>
<td>472</td>
<td></td>
<td>nd</td>
<td></td>
</tr>
</tbody>
</table>

$^1$1 represents not different than wild type.

$^2$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 conditions. 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 tabacum 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 CO2 and N2O 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 CO2 and N2O 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 CO2 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 N2O emission from soil.

In contrast, GM plant residues with higher lignin and C:N ratio may cause reduced CO2 emission from their biodegradation and lower N2O 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 CO2 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 CO2 and N2O 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 CO2 and N2O 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 CO2 and N2O 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 CO2 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 microsites around plant that has reduced fertility. These environmental conditions can result in more N2O 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 CO2 and N2O 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 CO2 in aerobic and N2O 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 CO2 and N2O 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 CO2 and N2O 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 CO2 and N2O 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
plants (e.g., knockout of KNA7 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 CO2 and N2O from soil. Furthermore, the influence of such mutations on phenological 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 an important role in overall contribution of plant in influencing emission of CO2 and N2O from soil. The plants with higher root:shoot ratio may contribute greater part in reduction of their biodegradation and in return emission of CO2 and N2O (when environmental conditions met for N2O 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 CO2 and N2O emissions in response to their biodegradation when they die.

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