Can cell wall network explain crop residue decomposition and soil organic matter dynamic? A new insight into residue quality

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Abstract
This study aimed at determining the chemical characteristics of roots that regulate their C mineralization on the long term in soil. The chemical composition of maize roots from sixteen genotypes was characterized in details before soil decomposition. Roots were also incubated in soil for 796 days under laboratory conditions (15°C, -80 kPa). The chemical quality of maize roots differed markedly between genotypes notably in term of cell wall polysaccharides contents and quality, lignins contents and quality and esterified phenolic acids contents. Statistical relationships were established between the fate of C from roots and their initial chemical characteristics. The role of the intimate associations between the lignin fraction and cell wall polysaccharides in a cohesive network, and the role of esterified PCA as one of the main interconnecting agents between polymers in graminaceous cell walls, are of primary importance and could improve the prediction of residue decomposition in soils.

Key Words
Roots, decomposition, chemical quality, cell wall

Introduction
The intrinsic biochemical properties of crop residue, more commonly termed litter quality; strongly influence their decomposition in soil and the associated C and N fluxes (Swift \textit{et al.} 1979). Quality of crop residue has long been approached through their initial C-to-N ratio which is now considered as a general index of quality mainly related to soil N dynamic (Vanlauwe \textit{et al.} 1996; Heal \textit{et al.} 1997). However, this ratio does not account for the availability of C and N, which is often essential to describe the decomposition kinetics (Recous \textit{et al.} 1995). Crop residues have a complex composition with a soluble fraction and an insoluble fraction corresponding essentially to the cell walls. The cell wall composition and the quality of their constitutive polymers have a great effect on their decomposition in soil and on the associated C and N fluxes (Bertrand \textit{et al.} 2006; 2009). The principal cell wall polymers are polysaccharides (such as cellulose and hemicelluloses) and lignin. In Gramineae, arabinoxylans represent the main type of hemicelluloses mainly substituted by arabinose and hydroxycinnamic acids, namely ferulic acid (FA) and p-coumaric acid (PCA), are the principal interconnecting agents between polymers (Kato and Nevis 1985). The chemical composition of cell wall polymers, as well as their interactions, influences the accessibility of these components to decomposers (Chesson 1988). Roots are one of the major sources of C contributing to soil organic matter build-up (Rasse \textit{et al.} 2005), and the understanding of their kinetics of decomposition in soil needs to be improved. Indeed, few results were published concerning the effect of chemical quality on root decomposition in soil (Herman \textit{et al.} 1977). Roots are particularly rich in cell walls and are more lignified than aerial plant parts (Machinet \textit{et al.} 2009). Therefore the nature and the structure of these cell walls could significantly influence the kinetics of C mineralization in the medium and long terms. The aims of this work were (i) to better understand the role of cell wall chemical characteristics on root decomposition in soils and (ii) to improve the designing of parameters that could be used to describe residue quality in C models.

Methods
\textit{Soil and maize roots}
Two sets of maize (\textit{Zea mays} L.) brown-midrib isogenic lines, within the genetic background of inbreds F2 (F2, F2bm1, F2bm2, F2bm3 and F2bm4) and F292 (F292, F292bm1, F292bm2, F292bm3 and F292bm4), and a set of six maize hybrids (F7026bm3*F2bm3, Mexxal, Anjou 285, Anjou 258, Colombus and Manfusa) were cultivated in 2005 in experimental fields at the INRA Lusignan experimental station (49°26′N, 0°07′E, France) and were harvested at physiological maturity. Only the roots were kept for experiments and were cut to a diameter of 2 to 3 mm before incubation in an agricultural loamy soil.
Soil laboratory incubation

Soil samples and maize roots were mixed at a rate equivalent to 2 g C/kg dry soil and incubated for 796 days at 15°C. Inorganic N was added to the soil as KNO₃ to avoid N limitation during the decomposition process. Soil moisture was kept at a potential of -80 kPa throughout the incubation period by weighing at weekly intervals and readjusting with deionised water when necessary. A control incubation experiment was performed in the same way but without the addition of residues. Carbon mineralization was measured in the presence of a CO₂ trap (10 ml 1 M NaOH) at regular intervals up to day 796 after the beginning of incubation.

Chemical characteristics

Maize root residues before decomposition in soil were analysed for total C and N, soluble, neutral detergent fiber (NDF), acid detergent fiber (ADF) and acid detergent lignin (ADL) according to Goering and Van Soest (1970). Cell walls were extracted from maize roots by neutral detergent fiber (NDF) to remove cytoplasmic components (proteins, wax, pigments, tannin, etc...). Polysaccharides were analyzed according to Blakeney et al. (1983) on roots after NDF extraction (cell walls). The released monosaccharides were separated and quantified by high performance anion-exchange chromatography (HPAEC). Klason lignin was determined as the insoluble residue remaining after a two step sulphuric acid hydrolysis of the cell wall polysaccharides (Monties 1984). Lignin monomer composition was determined by thioacidolysis. This reaction enables the specific disruption of labile-ether inter-monomer linkages, which represent the non-condensed lignin fraction (Lapierre et al. 1986). Monomer products were analyzed as trimethylsilyl derivatives of guaiacyl (G) and syringyl (S) by capillary column gas chromatography. Ester-linked hydroxycinnamic acids (ferulic acid (FA) and p-coumaric acid (PCA)) were released by alkaline extraction and detected using a Waters photodiode array UV detector.

Results

The mineralization of maize roots varied markedly amongst genotypes and, as expected, was higher than that of control soil (Figure 1). At the end of the incubation (796 days), the total amounts of mineralized C were significantly smaller in F2bm1 (41.6 ± 2.2% of added C) than in Manfusa (70.1 ± 1.9% of added C) (P≤0.05). The observed differences in cumulative mineralized C over the entire incubation period resulted mainly from differences in the rates of C mineralization during the first 40 days. Total N contents of roots varied from 0.5 to 1.3% of dry matter. These contents lead to C to N ratio from 37 (F2bm1) to 97 (Manfusa). The NDS soluble fraction accounted for < 22% of dry matter; therefore cell wall contents were high. Glucose content of roots ranged from 30.7% to 41.1% while the arabinose to xylose ratio slightly varied between genotypes, indicating a similar level of xylan substitution by arabinose. The amount of Klason lignin (KL) varied from 15.2% to 19.4% DM and the S unit ranged from 25.1 to 90.5 µmol/g of cell wall, while the amounts of G unit varied from 21.2 to 54.2 µmol/g of cell wall (Table 1). Furthermore, the relative proportion of S unit was smaller than that of G unit in all bm3 mutants, leading to S to G ratios <1 which were only found in these genotypes. Ester-linked PCA were more abundant than ester-linked FA and ranged from 1.6% to 3.6% of cell wall (data not shown).

Simple correlation was performed to further establish the relationships between the cumulative amounts of mineralized C at different steps of decomposition and the initial chemical characteristics of maize roots. On the short term, the amounts of C-CO₂ were positively correlated with the soluble fraction over the first 10 days, and particularly highly correlated with the soluble C at day 3 (P≤0.001). Thus, the amounts of C-CO₂ were slightly but significantly negatively correlated with arabinose between days 3 and 7, the A/X ratio between days 7 and 14 and the KL/Soluble ratio between days 3 and 14 (P≤0.05). They were also negatively correlated with galactose during the whole incubation period. On the medium to long term, there was a negative relationship between the C mineralized and the Van Soest lignin/Soluble ratio from day 10 until day 796, and as expected the effect of lignin fractions on C mineralized became important. The amounts of mineralized C were strongly negatively correlated with the lignin fraction.

A multiple-regression analysis was attempted to explain more comprehensively the variations of the C mineralization kinetics observed among the 16 genotypes of maize roots. When using all chemical characteristics as explanatory variables, the best-fitting regression equation included the Van Soest lignin (LVS)/ Van Soest Cellulose (CVS) ratio, ester PCA and Van Soest Hemicellulose (HVS) according to the following equation (p<0.001, residual standard error RSE = 52.4, Figure 2). This three-variates-based equation accounted for 93% of the observed cumulative amounts of C-CO₂ (Figure 2).
Figure 1. Cumulative amounts of carbon mineralized in control soil (without maize roots, dotted lines) and after addition of maize root (full lines). Data are means of 4 incubation replicates.

Figure 2. Relationships between the cumulative amounts of C mineralized after 796 days and equations of the multiple-regression model. Genotypes were identified by numbers 1 to 16.

Conclusion
The 16 maize root genotypes used presented significant variations in terms of chemical characteristics that translated into large differences in kinetics and cumulative C mineralization during their decomposition. This material was therefore very suitable for investigating relationships between quality and decomposition. The detailed analysis of chemical composition, by different methods evidenced the role of soluble C on the short term, lignin fraction of the longer term, but also the importance of the intimate associations between the lignin fraction and cell wall polysaccharides in a cohesive network. The role of esterified PCA as one of the main interconnecting agents between polymers in graminaceous cell walls was shown by regression analysis, allowing to improve systematically the prediction of residue decomposition in soils despite its negligible quantitative importance in root tissues.

References


