UGent/INRA – Molter Final report

1.	Introdu	iction	.2
2.	Method	lology	.2
3.	Results	& discussion	.3
3	8.1. Soil	l fractions	.3
	3.1.1.	Dry weight and organic matter properties	.3
	3.1.2.	¹³ C tracer	.3
3	3.2. Spe	ecific compounds analysis	.4
	3.2.1.	Performance of analyses of amino-sugars from density separates	.4
	3.2.2.	Quantification of total amino-sugars	.5
	3.2.3.	¹³ C tracer within specific compounds	.8
4.	Conclus	sions	.9
5.	Future	collaboration with host institution & valorisation1	0
6.	Referen	nces1	0

1. Introduction

Since one century, forest ecosystems have been submitted to a global warming of 0.7°C, partly imputable to human activities (Courtillot et al., 2007). Climate modeling predicts that this global warming will still increase during the forthcoming decades (IPCC, 2007), what may strongly impact biological activity in soil and biogeochemical cycling of carbon (C) and nutrients. Thus, large amount of soil organic carbon is expected to be mineralized, raising atmospheric concentration in CO₂, and enhancing global warming and ocean acidification (Orr et al., 2005). However, this mechanism still remains difficult to assess due to the limited knowledge of parameters controlling soil organic matter (SOM) mineralization or sequestration in soil.

The crucial role of mineral-organic associations (MOAs) in C sequestration has been evidenced by numerous studies (von Lützow *et al.*, 2007). Aggregates at the microscopic scale, or organic compounds sorbed on mineral particles at the nanometric scale are thus physically protected from decomposer activities for duration expanding from several years to centuries (Chenu & Plante, 2006; Kleber *et al.*, 2007). Little is still known about how SOM is associated to mineral particles. It has been recently suggested that the microbial processing of organic C derived from the litter input would be mandatory to initiate the incorporation of fresh material into MOAs (Hatton *et al., submitted*).

Amino-sugars (AS) are considered as molecular markers for the presence of microbiallyprocessed OM because they are predominantly synthesized by micro-organisms and fated to their cell walls. They represent up to 10% of total N and 1 to 5% of the total carbon (Amelung et al., 2006). In spite of such a little contribution to C and N stocks, AS are suspected to be remarkably resistant to degradation. Indeed, the amount of soil AS exceeds the amount of AS present in soil microorganisms, which suggest that these compounds remain unalterated after cell death. Micro-organisms differ in their composition in AS and present specific cell walls characteristics; Galactosamine (GalN) and Muramic acid (MurA) being indicative of Bacteria and Glucosamine (GluN) of Fungi (Amelung *et al.*, 2001; Glaser, 2005). Zhang *et al.* (1996) used these cell walls specificities to assess the relative contribution of bacterial and fungal compounds.

The scientific aim of this project and of the long-term exchange scientific visit was to trace the incorporation of ¹³C tracer derived from labelled glycine (Gly) and beech leaf litter (LL) in AS entrapped into aggregates or coating mineral particles isolated by density fractionation by the use of Liquid Chromatography coupled to Isotope Ratio Mass Spectrometer (LC-IRMS). By following the incorporation of substrate-derived C in biomarkers specific of the micro-organisms isolated from different types of MOAs, we intended to investigate whether the microbial processing of plant residues is a crucial stage prior to association with minerals and quantifying the rate of this mechanism in different compartments of soil.

2. Methodology

To explore the dynamics of litter residues and the role of microbial transformation in their association with mineral particles, we took advantage of ¹³C-glycine (98% ¹³C excess) and ¹³C-beech litter (3.1% ¹³C excess) incubations conducted at 20°C in the laboratory over 12 weeks on an acidic forest soil, what is equivalent to ca. 1.5 years *in situ*. Both substrates were applied in equal amount of N than the natural annual input,

i.e. 0.015 mgN.g_{soil}⁻¹. This gives 0.026 mgC.g g_{soil}⁻¹ for glycine substrate (Gly) and 1.066 mgC. g_{soil}⁻¹ for leaf litter substrate (LL).

Prior the visit control soils, soils incubated with labelled LL for 12 weeks and soils incubated with labeled Gly for 7 days and 12 weeks were sequentially density isolated according to Sollins *et al.* (2006). This method isolates MOAs of distinct physico-chemical properties and with contrasted ability to incorporate litter-derived components (Hatton *et al., submitted*). Five density fractions containing plant debris (<1.65 g.cm⁻³), plant aggregates (1.65-1.85 g.cm⁻³), mineral aggregates (1.85-2.4 g.cm⁻³), Quartz and Feldspar (2.4-2.65 g.cm⁻³) and Quartz and Oxides (>2.65 g.cm⁻³) were isolated.

Soil AS were extracted at Ghent based on the procedure described by Bodé et al. (2009). The four weeks spent in the host laboratory were devoted to sample preparation and analysis:

Weeks # 1, 2 and 3	Sample preparation for AS isolation and purification from bulk sample. Density fractions and bulk soils were extracted as duplicates for AS according to Bodé et al. (2009).
Week # 4	Extracts were analyzed for GluN, GalN and MurA by LC-IRMS according to Bodé et al. (2009).

3. Results & discussion

3.1. Soil fractions

3.1.1. Dry weight and organic matter properties

Mass recoveries were almost total. Dry weight strongly peaked in Quartz and Feldspar fractions, with 81.6% of the total soil mass. Mineral aggregates represented 10.2% of dry weight, while other fractions all ranged from 1.7 to 3.9%. Recovery rates for total C and N exceeded 77%, which is consistent with previous results from the same soil (Hatton *et al., submitted*). Plant debris and aggregates concentrated most of C and N (>83%), while Quartz and Feldspar fractions never exceed 16% and Quartz and Oxides fractions 0.7%. Good agreements found in soil mass, total C and N in between labelled and control treatments did not reveal bias of treatments and procedure of physical fractionation.

C/N ratios decreased with increasing fraction density concomitantly to the increase in natural abundances ¹⁵N and ¹³C values - measured in control treatment. Altogether, these indicators of decomposition indicate that, the proportion of microbially-transformed OM increases. Our results are consistent with what have been observed before (Golchin *et al.*, 1994a; Golchin *et al.*, 1994b; Hatton *et al.*, *submitted*; Kramer *et al.*, 2009; Sollins *et al.*, 2006).

3.1.2. ¹³C tracer

3.1.2.1. Bulk soil

Soils incubated with LL for 12 weeks contained 112% of the tracer initially applied, which reveal an incomplete mixing of the labelled substrate with the soil. Only 24% and 18% were found in soils incubated with glycine for 7 days and 12 weeks, respectively.

3.1.2.2. Compartments of soil

3.1.2.2.1. Glycine experiment

71% of the tracer found in the bulk soil was recovered after density fractionation. The tracer distribution though the sequence of density fractions did not vary after 7 days and 12 weeks of incubation (Figure 1). They both contain 17-18% of the tracer in plant debris, 20-21% in plant aggregates, 46-48% in mineral aggregates, 14-15% in Quartz and Feldspar and 0.2-0.3% in Quartz and Oxides fractions.

3.1.2.2.2. Leaf litter experiment

More than 92% of the litter-derived tracer was recovered after density fractionation. The distribution of the tracer is different when the tracer has been applied as LL -plant debris contain 56% of the ¹³C tracer, plant aggregates 22%, mineral aggregates 16%, low reactivity minerals 6% and high reactivity minerals 0.3% (Figure 1). The distribution of the litter-derived tracer is similar to what has been observed *in situ* 3 years after ¹⁵N-labelled litter deposition (Hatton *et al., submitted*), suggesting that litter-derived C and N follow the same pathways though soil MOAs. This is in accordance with previous study that tracked the bomb-¹⁴C signal (Prior *et al.,* 2007; Sollins *et al.,* 2009; Sollins *et al.,* 2006; Swanston *et al.,* 2004; Torn *et al.,* 2009).



¹³C tracer within soil compartments

Figure 1: Distribution of the ¹³C tracer through soil compartments isolated by sequential density fractionation (n=3). The tracer was applied as labelled glycine or leaf litter and sampled after 7 days (Gly-7days) and 12 weeks (Gly-12weeks) when incubated with glycine and after 12 weeks with leaf litter (LL-12weeks).

Overall, these findings highlight two contrasted patterns of C association within soil MOAs depending on the substrate chemistry.

3.2. Specific compounds analysis

3.2.1. Performance of analyses of amino-sugars from density separates

Amino-sugar were successfully extracted and analysed for all the studied soil fractions, except for the densest fractions. This confirms the do-ability of the AS extraction and the LC-IRMS analyses onto density-separated soils. The densest fractions, however, never provided exploitable results. We suspect oxides found in these fractions to infer on the efficiency of the AS extraction and to cause the clogging of the LC-IRMS column. Further adjustments are needed to remove oxides from the extract (Methanol).

3.2.2. Quantification of total amino-sugars

3.2.2.1. Bulk soils

Glucosamine, GalN and MurA concentrations remained constant within treatments at 1.30 mg.g_{soil}⁻¹ ± 0.27, varying from 1.2 to 1.5 mg.g_{soil}⁻¹ (table 1). Altogether, they represent 1.90 to 2.25% of the total soil C, which is in line with what have been published before (Amelung *et al.*, 2001; Glaser, 2005).

Glucosamine is the most abundant AS with 50-52% of the total AS content, followed by GalN and MurA with 24-26% and 23-24%, respectively (table 1). This is in accordance with previous results from Decock *et al.* (2009). Muramic acid content was higher after 7 days of glycine decay than after 12 weeks. Both concentrations are much higher than those reported by Zhang and Amelung (1996).

In soils incubated with Gly, C/N ratios declined from 17.4 to 15.6 after 7 days and 12 weeks of incubation. This change in C/N ratios was also observed by Liang et al. (2007) during the first weeks after leaf amendment.

3.2.2.2. Compartments of soil

3.2.2.2.1. Glycine experiment

Plant debris, plant aggregates and mineral aggregates recovered 51% and 57% of the total AS content measured in the bulk soil. These three lightest fractions accounted for 53% and 60% of total GluN, 54% and 58% of total GalN and 42% and 48% of total MurA 7 days and 12 weeks after glycine application, respectively (table 1; figure 2).

After 7 days, GluN and GalN were equally distributed through these three lightest fractions. Muramic acid concentrations remained stable in between plant debris and plant aggregates and significantly increased in mineral aggregates that concentrated 35% of total MurA.

After 12 weeks, GluN, GalN and MurA concentrations remained equally distributed in plant debris and aggregates. Glucosamine and GalN concentrations significantly increased in mineral aggregates to account for 32% of both total GluN and GalN. Muramic acid was also concentrated in mineral aggregates, but only represent 26% of total MurA instead of 35% after 7 days.

The GluN to MurA ratios decreased from plant debris to mineral aggregates fractions at 7 days, while the ratios did not much vary at 12 weeks (table 1). This suggests that Fungi tended to be more represented than Bacteria in plant debris and plant aggregates in the early stage of the incubation, a tendency that disappeared with time.

3.2.2.2.2. Leaf experiment

Plant debris, plant aggregates and mineral aggregates recovered 43% of the total AS found in the bulk soil. They accounted for 54% of total GluN, 44% of total GalN and 31% of total MurA 12 weeks after leaf litter application (table 1; figure 2).

Glucosamine, GalN and MurA were equally distributed in plant debris, plant aggregates and mineral aggregates fractions. The concentration in GluN did not significantly vary much in between plant debris and plant aggregates fractions, but tended to decrease in mineral aggregates. This is traduced by a clear decrease of both GluN to GalN and Glu to MurA ratios in those fractions, which could indicate a tendency for bacterial enrichment over fungal OM with increasing fraction density or a tendency for fungal enrichment over bacterial OM with decreasing density.



Figure 2: Distribution and recovery after fractionation of glucosamine, galactosamine and muramic acid (n=2) through different compartments of soils isolated by density (Hatton *et al., submitted*). Labelled glycine and leaf litter were incubated with soils, sampled after 7 days (Gly-7days) and 12 weeks (Gly-12weeks) when incubated with glycine and after 12 weeks with leaf litter (LL-12weeks), and sequentially density fractionated (Sollins *et al.*, 2006). Missing bars indicate missing values.

Tableau 1: Carbon, nitrogen, amino-sugars contents and ratios of bulk and density fractionated soil fractions incubated with labeled glycine (Gly), leaf litter (LL) or no
substrate (control) (n≥2). Soils incubated with labeled glycine were sampled after 7 days and 12 weeks. Soils incubated with LL were incubated for 12 weeks. <i>n.a.</i> stands
for not available.

Treatments	Soil fractions	Carbon		Nitrogen		Glucomamine (GluN)								Galactosamine	GalN)								Muramic acid (Mur)									GluN/GalN	GluN/Mur
		mg.gsoil-1	%	mg.gsoil-1	1 %	ug.gsoil-1	SÉ %	% %SE	% of the total AS	%SE	ug.gC-1	SE	ug.gN-1	SE	ug.gsoil-1	SE	% %S	E % of the tota	al AS %SE	ug.gC-	1 SE	ug.gN-	1 SE	ug.gsoil-1	ŚE	% %	SE % of the	total AS %	SE ug	.gC-1 S	E ug.	.gN-1	SE		
-																																			-
Gly-7days	Bulk soil	23.68	100	1.36	100	605	196 10	00 32	55	10	26	8	446	144	315	106	100 33	28	5	13	4	233	78	160	136	100 8	85 1	,	15	7 4	6 1	118	101	1.9	3.8
	Plant debris Plant aggregates Mineral aggregates Quartz & Feldspath Quartz & Oxides Recovery	7.45 5.00 8.91 2.41 0.05 23.82	31 21 37 10 n.a. 101	0.29 0.26 0.71 0.20 0.00 1.47	20 18 48 14 0.33 109	115 93 116 n.a. 53	26 19 17 19 41 19 n.a. n. n.a. n.	9 4 5 3 9 7 a. n.a. a. n.a.	61 55 46 n.a. n.a.	2 1 n.a. n.a.	15 18 13 n.a. n.a.	4 3 5 n.a. n.a.	398 353 163 n.a. n.a.	91 63 58 n.a. n.a.	50 47 74 n.a. 170	10 7 23 n.a. i n.a. i	16 3 15 2 23 7 n.a. n.a 54	26 28 30 a. n.a. a. n.a.	0 0 n.a. n.a.	7 9 8 n.a. n.a.	1 3 n.a. n.a.	171 178 103 n.a. n.a.	34 26 33 n.a. n.a.	22 26 55 n.a. n.a. 103	1 4 10 n.a. n.a.	14 16 35 n.a. n n.a. n 65	1 1: 2 1: 7 2: .a. n. .a. n.	3 5 1 a. r. a. r.	2 0 3 1.a. 1 1.a. 1	3 (5 1 6 - n.a. n. n.a. n	0 7 1 9 1 7 1.a. n 1.a. r	77 97 77 n.a. n.a.	4 14 15 n.a. n.a.	2.3 2.0 1.6 n.a. n.a.	5.2 3.6 2.1 n.a. n.a.
Gly-12weeks	Bulk soil	28.22	100.00	1.81	100	673	10	00	50	n.a.	24	n.a.	372	n.a.	341	n.a.	100 <i>п.</i> ғ	. 25	n.a.	12	n.a.	188	n.a.	302	n.a.	100 <i>n</i>	.a. 24	4 n	1.a.	11 n).a. 1	167	n.a.	2.0	n.a.
	Plant debris Plant aggregates Mineral aggregates Quartz & Feldspath Quartz & Oxides Recovery	7.77 4.72 8.20 2.72 0.05 23.48	27.54 16.73 29.06 9.65 0.19 77	0.29 0.24 0.63 0.23 0.00 1.39	21 17 45 16 0.24 77	109 81 216 n.a. <i>n.a.</i> 60	36 10 20 11 16 31 n.a. n. n.a. n.	6 5 2 3 2 2 a. n.a. <i>a. n.a</i> .	55 54 53 n.a. n.a.	4 0 1 n.a. n.a.	14 17 26 n.a. <i>n.a</i> .	5 4 2 n.a. <i>n.a</i> .	378 334 343 n.a. <i>n.a.</i>	126 83 25 n.a. <i>n.a.</i>	49 41 108 46 <i>n.a.</i> 245	23 10 13 n.a. <i>n.a.</i>	14 7 12 3 32 4 14 n.a 72	24 27 26 	5 1 1 <i>n.a.</i>	6 9 13 n.a. <i>n.a</i> .	3 2 n.a. <i>n.a</i> .	170 168 172 n.a. <i>n.a.</i>	80 40 21 n.a. <i>n.a.</i>	37 27 80 27 n.a. 171	7 8 7 n.a. <i>n.a</i> .	12 9 26 9 n n.a. n 57	2 2 3 1! 2 2 .a. n. .a. n.	 a. n a. n	9 1 0 1.a.	5 1 6 2 10 121 n n.a. n	1 1: 2 1 1 1 a	129 112 126 10 n.a.	23 34 11 n.a. n.a.	2.2 2.0 2.0 n.a. n.a.	2.9 3.0 2.7 n.a. n.a.
LL-12weeks	Bulk soil	27.17	100.00	1.66	100	797	137 10	00 17	52	1	29	5	481	82	369	60	100 16	24	0	14	2	223	36	330	25	100	8 2	3	2	12	1 1	199	15	2.2	2.4
	Plant debris Plant aggregates Mineral aggregates Quartz & Feldspath Quartz & Oxides Recovery	11.19 5.32 7.33 2.58 0.13 26.55	41.19 19.59 26.98 9.49 0.47 93	0.44 0.30 0.61 0.19 0.01 1.54	28 20 39 12 0.63 93	137 126 85 90 <i>n.a.</i> 55	44 11 13 10 31 1 11 1 n.a. n.	7 6 6 2 1 4 1 1 <i>a. n.a.</i>	56 56 45 50 n.a.	3 1 1 n.a.	12 24 12 35 n.a.	4 2 4 4 n.a.	313 417 140 482 n.a.	101 43 51 57 n.a.	68 64 67 46 n.a. 245	22 5 20 4 n.a. 1	18 6 17 1 18 5 12 1 1.a. n.a 66	27 29 36 25 n. n.a.	2 1 2 1 <i>n.a.</i>	6 12 9 18 <i>n.a.</i>	2 1 3 2 n.a.	155 213 110 246 <i>n.a.</i>	51 17 33 22 n.a.	37 32 34 42 n.a. 146	0 8 14 8 n.a.	11 10 10 13 n.a. n 44	0 11 2 11 4 11 3 21 .a. n.	7 5 9 5 a. r	4 2 1 2 1.a.	3 (6 1 5 1 16 1 n.a. n	D 8 1 1 2 5 3 2 1.a. 7	85 106 57 226 7.a.	1 26 23 45 n.a.	2.0 2.0 1.3 2.0 <i>n.a.</i>	3.7 4.0 2.5 2.1 <i>n.a.</i>
Control	Bulk soil	26.60	100.00	1.60	100	680	167 10	0 25	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	338	47	107 15	in.a.	n.a.	n.a.	n.a.	n.a.	n.a.	240	n.a.	100 <i>n</i>	.a. n.	a. n	1.8.	n.a. n	ı.a. r	n.a.	n.a.	n.a.	n.a.
	Plant debris Plant aggregates Mineral aggregates Quartz & Feldspath Quartz & Oxides <i>Recovery</i>	7.24 3.40 11.81 2.42 0.04 24.90	27.21 12.78 44.39 9.09 0.15 98	0.30 0.18 0.89 0.18 0.00 1.56	19 12 57 12 0.23 98	154 64 207 98 n.a. 77	20 23 15 9 20 30 3 14 n.a. n.	3 3 9 2 0 3 4 0 a. n.a.	62 57 61 46 n.a.	0 1 0 n.a.	21 19 18 40 n.a.	3 4 2 1 <i>n.a.</i>	509 352 232 534 n.a.	68 80 23 17 n.a.	63 31 131 48 <i>n.a.</i> 272	7 6 11 2 n.a. 1	19 2 9 2 39 3 14 1 <i>n.a. n.a</i> 81	25 27 39 22 a. n.a.	0 0 1 n.a.	9 9 11 20 <i>n.a.</i>	1 2 1 1.a.	209 170 146 261 <i>n.a.</i>	24 35 12 13 n.a.	30 17 n.a. 63 n.a. 110	4 3 n.a. 0 n.a.	13 7 n.a. n 26 n.a. n 46	2 1: 1 11 .a. n. 0 3: .a. n.	3 3 a. r. 2 a. r.	0 0 1.a. 7 1.a. 1	4 1 5 1 1.a. n. 26 (n.a. n	1 1 1 9 1 <i>a. n</i> 0 3 1 <i>a. r</i>	100 91 n.a. 346 n.a.	15 19 <i>n.a.</i> 2 <i>n.a.</i>	2.4 2.1 1.6 2.0 <i>n.a.</i>	5.1 3.9 n.a. 1.5 n.a.

3.2.3. ¹³C tracer within specific compounds

At the present stage, two fractions can be readily compared through the different treatments, namely plant debris and plant aggregates fractions.

3.2.3.1. Glycine experiment

In the two lightest fractions, 0.04% and 0.05% of the tracer initially applied as labelled glycine was found in GluN, GalN and MurA, after 7 days and 12 weeks, respectively. This indicates no effect of the duration of the incubation in soils incubated with glycine.

The tracer found in AS were unequally distributed. After 7 days of glycine decay, 88% were found in GluN, 5% in GalN and 7% in MurA (Figure 3). Twelve weeks after glycine application 85% of the tracer found in GluN, 6% in GalN and 9% in MurA. The patterns of tracer incorporation within AS suggest that the uptake of glycine is mainly governed by Fungi.

3.2.3.2. Leaf litter experiment

After 12 weeks, 0.10% and 0.05% of the tracer initially applied as labelled LL were recovered in plant debris and plant aggregates. Glucosamine contained 50% and 45%, GalN 13% and 8%, and MurA 37% and 47% of the total AS tracer in plant debris and plant aggregates fractions (Figure 3). The fact that MurA is more efficient than GalN in incorporating the tracer could be explained by its faster turnover (Liang *et al.*, 2007; Zhang & Amelung, 1996). Overall, these results suggest that Bacteria and Fungi are both involved in the incorporation of litter-derived C.





Figure 3: Distribution of a ¹³C tracer among glucosamine (GluN), Galactosamine (Gal) and Muramic acid (MurA) in plant debris and aggregates fractions as isolated by density (Hatton *et al., submitted*).

4. Conclusions

The visit was a great opportunity to exchange technical expertises between the applicant's institution (INRA Nancy, France) and the host's institution (Laboratory of Applied Physical Chemistry, Ghent University, Belgium), which have developed complementary skills. The host laboratory has, indeed, developed extensive experience on quantification of C isotope in AS (Bodé *et al.*, 2009; Decock *et al.*, 2009), whereas the applicant's institute has just acquired a new LC-IRMS system, allowing these analyses. The collaboration offered a great opportunity to the French laboratory to get a LC-IRMS technology transfer from Belgium and would permit to compare and inter-calibrate two different LC-IRMS systems.

Our investigations showed that the tracing of compound-specific ¹³C-analysis is doable onto density-separated soil fractions. We distinguished two reasons that can explain missing data: a) analytical problems that can be overtaken by repeating the measure and

b) technical limitations associated to the presence of pedogenic oxides, which require some technical adjustments.

The quantification of the ¹³C tracer in density separates revealed two contrasted patterns of C association within soil MOAs depending on the substrate chemistry.

The quantification of total soil AS evidenced that the different compartment of soil investigated do not have the same composition in AS, a composition that varies as a function of the type of AS, the time of decay and the substrate quality. A full determination of the AS contents within all density separates is necessary to decipher whether the rest of the AS is in denser fractions or in the soluble fraction.

The quantification of ¹³C tracer in AS provided information on the extent to which the microbial processing of organic C derived from the labelled LL or Gly is mandatory to initiate the incorporation of fresh material into plant debris and plant aggregates. Our results suggest that the activity of the decomposers is governed by the chemistry of the substrate. Glycine would be rapidly decomposed by microorganisms, mainly Fungi, and incorporated into soil AS (\leq 7 days), while would take longer for LL residues to get decomposed by both Bacteria and Fungi.

Additional data and technical adjustments are needed to get the full picture of AS composition and isotopic enrichment though the full sequence of soil compartment.

5. Future collaboration with host institution & valorisation

These preliminary results are very promising. Work is still in progress to overcome the technical limitations associated to the presence of pedogenic oxides. Thus, we are confident getting soon all the values we need to answer our scientific question, which would allow us to write a scientific paper.

The collaboration is going to generate data on AS dynamics that will complete the Ghent datasets to parameterize the a biogeochemical model for individual organic molecule dynamics (Derrien & Amelung, 2010).. By combining both expertises, we expect to make progresses on the dynamics of specific molecular biomarkers in soils.

6. References

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