Plant and Soil (2005) 273: 307–326
DOI 10.1007/s11104-004-8128-y

Influence of biochemical quality on C and N mineralisation from a broad variety of plant materials in soil

Lars S. Jensen[1,7], Tapio Salo[2], Fridrik Palmason[3], Tor Arvid Breland[4], Trond M. Henriksen[5], Bo Stenberg[6], Anders Pedersen[1], Christina Lundström[6] & Martti Esala[2]

[1]*Department of Agricultural Sciences, Royal Veterinary & Agricultural University, Thorvaldsensvej 40, DK-1871 Frederiksberg C, Denmark.* [2]*MTT, Agrifood Research Finland, Environmental Research, FIN-31600 Jokioinen, Finland.* [3]*Agricultural Research Institute Keldnaholt, IS-112 Reykjavik, Iceland.* [4]*Department of Plant and Environmental Sciences, Norwegian University of Life Sciences, P.O. Box 5003, N-1432 Ås, Norway.* [5] *The Norwegian Crop Research Institute, Apelsvoll Research Centre, N-2849 Kapp, Norway.* [6]*Department of Soil Science, Swedish University of Agricultural Sciences, Division of Precision Agriculture, P.O. Box 234, SE-532 23 Skara, Sweden.* [7]*Corresponding author**

Received 22 August 2004. Accepted in revised form 23 December 2004

Key words: decomposition, nitrogen mineralisation, plant residue quality, van Soest analysis

Abstract

We studied C and N mineralisation patterns from a large number of plant materials (76 samples, covering 37 species and several plant parts), and quantified how these patterns related to biological origin and selected indicators of chemical composition. We determined C and N contents of whole plant material, in water soluble material and in fractions (neutral detergent soluble material, cellulose, hemicellulose and lignin) obtained by stepwise chemical digestion (modified van Soest method). Plant materials were incubated in a sandy soil under standardised conditions (15 °C, optimal water content, no N limitation) for 217 days, and CO_2 evolution and soil mineral N contents were monitored regularly. The chemical composition of the plant materials was very diverse, as indicated by total N ranging from 2 to 59 mg N g^{-1}, (i.e. C/N-ratios between 7 and 227). Few materials were lignified (median lignin = 4% of total C). A large proportion of plant N was found in the neutral detergent soluble (NDS) fraction (average 84%) but less of the plant C (average 46%). Over the entire incubation period, holocellulose C content was the single factor that best explained the variability of C mineralisation ($r = -0.73$ to -0.82). Overall, lignin C explained only a small proportion of the variability in C mineralisation ($r = -0.44$ to -0.51), but the higher the lignin content, the narrower the range of cumulative C mineralisation. Initial net N mineralisation rate was most closely correlated ($r = 0.76$) to water soluble N content of the plant materials, but from Day 22, net N mineralisation was most closely correlated to total plant N and NDS-N contents (r varied between 0.90 and 0.94). The NDS-N content could thus be used to roughly categorise the net N mineralisation patterns into (i) sustained net N immobilisation for several months; (ii) initial net N immobilisation, followed by some re-mineralisation; and (iii) initially rapid and substantial net N mineralisation. Contrary to other studies, we did not find plant residue C/N or lignin/N-ratio to be closely correlated to decomposition and N mineralisation.

* FAX No: +45-35283468. E-mail: lsj@kul.dk

Introduction

Return of organic materials such as crop residues, catch crops and green manures has a decisive influence on carbon (C) and nitrogen (N) turnover in agricultural soils. The synchronisation of N supply with plant demand is important for both environmental and agronomic reasons. This applies particularly to cropping systems where mineral fertilisers are completely excluded, i.e. organic farming (Pang and Letey, 2000), or of limited availability, as in the developing countries (Palm et al., 2001b). Consequently, good knowledge of factors affecting decomposition dynamics and the resulting plant-available N in agricultural systems is required.

Over the past decade this issue has attracted much attention (Cadisch and Giller, 1997), and a range of studies have been published on the major factors influencing plant litter decomposition in both natural (e.g., Aerts, 1997; Cornelissen and Thompson, 1997) and agricultural ecosystems (e.g., Palm et al., 2001a). Initial litter quality, in particular the biochemical composition (soluble materials, hemicellulose, cellulose and lignin) as determined by stepwise chemical digestion of plant materials, has been shown to have a major bearing on decomposition and N release patterns and hence may constitute an adequate basis for calibration and initialisation of dynamic models of soil C and N turnover (Henriksen and Breland, 1999a; Thuriès et al., 2002; Trinsoutrot et al., 2000). However, simpler indices of degradability, such as the total N concentration or the C/N-ratio, are commonly found to correlate with mineralised C and N at some stage of decomposition (e.g. Nicolardot et al., 2001). These simple indices are often misinterpreted as causal factors, whilst the gross biochemical composition and the spatial arrangement of constituents in the plant tissue are more likely to be the determining factors (Magid et al., 2004).

The stepwise chemical digestion (SCD) method; (Goering and van Soest, 1970) commonly used for proximate analysis of biochemical composition of organic materials is quite laborious, however. Near-infrared reflectance (NIR) spectroscopy has been proposed as an alternative, indirect method, which is quick and cost-effective and has been successfully used for various quality characterisations, including plant litter composition and decomposability (Foley et al., 1998; Gillon and David, 2001; Shepherd et al., 2003).

Most decomposition studies in agricultural ecosystems have been restricted to a limited number of plant materials or other organic residues. In some studies based on larger sample sets, the decomposition data included have been obtained under highly variable experimental conditions, e.g. the large amounts of data gathered in the "Organic Resource Database" (Palm et al., 2001a). In order to obtain a very broad dataset on quality, decomposition and N release of a range of plant materials from agricultural crops measured under standardised conditions, a joint Nordic project was initiated with the objective of developing NIR calibrations as a cost-effective and reliable tool for characterising degradability of crop residues in a dynamic model of C and N turnover in soil (Jensen et al., 2004; Stenberg et al., 2004). The major objectives of the present work were to investigate the C and N mineralisation patterns when plant materials from this broad quality range were incubated in soil under standardised conditions, and to study how these patterns related to biological origin and selected indices of chemical composition, including distribution of C and N among fractions obtained by SCD. We placed the emphasis on simple, static relationships, whereas subsequent work (Bruun et al., 2005; Jensen et al., 2004) has been focused on empirical and mechanistic modelling approaches, respectively.

Materials and methods

Plant materials

A total of 249 crop plant materials were collected in the Nordic countries during the growing season of 2000 (Stenberg et al., 2004). The materials were selected to encompass as wide a quality range as possible with respect to C/N-ratio and distribution of C and N in biochemical fractions. More than 50 temperate crop species within several crop types (e.g. cereals, pasture grasses, legumes, vegetables, fibre and energy crops and catch crops) and six plant fractions (green leaves, stems, mature straw, pods and spikes, and whole

Table 1. Plant Species and plant parts included in the study, number of materials for each species and plant part, and numbers (in brackets) of materials selected for the incubation study

			Plant parts						
Class	English name	*Latin name*	Whole plant	Green leaves	Stem	Mature straw	Pods & spikes	Other	Total
Cereals	Oats	*Avena sativa*	1(1)	2		1			4(1)
	Spring barley	*Hordeum vulgare distichon*	1	7(1)	6(1)	1(1)	6(1)		21(4)
	Winter barley	*Hordeum vulgare distichon*		1		1(1)			2(1)
	Winter rye	*Secale cereale*		1(1)		1			2(1)
	Winter triticale	*Secale cer.x Triticum aest.*				1			1
	Winter wheat	*Triticum aestivum*	2	8(2)	8(5)	7	6(2)		31(9)
	Subtotal								61(16)
Ley and pasture grasses	Smooth meadowgrass	*Poa pratensis*	3	2	1	1(1)			7(1)
	Cock's-foot	*Dactylis glomerata*	2(1)	2	2(1)				6(2)
	Perennial ryegrass	*Lolium perenne*	3	1	1				5
	Hungarian brome	*Bromus inermis*		1	1				2
	Italian ryegrass	*Lolium multiflorum*	1	1					2
	Westerwolds ryegrass	*Lolium multiflorum*	3(2)						3(2)
	Meadow fescue	*Festuca pratensis*	4	1	1				6
	Meadow foxtail	*Alopecurus pratensis*	1			1(1)			2(1)
	Red fescue	*Festuca rubra*	1			1(1)			2(1)
	Ryefescue	*Festuca prat.* × Lolium multifl.	1	1	1				3
	Tall fescue	*Agrostis capillaris*	1			1			2
	Timothy	*Phleum pratense*	5			1			6
	Tufted hair-grass	*Deschampsia caespitosa*		1		1		1	2
	Subtotal								48(7)
Legumes	Alfalfa	*Medicago sativa*	1	1(1)	1				3(1)
	Black medic	*Medicago lupulina*	1						1
	Broad bean	*Vicia faba*	1(1)						1(1)
	Common birds-foot-trefoil	*Lotus corniculatus*	4						4
	Common vetch	*Vicia sativa*	1						1
	Crimson clover	*Trifolim incarnatum*	3	1(1)	1			1(1)	6(2)
	Egyptian clover	*Trifolium alexandrinum*	1(1)						1(1)
	Nootka lupin	*Lupinus nootkatensis*	2(1)						2(1)
	Pea	*Pisum sativum*	2			4(2)			6(2)
	Persian clover	*Trifolium resupinatum*	2		1(1)				3(1)
	Red clover	*Trifolium pratense*	4(1)	1(1)	1(1)				6(3)
	Ribbed melilot	*Melilotus officinalis*	2(1)						2(1)
	White clover	*Trifolium repens*	7(2)						7(2)

Table 1. Continued.

Class	English name	*Latin name*	Plant parts						
			Whole plant	Green leaves	Stem	Mature straw	Pods & spikes	Other	Total
	Winter vetch	*Vicia villosa*	6						6
	Yellow lupin	*Lupinus luteus*	1	1(1)	1(1)				3(2)
	Subtotal								52(17)
Other arable crops	Maize	*Zea mays*	6(2)	6(1)	6(3)		6(1)		24(7)
	Oilseed rape	*Brassica napus oleifera*	2(1)	1(1)	3(2)	1	3	3(1)	13(5)
	Sugarbeet	*Beta vulgaris*		5(2)					5(2)
	Sunflower	*Helianthus annuus*				1(1)			1(1)
	Swede	*Brassica napus L. napifera Metzg.*	1(1)						1(1)
	Turnip rape	*Brassica rapa oleifera*		1(1)	1	2(1)			4(2)
	Subtotal								48(18)
Fibre and energy crops	Elephant grass	*Miscanthus gigantus*		3	3(1)				6(1)
	Flax (fibre/oil)	*Linum usitatissimum*	5(3)	1(1)	4(3)				10(7)
	Hemp	*Cannabis sativa*		1(1)	1(1)	1(1)			3(3)
	Subtotal								19(11)
Vegetable crops	Cabbage	*Brassica oleraceae*		5(1)					5(1)
	Carrot	*Daucus carota*		2(1)					2(1)
	Leek	*Allium porri*			2			2(1)	4(1)
	Onion	*Allium cepa*		1(1)					1(1)
	Potato	*Solanum tuberosum*	2						2
	Subtotal								14(4)
Catch crops	Chicory	*Cichorium intybus*	1	2					3
	Oil radish	*Raphanus sativus*	1	1(1)					2(1)
	Phacelia	*Phacelia tenacetifolia*		1(1)					1(1)
	Yellow mustard	*Sinapis alba*				1(1)			1(1)
	Subtotal								7(3)
Total			85(18)	63(20)	46(20)	28(11)	21(4)	6(3)	249(76)

above-ground plants) were represented (see Table 1 for details). The materials were dried at 40 °C for 48 h immediately after sampling and stored. The bulk sample of plant material (500–1000 g DM) was not cut or ground more than necessary at this stage, but a representative sub-sample (100 g DM) was kept separate and prior to further NIR or chemical analyses gathered in one laboratory for milling of all samples to a particle size less than 1 mm, but not completely powdered (Palm and Rowland, 1997).

In order to achieve a manageable number of samples for use in the incubation studies reported here, a representative sub-set was selected from the 249 sample archive, based on information in NIR spectra of the materials (Stenberg et al., 2004). Briefly, NIR spectra were measured on all 249 samples with a NIRSystem 6500 (Foss Tecator) scanning monochromator. Each spectrum constituted of every second nanometre wavelength between 1100 and 2500 nm. In order to achieve the most representative sub-set possible based on the entire information in the NIR-spectra, standardised Mahalanobis distances between samples (Shenk and Westerhaus, 1991) were used to select 76 samples for the incubation study. SCD was also carried out for this sub-set according to Goering and van Soest (1970). In addition, hot water soluble material was determined according to TAPPI (1978), producing a water non-soluble fibre fraction. All extractions were carried out using a digestion apparatus (ANKOM Technology, NY, USA) and the extraction procedure was adopted from Henriksen and Breland (1999a) to allow determination of element contents in each of the remaining fibrous fractions. Contents of C and N were measured in each of the fibrous fractions and in whole plant material by an elemental analyser and mass-spectrometer (ANCA-SL & 20–20, PDZ Europa, UK). Carbon and nitrogen in water soluble material (WS), neutral detergent soluble material (NDS), hemicellulose, cellulose and lignin were then derived by subtraction. The WS fraction was then subtracted from the NDS fraction to give neutral detergent but not water soluble (NDNWS) material. Hemicellulose and cellulose were added together to constitute the holocellulose fraction. All values were calculated as mg C or N g^{-1} plant dry matter. For four samples WS was not analysed and NDNWS could therefore not be calculated, hence only NDS values are given.

Sampling and preparation of incubation soil

A 350 kg portion of a sandy soil was collected in June, 2000, from a field (recent cropping history of the field included oats, grass-clover and barley; the latter being the last crop) at Häme experimental station (61° 20′ N, 24°13′ E, 103 m a.s.l) in southern Finland. Briefly, the top layer (0–7 cm) of the soil was sampled and gently sieved through 4 mm mesh on the same day. The soil contained 4.7% clay, 7.3% silt, 88.0% sand, 1.8% organic C and 0.14% total N. In order to boost a rich and potent decomposer community and thus alleviate possible limitations due to poor colonisation of fibrous material (Henriksen and Breland, 1999a, 2002), the sampled soil was pre-incubated at 15 °C with easily degradable plant material consisting of red clover (3.5% N) and timothy (2.2% N). Both materials were added at a rate of 5 g dry matter kg^{-1} dry soil, and soil moisture was adjusted to a gravimetric water content of 16% (equivalent to 40% of water holding capacity) which was monitored every week and replenished if necessary. After 53 days of pre-incubation, when the plant material-derived CO_2 evolution had levelled off, soil was portioned into 18 kg plastic bags and frozen at −18 °C. In November 2000, the frozen soil was distributed as frozen cargo among the participating groups, and kept at −18 °C until the start of the incubations. Before starting each incubation, the soil was thawed at room temperature for 24 h, and was further pre-incubated for 14–16 days at 15 °C in order to diminish the effect of freeze-thaw on C and N turnover. The soil was then gently mixed in the laboratory and if necessary moistened to slightly less than field capacity (−10 kPa).

Incubation experiments

The 76 plant materials in the sample sub-set described above were distributed among the Nordic countries, where two incubation experiments were conducted in each of the five different laboratories. Each incubation experiment consisted of 7–8 unique plant materials, one reference material common to all incubations (whole plant timothy: *Phleum pratense* L.) and the soil without added plant material as a control.

For each replicate, 1.00 g plant material (DM) was mixed as homogeneously as possible with 50.0 g DM of the sandy soil in a small plastic beaker, and the soil was compacted to approximately 1.1 g cm^{-3}. In some cases (coarse plant materials like straw) soil could only be compacted to a slightly lower density. All plant materials were cut by hand into pieces less than 1 cm in length just prior to mixing with the soil; careful sampling of all particle sizes was made to ensure a representative sub-sample.

Altogether 30 beakers were set up for each plant material, in order to provide sufficient samples for three replicates in all subsequent CO_2-C and soil mineral N measurements.

Water content was adjusted in all beakers to field capacity (−10 kPa corresponding to 48% of water holding capacity and a gravimetric water content of 18.8%) at the start of the incubations. The moisture was checked weekly by weighing and water added if necessary. Beakers were kept covered with polyethylene in boxes.

Our objective was to investigate decomposition and N release pattern as affected solely by the inherent quality attributes of the plant residues and not by external conditions, e.g. availability of soil mineral N. Decomposition of some of the high C/N-ratio materials would be limited by a sub-optimal N availability (Henriksen and Breland, 1999b; Recous et al., 1995). The amount of available N needed (in plant material and soil) for unlimited decomposition was estimated to be 33.5 mg N g^{-1} plant material C added (Henriksen and Breland, 1999b; Recous et al., 1995). The mineral N contents of all soil samples after pre-incubation, but prior to set-up of the experiment, was approximately 100 mg N kg^{-1}. Taking this external soil mineral N and the plant-internal N into account, we therefore added mineral N to reach a minimum value of 33.5 mg N g^{-1} plant C. This implied that mineral N was added to the soil as KNO_3 solution during the initial adjustment of the water content to plant materials containing less than 8.5 mg N g^{-1} (C/N-ratios > 47).

Incubations were carried out either in small growth chambers (Termaks 6000 or similar) or in constant temperature rooms, all capable of maintaining a temperature of 15 ± 1°C. Temperature was recorded using data-loggers during the incubations.

For measurement of CO_2 evolution during intervals of increasing length, three randomly chosen replicate beakers from each treatment were enclosed in individual incubation jars (2 or 3 L) with alkali traps (5–10 mL of 3–3.5 *M* NaOH). Three empty incubation jars were included to serve as blanks for CO_2 determination. Soil beakers and alkali traps were exchanged on approximately Days 2, 4, 7, 10, 15, 22, 31, 42, 58, 79, 105, 133, 168 and 217.

NaOH was titrated with 0.1–1 *M* HCl either by manual titration after addition of excess $BaCl_2$ to precipitate carbonate and with phenolphthalein as an indicator (Anderson, 1982) or by automatic double infliction-point titration (pH 8.3 to pH 3.7).

For measurement of soil mineral-N content on Day 0 and then approximately on Days 4, 10, 22, 42, 79 133 and 217 of the experiment, three replicate beakers from each treatment were sampled destructively and soil mineral N was extracted with 1 *M* KCl (20 g soil DW to 100 ml extractant). Ammonium-N and nitrate-N were determined in the extracts by standard colorimetric methods using standard autoanalyser or flow-injection analysis (Keeney and Nelson, 1982).

Calculations and statistics

Carbon mineralisation from each of the plant materials was calculated by subtraction of CO_2 evolution measured for the control soil. Net N mineralisation in each of the treatments (plant materials and unamended control) was calculated by subtracting the soil mineral N content of the treatment at Day 0 from mineral N at all subsequent measurements. Net N mineralisation from the plant materials was then calculated by subtracting the net N mineralisation of the control soil.

We used correlations analyses (PROC CORR of the SAS® software, Littell et al., 1996) for estimating Pearson correlation coefficients between initial plant material properties (C and N in total plant material and in SCD fractions) and C and N mineralisation.

Results

Plant residue quality

The 76 samples selected for the incubation study represented 37 of the 52 species collected initially.

They represented the sampled crop classes and plant parts reasonably well (Table 1). One quarter of the materials incubated was whole-plant material, mainly from younger plants, while the other three quarters were plant fractions (green leaves, stem, mature straw, pods and spikes).

The gross biochemical composition of the materials was very diverse, as reflected by the contents of C and N in the whole-plant material and in the fractions obtained by SCD of the incubated plant materials (Table 2). Total plant C ranged only from 378 to 544 mg C g^{-1} (mainly due to differences in ash content), while total plant N ranged from 2 to 59 mg N g^{-1}. Consequently, total C/N ranged from 7 to 227, with a somewhat right-skewed distribution. The total soluble fraction (WS + NDNWS = NDS, Table 2) was highly variable, ranging from 43 to 396 mg C g^{-1} and between 1 and 53 mg N g^{-1}. Overall, only a few of the materials were lignified. The median lignin proportion was 4% of total C, the 90% fractile 14% of total C and the maximum lignin 23% of total C (Figure 1). Compared with the C distribution, much more of the total N was in the soluble fractions, on average 40 and 44% of total N in the WS and NDNWS fractions, respectively, compared to

Table 2. Selected descriptive statistics for the content of C and N in the whole plant materials and in the fractions obtained by SCD

Parameter	Min	Max	Median	Mean	Std.dev.	Skewness	Kurtosis
Whole plant (mg C g^{-1}, mg N g^{-1} or ratio)							
Total C	378.1	543.8	449.4	449.1	28.0	0.42	2.31
Total N	2.18	59.12	13.35	17.14	13.94	1.26	0.81
Total C/N	7	227	32	52	47	1.65	2.48
In plant fractions (mg C g^{-1}, mg N g^{-1} or ratio)							
Water soluble[a] C	11.0	226.5	112.5	112.2	54.9	0.15	−0.86
Water soluble N	0.41	33.92	5.13	7.02	7.28	2.14	4.68
Water solulble C/N	4	255	21	30	34	4.39	25.8
NDNWS[a,b] C	4.0	256.0	79.4	91.7	50.5	0.77	0.43
NDNWS N	0.67	25.22	5.42	7.54	6.65	1.21	0.52
NDNWS C/N	3	63	15	18	11	1.62	4.04
Neutral detergent soluble C	42.6	395.6	187.2	205.8	90.4	0.24	−1.21
Neutral detergent soluble N	1.44	53.45	11.39	14.88	12.83	1.32	1.0
Neutral detergent soluble C/N	5	92	18	22	16	2.31	6.71
Hemicellulose C	9.3	205.0	67.0	79.5	47.0	0.54	−0.71
Hemicellulose N	0.04	7.93	0.86	1.30	1.49	2.31	6.12
Hemicellulose C/N	5	1760	86	234	381	2.64	6.63
Cellulose C	31.4	265.0	140.56	136.4	59.0	0.02	−0.92
Cellulose N	0.07	4.75	0.46	0.62	0.62	4.25	26.52
Cellulose C/N	14	988	294	358	247	0.71	−0.28
Holocellulose[c] C	66.2	366.0	240.1	215.9	87.4	−0.21	−1.22
Holocellulose N	0.30	9.76	1.33	1.93	1.79	2.49	6.88
Holocellulose C/N	9	825	159	207	177	1.33	1.76
Lignin C	0.3	103.8	18.52	27.5	24.1	1.06	0.48
Lignin N	0.01	1.35	0.32	0.40	0.29	0.83	0.48
Lignin C/N	15	294	67	75	53	1.98	5.36
Lignin (DM)-to-N ratio	0.01	72	3.42	8.33	12.0	2.73	9.88

[a] $n = 76$, except for water soluble (WS) and NDWS, where $n = 72$.
[b] NDNWS = Neutral detergent, not water soluble. Derived by difference between NDS and WS.
[c] Holocellulose = hemicellulose + cellulose.

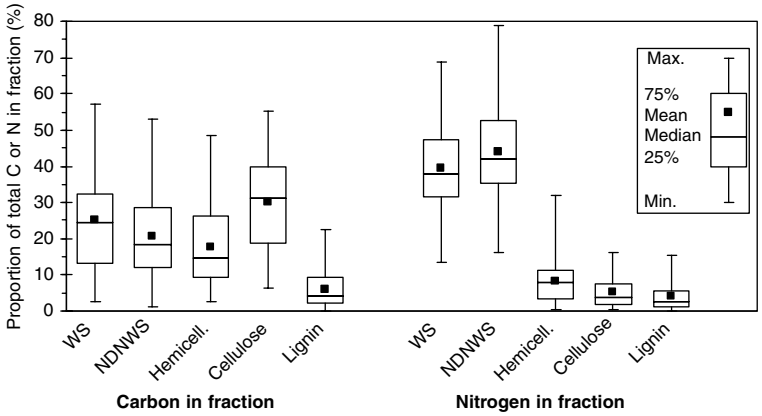

Figure 1. Box and whiskers plot of the relative distribution (max., min., 25% and 75% fractiles, median and mean values) of total C and N between water soluble (WS), neutral detergent but not water soluble (NDNWS), hemicellulose, cellulose and lignin fractions ($n = 76$, except for WS and NDNWS where $n = 72$).

25 and 21% of total C, respectively (Figure 1). The small quantity of N remaining was mainly found in the hemicellulose fraction. Because of the high proportion of total plant N in the soluble fraction, the NDS C/N-ratios were much lower than total C/N and ranged from 5 to 92 vs. 7 to 227, respectively (median 18 vs. 32, Table 2). Correspondingly, the C/N-ratios of the structural holocellulose (hemicellulose + cellulose) fractions were much higher (median 159) than total C/N (median 32).

The soluble and holocellulose (hemicellulose + cellulose) C fractions represented most of the total C; hence highly significant, negative correlations existed between these (Figure 2a and Table 3). A similarly strong correlation was not found between soluble C and total plant N, but more than half of the variability in soluble C could be described by the log-transformed N content (Figure 2b). Owing to the high proportion of the total N in the soluble fractions, there was a very high correlation between total N and either of the soluble N fractions (Figure 2d), with an almost absolute linear relationship between NDS-N and total N (average slope 0.91). Although a much smaller proportion of C than of N was soluble, NDS-C and NDS-N were highly correlated ($r = 0.74$, Table 3).

Plant residue C mineralisation

Initial C mineralisation rate was highly correlated to the contents of water soluble C, total plant N and NDS-N ($r = 0.79$, 0.73 and 0.75, respectively at Day 4, Table 4). The importance of these parameters in describing C mineralisation decreased later in the incubation period, whereas NDS-C and holocellulose C became increasingly important (Figure 3). Overall, lignin C explained only a small proportion of the variability in C mineralisation ($r = -0.44$ to -0.51). However, the higher the lignin content, the narrower the range of C mineralisation at both Day 42 and Day 217 (Figure 3, bottom row of plots).

Over the entire incubation period, the holocellulose C content was the single factor that best explained the variability in C mineralisation at all sampling days in the incubation ($r = -0.73$ to -0.82, Table 4 and Figure 3), explaining more than half the variability ($r^2 > 0.5$) at all sampling days during the incubation. Consequently, the C mineralisation patterns of the sample population were best categorised by the content of holocellulose C (Figure 4). Almost all materials with less than 150 mg holocellulose C g^{-1} (mostly green, fresh materials) showed relatively rapid initial C mineralisation, most of them releasing more than 50% of added C as CO_2 within less than 2 months, and between 50 and 80% by 217 days. Materials with 150–250 mg holocellulose C g^{-1} showed similarly rapid initial C mineralisation, but less than 60% of added C was mineralised within the incubation period. Materials with more than 250 mg holocellulose C g^{-1} generally had much lower initial minerali-

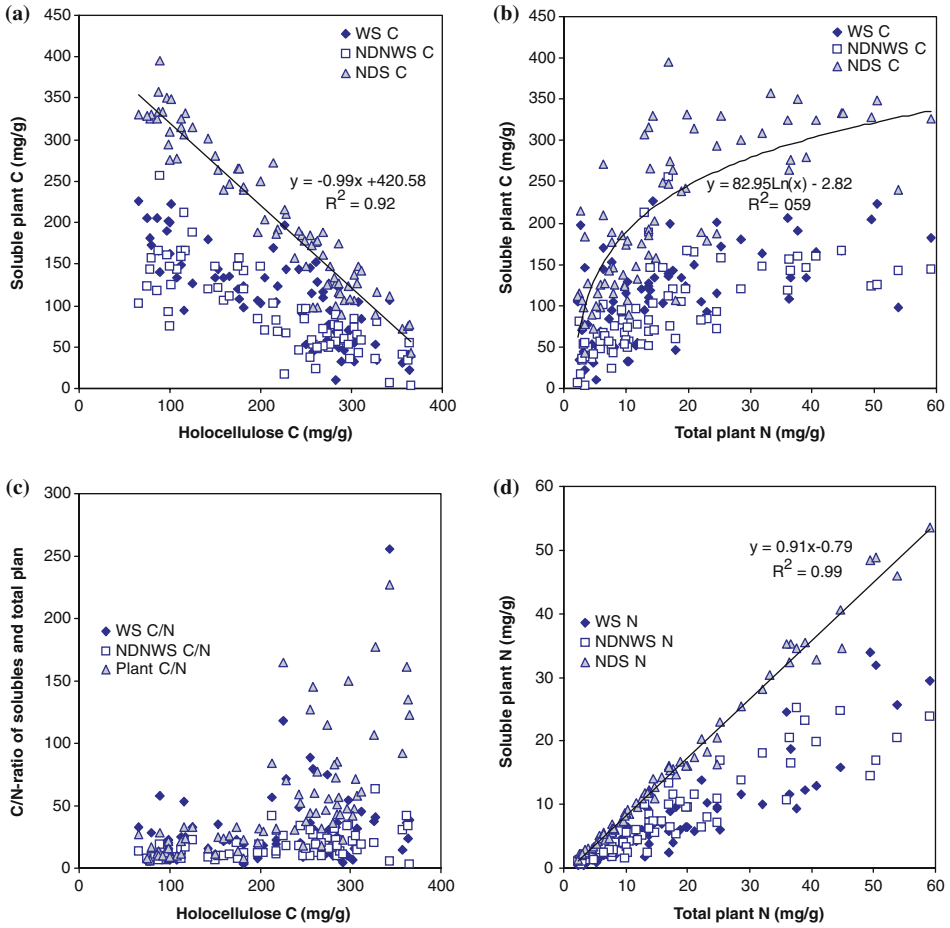

Figure 2. Relationships between soluble plant C [in water (WS), neutral detergent but not water (NDNWS), and neutral detergent (NDS)] vs. (a) holocellulose or (b) total plant N, (c) C/N-ratio of soluble materials and total plant vs. holocellulose C and (d) soluble plant N (WS, NDNWS, NDS) vs. total plant N ($n = 76$). Lines in a, b and d indicate regressions for the NDS fractions.

sation rates, although the proportion of added C mineralised after 217 days was in the same range as for the group with intermediate holocellulose content.

Plant residue net N mineralisation

Net N mineralisation was significantly correlated to all the SCD-C fractions. However, the correlation was high only for holocellulose C and NDS-C in the last part of the incubation period ($r = -0.66$ – -0.73, Table 4), and in such a way that less than 150 mg NDS-C g^{-1} was always associated with sustained immobilisation, whereas more NDS-C was associated with anything from sustained N immobilisation to marked net N mineralisation at Day 217 (Figure 5, top row of plots). The initial net N mineralisation rate (Day 4) was closely correlated to total plant N, water soluble N and NDS-N ($r = 0.72$ – 0.76). From Day 22 and throughout the remainder of the 217-day incubation period, net N mineralisation was most closely correlated to total plant N and NDS-N (r ranged from 0.90 to 0.94, Table 4). The net N mineralisation patterns of the sample population therefore proved to be best categorised by the content of NDS-N (Figure 6). Materials with less than 10 mg NDS-N g^{-1} all showed relatively rapid initial immobilisation within the first 22 days, and most of them showed only slow re-mineralisation thereafter, hardly reaching above initial N content within the 217-days. This was due to a dominance of high C/N-ratio samples (average C/N = 88) in

Table 3. Pearson correlation coefficients (r) between residue quality parameters (C and N in SCD fractions, mg g^{-1})

		Carbon (mg C g^{-1} DM)								Nitrogen (mg N g^{-1} DM)							
		Total	WS	NDNWS	NDS	Hemi	Cell	Holo	Lign	Total	WS	NDNWS	NDS	Hemi	Cell	Holo	Lign
C	Water soluble (WS)	-0.22^{NS}	1														
	NDNWS[a]	-0.11^{NS}	0.43^{*}	1													
	ND[b] soluble (NDS)	-0.18^{NS}	**0.86***	**0.83***	1												
	Hemicellulose (Hemi)	0.08^{NS}	-0.56^{*}	-0.58^{*}	-0.68^{*}	1											
	Cellulose (Cell)	0.45^{*}	**−0.77***	**−0.71***	**−0.88***	0.35	1										
	Holocellulose[c] (Holo)	0.35	**−0.82***	**−0.80***	**−0.96***	**0.77***	**0.86***	1									
	Lignin (Lign)	0.54^{*}	-0.47^{*}	−0.31	-0.47^{*}	-0.17^{NS}	0.70^{*}	0.38	1								
N	Plant total N	−0.32	0.58^{*}	0.63^{*}	**0.73***	-0.55^{*}	-0.67^{*}	-0.75^{*}	−0.38	1							
	Water soluble (WS)	−0.36	0.54^{*}	0.40	0.56^{*}	-0.46^{*}	-0.52^{*}	-0.60^{*}	−0.33	**0.91***	1						
	NDNWS	−0.27	0.56^{*}	**0.77***	**0.78***	-0.57^{*}	**−0.71***	-0.79^{*}	−0.36	**0.92***	0.69^{*}	1					
	ND soluble (NDS)	−0.33	0.60^{*}	0.63^{*}	**0.74***	-0.57^{*}	-0.68^{*}	-0.77^{*}	−0.38	**0.99***	**0.93***	**0.91***	1				
	Hemicellulose (Hemi)	-0.22^{NS}	0.22^{NS}	0.31	0.33	0.00^{NS}	-0.45^{*}	−0.30	-0.41^{*}	0.59^{*}	0.41^{*}	0.50^{*}	0.51^{*}	1			
	Cellulose (Cell)	0.01^{NS}	0.02^{NS}	0.32	0.25	−0.39	-0.11^{NS}	−0.28	0.11^{NS}	0.47^{*}	0.31	0.54^{*}	0.42^{*}	0.34	1		
	Holocellulose (Holo)	-0.18^{NS}	0.21^{NS}	0.36	0.36	-0.13^{NS}	-0.41^{*}	−0.35	−0.30	0.65^{*}	0.46^{*}	0.59^{*}	0.56^{*}	**0.95***	0.63^{*}	1	
	Lignin (Lign)	0.39	-0.21^{NS}	0.06^{NS}	-0.06^{NS}	-0.39^{*}	0.35	0.02^{NS}	0.58^{*}	0.09^{NS}	-0.03^{NS}	0.12^{NS}	0.06^{NS}	-0.06^{NS}	0.44^{*}	0.10^{NS}	1
C/N	Plant total C/N-ratio	0.34	-0.45^{*}	-0.62^{*}	-0.63^{*}	0.50^{*}	0.60^{*}	0.67^{*}	0.32	-0.68^{*}	-0.58^{*}	-0.66^{*}	-0.67^{*}	-0.44^{*}	−0.30	-0.47^{*}	-0.17^{NS}

[a]NDNWS = neutral detergent, not water soluble material. Derived by difference between NDS and WS.
[b]ND = neutral detergent.
[c]Holocellulose = hemicellulose + cellulose. NS = not significant ($P < 0.05$), *=significant at the $P < 0.0001$ level, all other significant at $P = 0.0001$–0.05. Correlations in bold denote $r^2 > 0.5$.

Table 4. Pearson correlation coefficients (r) between residue quality parameters (SCD) and mineralised C or N (mg C or N g^{-1} of added C) at different stages during incubation ($n = 76$)

		Carbon mineralisation							Nitrogen mineralisation						
		Correlation coefficient (r)													
	Day:	4	10	22	42	79	133	217	4	10	22	42	79	133	217
Carbon (mg C g^{-1})	Total plant C	−0.50	−0.52	−0.51	−0.49	−0.48	−0.48	−0.47		−0.30	−0.34	−0.35	−0.37	−0.36	−0.34
	Water soluble	**0.79**	0.78	**0.74**	0.70	0.67	0.66	0.64		0.41	0.49	0.54	0.60	0.56	0.61
	NDNW[a] soluble	0.33	0.43	0.52	0.58	0.60	0.59	0.56	0.32	0.40	0.44	0.49	0.52	0.54	0.57
	ND[b] soluble	0.67	0.73	**0.76**	**0.77**	**0.77**	**0.76**	**0.73**	0.29	0.49	0.56	0.61	0.67	0.66	0.70
	Hemicellulose	−0.54	−0.58	−0.58	−0.56	−0.53	−0.50	−0.47		−0.38	−0.44	−0.51	−0.54	−0.54	−0.55
	Cellulose	−0.65	−0.71	**−0.76**	**−0.78**	**−0.78**	**−0.78**	**−0.76**		−0.47	−0.52	−0.56	−0.62	−0.61	−0.64
	Holocellulose[c]	**−0.73**	**−0.79**	**−0.82**	**−0.82**	**−0.81**	**−0.79**	**−0.76**	−0.30	−0.52	−0.59	−0.65	−0.71	−0.70	**−0.73**
	Lignin	−0.44	−0.46	−0.47	−0.48	−0.50	−0.51	−0.51		−0.32	−0.35	−0.34	−0.36	−0.34	−0.37
Nitrogen(mg N g^{-1})	Total plant N	**0.73**	**0.77**	**0.74**	0.69	0.63	0.58	0.54	**0.72**	**0.86**	**0.90**	**0.94**	**0.94**	**0.94**	**0.92**
	Water soluble	0.70	0.72	0.68	0.61	0.54	0.49	0.44	**0.76**	**0.87**	**0.91**	**0.92**	**0.90**	**0.87**	**0.82**
	NDNW soluble	0.68	0.71	0.69	0.67	0.63	0.59	0.54	0.56	**0.69**	**0.76**	**0.81**	**0.83**	**0.86**	**0.88**
	ND soluble	**0.75**	**0.79**	**0.76**	**0.71**	0.65	0.60	0.56	**0.72**	**0.85**	**0.91**	**0.93**	**0.94**	**0.94**	**0.92**
	Hemicellulose	0.30	0.34	0.31					0.44	0.51	0.49	0.53	0.54	0.54	0.52
	Cellulose									0.38	0.37	0.45	0.44	0.47	0.49
	Holocellulose	0.33	0.38	0.34	0.31				0.47	0.55	0.53	0.59	0.60	0.61	0.60
	Lignin														
C/N-ratio of	Total plant N	−0.53	−0.60	−0.62	−0.62	−0.59	−0.55	−0.52	−0.31	−0.45	−0.50	−0.56	−0.62	−0.61	−0.64
	Water soluble			−0.31							−0.33	−0.37	−0.38	−0.39	−0.39
	NDNW soluble	−0.59	−0.62	−0.60	−0.56	−0.50	−0.45	−0.43		−0.39	−0.44	−0.50	−0.57	−0.56	−0.60
	ND soluble	−0.36	−0.44	−0.46	−0.45	−0.39	−0.33	−0.30	−0.38	−0.43	−0.45	−0.50	−0.55	−0.54	−0.55
	Hemicellulose	−0.38	−0.42	−0.44	−0.43	−0.40	−0.38	−0.38			−0.32	−0.36	−0.43	−0.40	−0.43
	Cellulose	−0.35	−0.42	−0.43	−0.43	−0.40	−0.34	−0.30	−0.37	−0.48	−0.50	−0.55	−0.59	−0.58	−0.60
	Holocellulose	−0.47	−0.55	−0.59	−0.60	−0.57	−0.54	−0.51	−0.35	−0.48	−0.51	−0.56	−0.64	−0.61	−0.64
	Lignin	−0.41	−0.47	−0.48	−0.47	−0.45	−0.43	−0.39	−0.32	−0.42	−0.46	−0.49	−0.53	−0.50	−0.53
Lignin(DM) / total N ratio		−0.48		−0.52	−0.52		−0.51	−0.49			−0.38	−0.40		−0.43	−0.48

[a]NDNW soluble = neutral detergent, not water-soluble material. Derived by difference between NDS and WS.
[b]ND soluble = neutral detergent.
[c]Holocellulose = hemicellulose + cellulose.
Only correlations significant at the $P < 0.01$ level are shown, correlations in bold denote $r^2 > 0.5$.

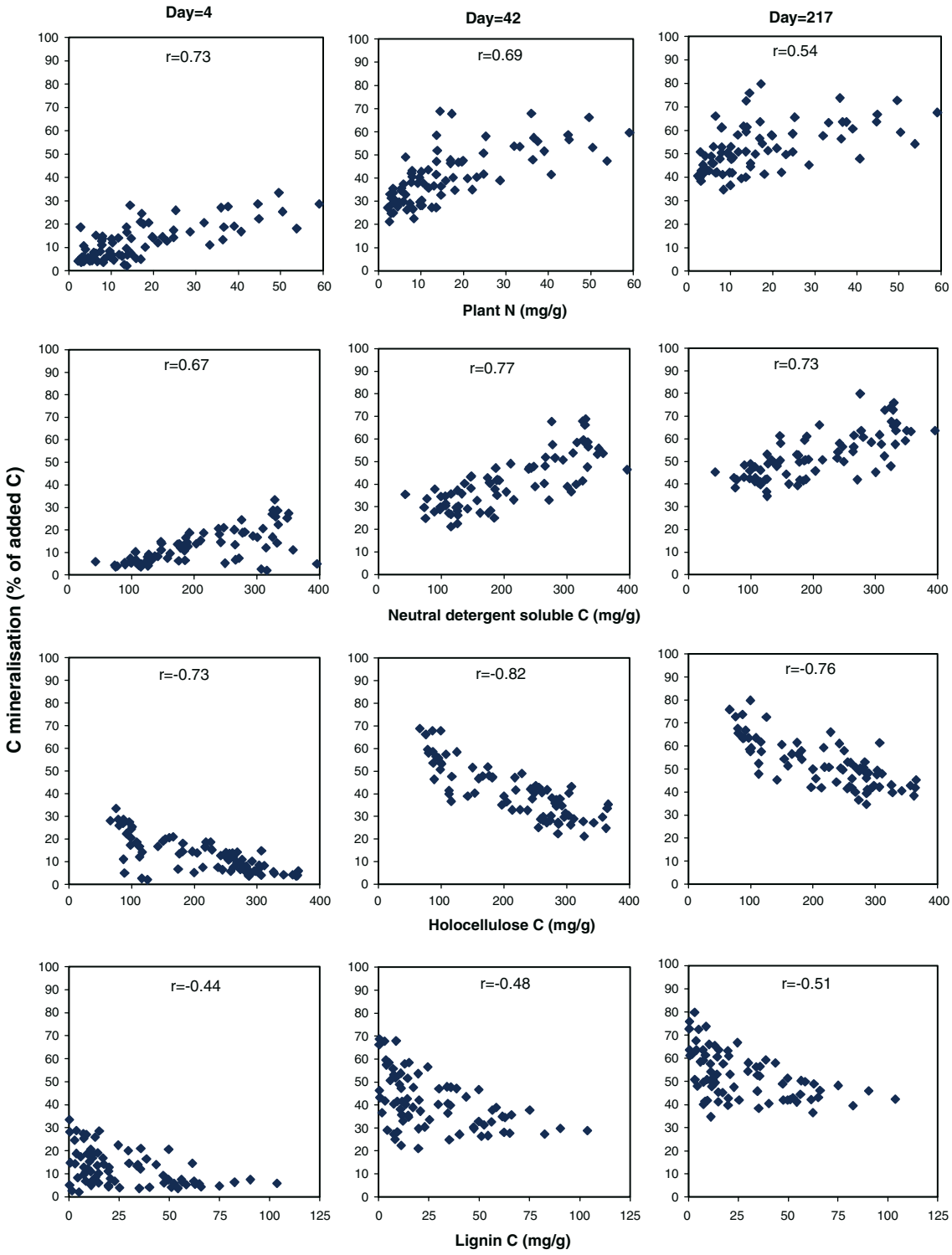

Figure 3. Relationships between C mineralisation after 4, 42 and 217 days of incubation and total plant N, neutral detergent soluble C (NDS), holocellulose C (hemicellulose + cellulose) and lignin C. Values given in figures (r) are Pearson correlation coefficients ($n = 76$).

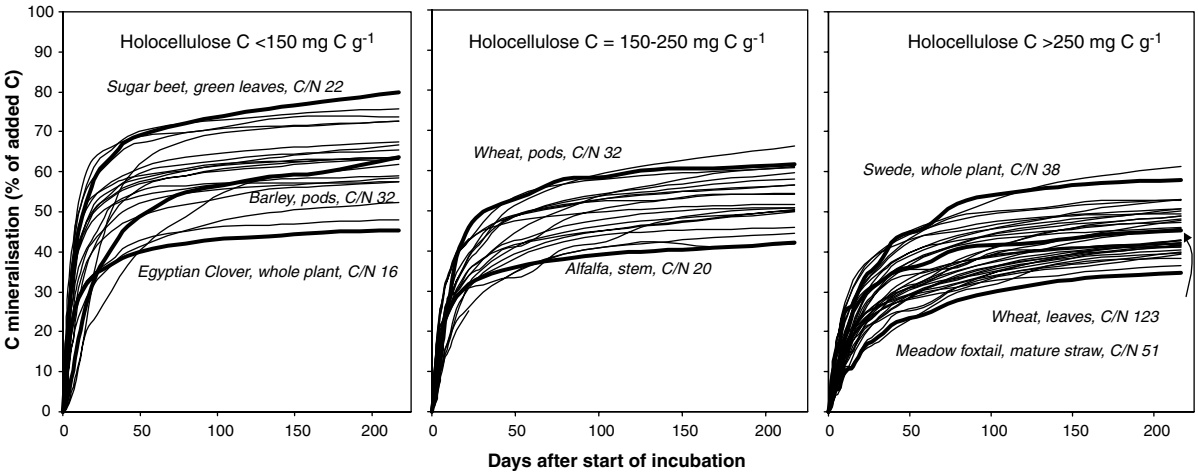

Figure 4. Carbon mineralisation during 217 days of incubation. Lines represent the average of replicates ($n = 3$) for each of the 76 plant materials incubated. Materials were grouped according to the content of holocellulose C. Labelled materials (bold lines) are highlighted to represent extremes in each group.

this group, with an over-representation of materials from cereals, grasses and alternative crops. Materials with 10–30 mg NDS-N g^{-1} showed a much more diverse pattern, including both rapid initial net immobilisation and mineralisation, but the majority of materials showed net N mineralisation by the end of the incubation period. Materials with more than 30 mg NDS-N g^{-1} generally had very high initial net N mineralisation rates, except a few with a short initial immobilisation period, followed by net N mineralisation, which after 217 days resulted in more variable mineral N levels than for the two first groups. This was caused by an over-representation of materials from legumes, catch crops and horticultural crops, which generally have low C/N-ratios (average C/N = 10).

Although C and N mineralisation rates on most sampling occasions were significantly correlated to both total plant C/N-ratio and C/N-ratio of the various SCD fractions, all of these correlations were relatively low ($r^2 > 0.5$, Table 4). This was mostly due to the asymptotic nature of the relationship between net N mineralisation at Day 217 and total plant C/N, as evident in Figure 5 (bottom row of plots).

Discussion

Sample properties range

Compared to most previous litter decomposition studies, the dataset produced in this Nordic project is both extensive and represents a very broad range of plant materials. Most studies of litter decomposition include less than 10 different litter materials investigated under similar conditions (e.g. Bending et al., 1998; de Neergaard et al., 2002; Henriksen and Breland, 1999a; Kumar and Goh, 2003; Quemada and Cabrera, 1995) and only a few include more than 20 or 30 (Constantinides and Fownes, 1994; Gillon et al., 1999; Joffre et al., 2001; Trinsoutrot et al., 2000), not all under similar experimental conditions. Although Seneviratne (2000) and Palm et al. (2001a) included more samples (102 and 1929 samples, respectively), their data were compiled from literature and other studies under variable conditions (i.e. different soils, temperature, experimental conditions, incubation period and sampling frequency), and neither of them contain as complete and detailed data on measured C and N content in the various plant material fractions. The materials included in the present study were selected carefully from a larger (249 samples) archive of plant samples (Stenberg et al., 2004), in order to achieve as broad and representative a range of plant qualities as possible. The correlation matrix (Table 3) between properties of the 76-sample incubation sub-set closely resembles the corresponding correlation matrix in Stenberg et al. (2004) for the 113 sample sub-set selected for SCD analyses from the full archive population. This strongly suggests that the incubation sub-set was representative with respect to all

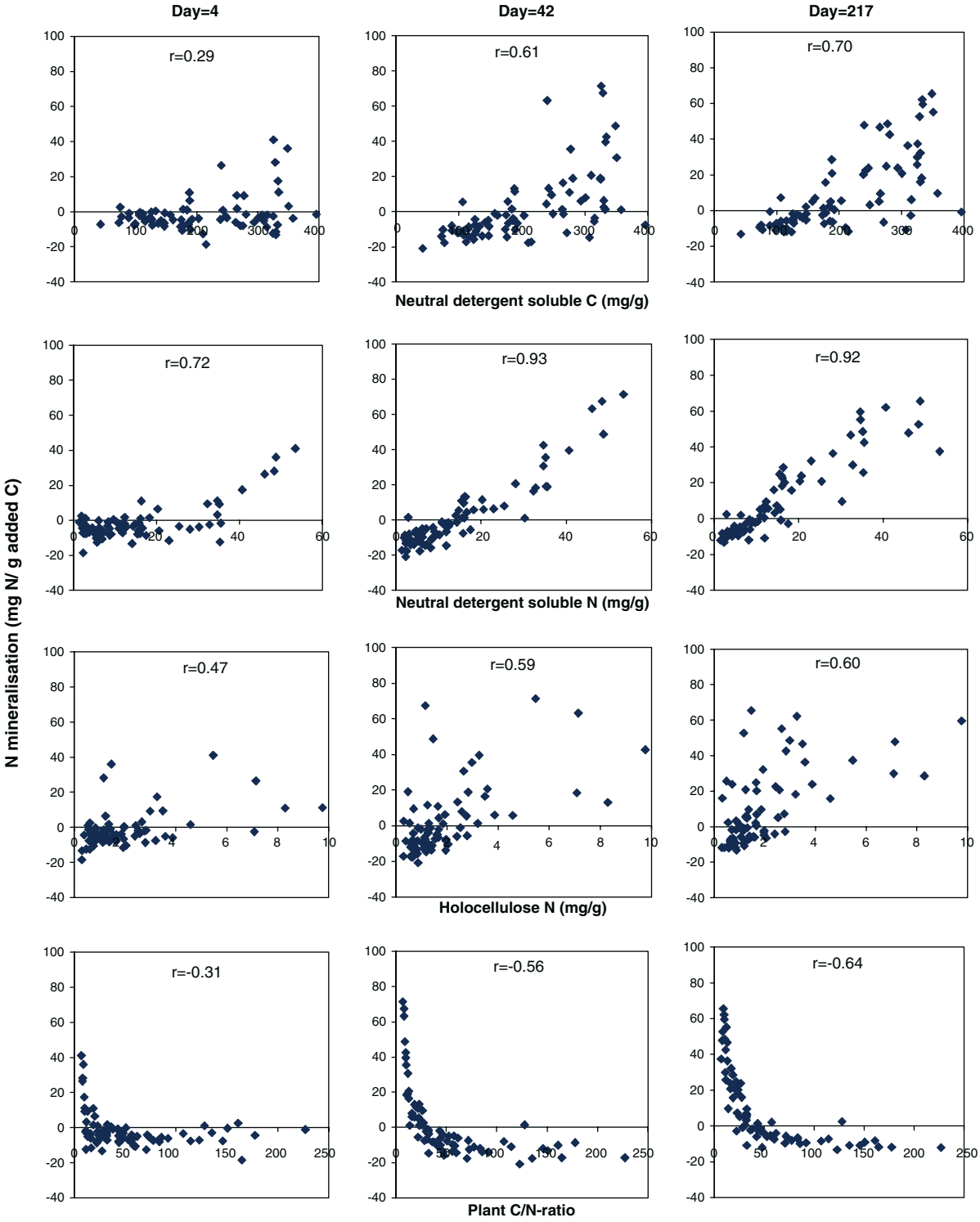

Figure 5. Relationships between net N mineralisation after 4, 42 and 217 days of incubation and neutral detergent soluble C and N (NDS), holocellulose N (hemicellulose + cellulose) and plant total C/N-ratio. Values given in figures (r) are Pearson correlation coefficients ($n = 76$).

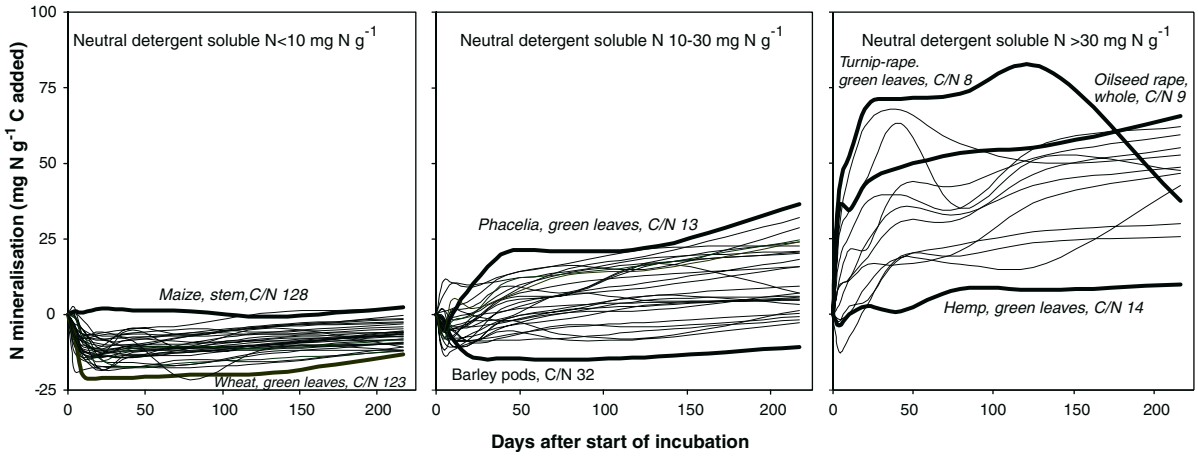

Figure 6. Net N mineralisation during 217 days of incubation. Lines represent the average of replicates ($n = 3$) for each of the 76 plant materials incubated. Materials were grouped according to the content of neutral detergent soluble (NDS) N. Labelled materials (bold lines) are highlighted to represent extremes in each group.

selected biochemical properties and indicates that the Mahalanobis distances technique for NIR-spectra (Shenk and Westerhaus, 1991) was appropriate for selecting the sample sub-set for the incubation study.

Our comprehensive sample population of plant materials covered a range in quality parameters that largely seemed to encompass most of the materials included in previous studies. In the Organic Resource Database, Palm et al. (2001a) found above-ground plant N content to vary between about 2.5 and 60 mg N kg^{-1} in the more than 1000 samples covered, which is very similar to the range found here (Table 2). Our range in plant N content is also identical to that found in a compilation by Seneviratne (2000) covering 102 plant samples. Similarly, Trinsoutrot et al. (2000) found N contents from 3 to 45 mg N kg^{-1}, a range comparable with a number of literature values cited in their study. Henriksen and Breland (1999a) found water soluble C between 16 and 156 and water soluble N between 0.5 and 9.5 mg g^{-1} for 10 different plant residues, which are somewhat lower values than in the present study. In our study, soluble N was highly right-skewed, with maximum values of water soluble N up to 34 mg N g^{-1} (Table 2). Most other studies report cellulose and lignin in percentage dry matter, and the ranges we observed (data not shown) of 7 to 58% (DM) cellulose and 0.1 to 23% (DM) lignin are similar to or slightly broader than those in other studies (Bending et al., 1998; Henriksen and Breland, 1999a; Quemada and Cabrera, 1995; Trinsoutrot et al., 2000).

When designing the initial sampling strategy for the full range of samples (249), an important criterion was to minimise co-variation between the amount of easily decomposable substances and the C/N-ratio of the materials. These properties are often inter-correlated and commonly the C/N-ratio is misinterpreted as a causal factor for decomposability. From Figure 2c it is clear that we did not completely avoid such inter-correlation. The non-structural samples (typically young, green plant leaves) samples with less than 200 mg holocellulose C g^{-1} all showed low C/N-ratios (between 7 and 32) and the overall correlation between holocellulose C and total C/N was significant ($r = 0.67$, Table 3). However, the remaining samples with more than 200 mg holocellulose C g^{-1} showed highly varying C/N-ratios (between 18 and 227). Consequently, we believe that the inter-correlation between these two properties was minimal for the majority of our incubated samples.

Experimental conditions

Our overall objective was to develop NIR models on plant residues as a tool for characterising their degradability and N release in soil, independent of external constraints. Therefore, we wanted to investigate decomposition and N min-

eralisation patterns as affected solely by the inherent quality attributes of the plant residues. This may be difficult to achieve experimentally, but we tried to remove or hold constant the variable external constraints that influence decomposition and nutrient turnover of organic materials under natural, *in situ* conditions. We did not want the decomposition of the high C/N-ratio materials to be limited by lack of available N, which may vary significantly in arable soils. Therefore, as detailed in the Materials and Methods section, we added inorganic N to reach a minimum level of soil mineral and plant N (33.5 mg N g^{-1} plant C), which was based on studies with maize and wheat residues (Henriksen and Breland, 1999b; Recous et al., 1995). Substantial soil mineral was also present for low C/N-ratio plant materials incubated without inorganic N addition, initially the non-amended soil contained approximately 100 mg N kg^{-1}. The net effect of mineral N availability on decomposition depends to some extent on the quality of the plant residues, though. Whereas addition of mineral N may stimulate decomposition of materials rich in cellulose and hemicelluloses, increased recalcitrance may be the result with material with high lignin concentration (Fog, 1988; Henriksen and Breland, 1999b; Recous et al., 1995). However, very few of our materials had high lignin contents. Consequently, we do not believe that the addition of mineral N appreciably retarded decomposition in our study. We rather have reasons to assume that N addition was needed for N-unlimited decomposition of the materials showing sustained or temporary net immobilisation (Figure 6, left), mainly owing to high contents of cellulose and hemicellulose. Under natural conditions, decomposition of these materials would be limited to some extent and the immobilisation and re-mineralisation patterns different depending on the soil mineral N content.

We chose not to grind the plant material in our study, and the input rate (2 g DM 100 g^{-1} soil) was relatively high. Both factors contribute to reduced plant material–soil contact as compared to adding finely ground material at lower rates. Ambus and Jensen (1997) found that non-ground plant residues produced less microbial activity and N immobilisation during the initial decomposition phase than coarsely ground material, presumably due to a less intimate plant residue–soil contact, but they found no significant effect on N dynamics in the long term. Henriksen and Breland (2002) concluded that reduced soil contact contributed to reduced decomposition rates by decreasing the possibility of decomposer organisms to invade the material, an effect which appeared to be stronger with fibrous than with herbaceous materials. However, in another study this constraint was seemingly alleviated if the decomposer community was boosted by pre-incubating soil with readily degradable plant material (Henriksen and Breland, 1999a), as was done in the present study. Reduced soil contact may also contribute to increased net mineralisation, particularly of N (Breland, 1994; Henriksen and Breland, 1999a, 2002). The major reason is reduced volume of detritusphere soil, the 4–5 mm zone surrounding the decomposing residue, which retains a significant part of decomposing residue C and N (Gaillard et al., 2003; Ladd et al., 1996). For readily degradable material in particular, various protective mechanisms may promote retention, such as increasing clay content (Ladd et al., 1996). For this reason, we chose a soil with very low clay content for the present study.

Our incubation experiment was set up to minimise effects of external, soil-specific factors such as N-availability, the decomposer community's capacity to colonise and degrade holocellulose, and retention of C and N in the detritusphere. Therefore, we believe that the experimental conditions were reasonably representative for natural conditions, where largely particulate plant residues are incorporated in a microbially active soil and with little interaction between plant material quality and soil-specific retention of C and N. A factor obviously differing between our study and field conditions was the onset of decomposition. We added dried residues, which presumably were susceptible to microbial invasion at the onset of the experiment. In the field, plant parts may retain their integrity for shorter or longer periods after incorporation in soil, particularly roots and belowground structures of perennial species. However, this could only be mimicked in an incubations study by adding fresh residues and this was judged impossible in a comparative study like this with a large number of different plant materials.

Plant residue C and N mineralisation

The C and N mineralisation patterns observed in this study are representative of most agricultural materials, as is evident from a comparison with patterns reported by others, e.g. Trinsoutrot et al. (2000) who found C mineralisation to range from 33 to 67% of applied C and N mineralisation of −28 to +50 mg N g^{-1} residue C applied over a 168-day incubation at 15 °C. They also found that the initial phase with rapid mineralisation or immobilisation lasted for a maximum of four weeks, which is very similar to our findings. Similarly, others have found that the initial rate and degree of net immobilisation may vary greatly between samples (Bending et al., 1998; Constantinides and Fownes, 1994; Hadas et al., 2004; Henriksen and Breland, 1999a). Some of our materials showed rapid immobilisation followed by re-mineralisation shortly afterwards (e.g. Phacelia green leaves, Figure 6, centre), while others showed slower but more prolonged net N immobilisation (e.g. barley pods, Figure 6, centre). Compared to most other studies, however, our study included some samples with extremely rapid and high net N mineralisation. These samples were characterised by very low C/N-ratios (less than 10) and were typically leaves of young plants (e.g. of turnip rape, Figure 6, right).

Factors explaining mineralisation patterns

As pointed out by Ruffo and Bollero (2003), multicolinearity between predictor variables, i.e. plant residue quality parameters, may invalidate multiple regression analysis on C or N mineralisation, as performed by Trinsoutrot et al. (2000) and others. In our dataset, a strong correlation exists between soluble (NDS) C and total or soluble N (Table 3, Figure 2), an observation also made by Ruffo and Bollero (2003). This multicolinearity would thus invalidate their use as predictor variables in a multiple regression analyses of the dataset, and hence we only present simple correlations here. In a separate paper, we report several multivariate analysis approaches for interpretation of the data (Bruun et al., 2004).

Early C mineralisation was highly correlated with both water soluble C and N, but the correlation coefficient decreased as decomposition proceeded (Table 4), as also observed by Trinsoutrot et al. (2000) However, compared to their study, C mineralisation in our study was much more closely related to cellulose-C and in particular holocellulose-C and less to lignin-C.

Early N mineralisation was best explained by the content of water soluble N, but from the third week onwards, contents of WS-N, NDS-N and total N (co-linear parameters, Table 3) were the most important parameters, explaining more than 80% of the variation (Table 4). This is in agreement with previous observations (Bending et al., 1998; Constantinides and Fownes, 1994; Trinsoutrot et al., 2000).

Neither C nor N mineralisation were at any time very closely correlated to the plant material C/N-ratio if evaluated on the correlation coefficients alone (Table 4). As is evident from Figure 5 (bottom plots) however, the relationship at the later stages of decomposition was very close and strongly hyperbolic, with a break-even point around a C/N-ratio of 35. As discussed by Stenberg et al. (2004), high C/N-ratios may be associated with significant analytical error (even if based on Dumas combustion in an elemental analyser). C/N-ratios larger than 500 are usually meaningless, a C/N-ratio of 200 is associated with an analytical standard deviation of ±50, and even a C/N-ratio of 45 (plant N ~10 mg g^{-1}) would have an analytical error of approximately ±3. However, most plant materials with a C/N-ratio higher than 45 will cause substantial and extended N immobilisation. Therefore the analytical error associated with the C/N-ratio is not very critical for prediction of net N mineralisation.

Contrary to many other studies (e.g., Constantinides and Fownes, 1994; Cornelissen, 1996; Kumar and Goh, 2003; Tian et al., 1995; Vanlauwe et al., 1996) we did not find the lignin (DM) to plant N ratio to be well correlated with the N mineralisation at any time. In our study the correlation coefficient was at all times lower (Table 4) than that for total residue C/N, as also found by Trinsoutrot et al. (2000). This may be due to the fact that our sample population was relatively little lignified (median 4.1% DM lignin) and that decomposition was carried out under non-N-limiting conditions, which were meant to eliminate the influence of plant N on decomposition rate.

Both de Neergaard et al. (2002) and Muller et al. (2003) tested whether the water soluble C and N fractions can be used as an appropriate index for the easily decomposable pool in a mechanistic model of C and N mineralisation, but found that the easily decomposable pool appeared to be larger than just the water soluble material. This is corroborated by our findings that the neutral detergent soluble C and N were among the best overall predictors for C and N mineralisation, respectively, from this broad range of materials (Table 4). The challenge when attempting to simulate decomposition and N release from organic materials is to derive the best possible initialisation and parameterisation from the simplest and most easily accessible measurements. Nicolardot et al. (2001) successfully used the initial plant residue C/N-ratio to parameterise several decomposition-related properties of each material. As indicated in our study, the neutral detergent soluble C and in particular N were relatively closely related to the total plant N content (Figures 2b and d). These fractions are often included in mechanistic decomposition models. Utilising their correlations with total plant N may consequently be a fruitful approach in initialising such models (Jensen et al., 2004).

Conclusions

Our study showed that the holocellulose and the neutral detergent soluble N fractions of plant materials exert a major influence on their C and net N mineralisation, respectively, across a broad range of plant species, types and parts. The vast majority (>90%) of the plant N was in the fraction extractable by neutral detergent (NDS). Furthermore, it seems that the NDS-N content can be used to roughly categorise the net N mineralisation patterns into (i) sustained net N immobilisation for several months; (ii) initial net N immobilisation during the first 1–4 weeks, followed by some re-mineralisation; and (iii) initially rapid and substantial net N mineralisation. Contrary to other studies, neither plant residue C/N nor lignin/N ratio were closely correlated to decomposition and N mineralisation in the present study.

Acknowledgements

This work was supported by the Nordic Joint Committee for Agricultural Research and funded through the Research Councils in the five Nordic countries (SJVF Denmark, Formas Sweden, Finnish Ministry of Agriculture and Forestry, Agricultural Production Fund Iceland and The Research Council of Norway). We would also like to thank senior citizen Kurt Stenberg who came to the rescue during a midnight incubation start-up.

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Section editor: S. Recous