Chemical Composition of Crop Biomass Impacts Its Decomposition

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Understanding the interaction between plant components and their subsequent decomposition provides insights on how plant quality differences may influence C sequestration within a given management system. Our hypothesis was that decomposition is a function of biochemical composition when all other variables are constant (e.g., particle size, temperature and moisture). Recognizing the challenges of reconciling laboratory and field studies, this study examined the decomposition dynamics of five selected crops with varying composition under controlled temperature and moisture regimes. Residue materials were partitioned into leaf, stem, and root organs to give a clearer indication of compositional control on decomposition. Plant quality varied among species (alfalfa [*Medicago sativa* L.], corn [*Zea mays* L.], cuphea [*Cuphea viscosissima* Jacq. · *Cuphea lanceolata* W.T. Aiton], soybean [*Glycine max* (L.) Merr.] and switchgrass *[Panicum virgatum* L.]). A two-component litter decomposition model was used to describe decomposition observed during 498 d. Stepwise multivariate regression indicated initial N concentration, starch, total lignin, and acid-insoluble ash (AI ash) were the four best predictors (r^2 = 0.83) of the rate of active component decomposition (k_a); however, initial composition poorly predicted the rate of passive decomposition (k_p). The best four-component model (r^2 = 0.43) identified by stepwise multiple regression for k_p included AI ash, hemicellulose, N concentration, and C/N ratio. Rate constants are a function of the incubation period, thus making direct comparison among separate experiments difficult. Chemical recalcitrance appears to slow root decomposition; such chemical recalcitrance to decay may partially explain why roots have been found to contribute more C to the SOC pool than surface residues.

Abbreviations: AI, acid insoluble; AS, acid soluble; SOC, soil organic carbon; SOM, soil organic matter.

The chemical composition of crop biomass impacts its subsequent decomposition. The rate of decomposition is an early facet of the dynamic process converting residue (above and below ground) into soil organic matter (SOM). For a net increase in soil organic C (SOC), C inputs into soil must exceed C efflux. Photosynthetic plants are the primary source of C incorporated into SOC (Hedges and Ertel, 1982) and the rate of C input will depend on land use management (e.g., cropping system and tillage practice). The rate of decomposition is dependent on residue quality, microfaunal, climatic, and soil factors (Parr and Papendick, 1978). On a global scale, climate is the best predictor of decomposition kinetics; however, within a climatic region, biomass chemistry is the best predictor of decomposition kinetics (Aerts, 1997). Silver and Miya (2001), using a global data set, reported that root chemistry appeared to be the primary controller of root decomposition while climate and environmental factors played secondary roles, unlike differences from leaf-litter, where climate and environment were the primary regulators. Within a given management system, many of the factors (e.g., climate and tillage) that influence SOC turnover will be similar. The quantity of residue returned to the soil influences SOC content (Follett, 2001); however, quality differences among residues become important when other factors (e.g., temperature, particle size, etc.) are held constant.

Residue factors include chemical composition, C/N ratio, lignin content, and the size of residue particles. As reviewed by Heal et al. (1997), there have been numerous experiments that focused on the relationship between decomposition and plant composition; both C/N and lignin/N ratios have been used to predict rates of decomposition (Melillo et al., 1989). Although a general trend exists that high lignin content retards decomposition (Heal et al., 1997), no universal relationship has been established (Wang et al., 2004). Residue C/N ratio is a common indicator of residue quality but is not necessarily an accurate predictor of decomposition rate (Franck et al., 1997; Gorissen and Cotrufo, 2000). Understanding the interaction among plant tissue components and their susceptibility to microbial degradation will enable more effective use of crop rotations and cover crops to effectively increase soil C (Stahl and Klug, 1996).

There are several mechanistic models available for evaluating SOM. The CENTURY model uses inputs for N and lignin concentration and a two-pool decomposition algorithm (Parton, 1996). The EPIC model separates plant residue into metabolic, structural, and passive pools in addition to three soil-C pools (Izaurralde et al., 2006). The decomposition algorithm in CQESTR, a model for estimating C sequestration in agricultural soils, uses only a constant rate, based on residue N factor (Rickman et al., 2001). The N factor provides different decomposition rates for legumes and cereal residues, assuming legumes are N "rich" and cereals are N "poor"

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(Rickman et al., 2001). The success of these models to predict changes in SOM accurately reflects the importance of parameters, including total C inputs, residue management, moisture, and temperature, on determining net C exchange. Litter turnover models are mathematically similar to SOM decomposition models in that they also account for multiple decomposing pools (Wieder and Lang, 1982). Improving models by providing additional information for decomposition algorithms is still valuable.

In this study, we selected five crops—alfalfa, corn, cuphea, soybean, and switchgrass—with varied agronomic uses and in which we expected divergent structural compositions. Corn and soybean are the predominate crops in the Midwest and alfalfa represents an important forage crop of the region (National Agricultural Support Service, 2003). Cuphea, a promising alternative crop, produces seeds high in medium-chain fatty acids (Graham, 1989) that can be used as a substitute to palm seed kernel oil. Cuphea oils also have potential use as industrial lubricants (Thompson, 1984). Switchgrass is a potential biofuel feedstock (Brown et al., 2000).

Our hypothesis was that the decomposition of these crops is a function of their biochemical constituents; provided all other variables are held constant (e.g., particle size, temperature, and moisture), an investigation of the potential of plant quality to influence decomposition can be performed. There are challenges to reconciling laboratory and field studies; however, laboratory studies allow examination of biochemical factors while controlling other parameters to avoid confounding effects. Understanding the interaction between plant components and their subsequent decomposition will provide insights into how plant quality may influence C storage within a given management system.

MATERIALS AND METHODS

Field-grown plants, corn (Pioneer 3893), soybean (NK S14-M7), and cuphea were collected at maturity; alfalfa (Wrangler) was collected at the third cutting; switchgrass (Sunburst) was collected in late August. Alfalfa and switchgrass were collected during their second growing season. Soil and plant samples were collected at the Swan Lake Research Farm of the North Central Soil Conservation Research Laboratory, which is located in Stevens County, in west-central Minnesota (45°41′ N, 95°48′W) at 370 m above sea level. Plant material was collected from a replicated field experiment in a randomized complete block design with four replications; each plot was 9.1 m wide by 22.9 m long. Based on preliminary root mass estimates (data not shown), two root collection methods were used to collect sufficient root biomass for chemical and decomposition analysis, which minimized the total number of required samples. We collected 16 pooled soil cores (2.5-cm i.d., 15-cm depth) from alfalfa and switchgrass plots after the aboveground material was removed by baling. The root samples were collected from the peripheral 1 m or outer rows to minimize disturbance in the plots. Root biomass in the surface 15 cm ha^{-1} for switchgrass and alfalfa was calculated from grams of root per cubic centimeter in soil cores. In the annual crops (corn, cuphea, and soybean), the ground was loosened with a shovel to 15 cm and plants with roots still attached were lifted out of the soil; the number of plants was recorded. We crudely estimated root biomass for corn, cuphea, and soybean per unit volume from the root mass per plant and number of plants per unit area. For many species, including those in this study, root density is greatest in the surface 15 cm (Allmaras et al., 1975; Russell, 1977; Frank et al., 2004; Sharratt and Gesch, 2004; Weaver, 1926). Soil samples were stored at 4°C. Soil was washed from the roots with water. After separating leaves and stems, removing soil from roots, and drying (45°C), plant tissue was ground with a Wiley mill to pass through a 0.425-mm sieve. Grinding to a small, uniform particle size standardized the material and eliminated the confounding effect of different particle sizes, which was necessary for interpreting relative decay rates. In the field, litter size would be reduced by soil organisms; therefore, this study does not examine the complete route that biomass may typically take to become part of the SOM.

Composition Analysis

A representative 0.5-g sample of plant tissue was extracted sequentially for soluble sugars, starch, hemicellulose, cellulose, acid-soluble (AS) and AI lignin. Briefly, soluble sugars were extracted with 80% hot ethanol, starch was removed enzymatically with amyloglucosidase, and hemicellulose and cellulose were extracted by H_2SO_4 (National Renewable Energy Laboratory, 1996b). An Agilent 1100 series high-pressure liquid chromatography (HPLC) system (Agilent Technologies, Palo Alto, CA) with an Aminex HPX-87N column (Bio-Rad Laboratories, Hercules, CA) separated and quantified soluble sugars, starch, and cellulose and an Aminex HPX-87P column (Bio-Rad Laboratories) quantified hemicellulose. Acid-soluble lignin concentration was determined spectrophotometrically at 205 nm (National Renewable Energy Laboratory, 1996a) and AI lignin and AI ash were determined by proximate method (National Renewable Energy Laboratory, 1995). Standards (Sigma-Aldrich, St. Louis, MO) were used to calibrate the HPLC and to determine recovery rates. Reported values were adjusted based on internal standard recovery rates. The total C and N of the plant material were determined with a LECO CN-2000 (LECO Corp., St. Joseph, MI).

Decomposition

Field-collected Barnes loam soil (fine-loamy, mixed, superactive, frigid Calcic Hapludoll) was air dried and then sieved (2 mm). The soil had 3.1% total C, 2.9% organic C, and an organic C/N ratio of 11.4. The equivalent of 50 g of oven-dry soil was mixed thoroughly by hand with 0.2 g of plant tissue in a 230-mL plastic bottle. A second bottle was established with 100 g of soil (oven-dry equivalent) with 0.4 g of plant tissue to determine the rate of N immobilization and mineralization relating to decomposition. The experiment was initiated, time zero, by adding water (60% water-filled pore space) to the soil, without preincubation, recognizing that this might overestimate the decomposition rate of the active fraction (Paul et al., 2001). Bulk density in the bottle was about 1.2 g cm^{-3}. Incubation conditions were a constant 25°C, 49% humidity, and dark (Paul et al., 2001). This is warmer than the mean annual temperature of the region of 6.1°C, with a winter average of −11.2°C and summer average of 19.4°C (National Climate Data Center, 2005); therefore, the decay rates reflect a potential rather than an actual field rate. Since the plant material was not sterilized, different amounts and types of microbes could have been introduced with the plant tissue. The bottles were covered loosely with Parafilm (Alcan Packaging, Neenah, WI) to minimize dehydration but allow CO_2 and O_2 exchange. Water was added to the bottles as necessary to maintain 60% water-filled pore space.

Decomposition was assessed in the first bottle by determining emission of CO_2 measured on consecutive days until Day 21, then on Days 24, 31, 43, 64, 92, 120, 148, 183, 218, 330, and 498. Initially, capping time was 1 h, but capping time increased incrementally to a maximum of 48 h to compensate for the reducing rate of emission. Carbon dioxide emission was calculated as the change in CO_2 concentration during the capping period. One 2.5-mL gas sample per sample jar was drawn using a gas-tight syringe and a 2-mL aliquot was injected into an evacuated 1.8-mL amber sample vial, thus overpressuring the sample vial. The sample

vials had Teflon–rubber-lined Al caps. Duplicate 50-μL gas samples were analyzed within 2 h of sample collection.

Carbon dioxide concentration was determined using a Varian CP-8200 auto sampler into a Porapak Q column (injection temperature, 150°C; column temperature, 80°C; detector temperature, 130°C; and filament temperature, 250°C) on a CP-3800 Varian gas chromatograph equipped with a thermal conductivity detector (Varian Inc., Palo Alto, CA). The flow rate was 32 mL min^{-1} using He as the carrier gas. The gas chromatograph was calibrated at each sampling date with a three-point external standard curve, using certified traceable standards to determine CO_2 concentration.

Decomposition is reported as a percentage of the original C remaining:

$$\text{net}\, C_{\text{evolved}} = C_{\text{amended}} - C_{\text{control}} \quad [1]$$

This equation establishes that residue C evolved (net C_{evolved}) is a function of C evolved in amended (C_{amended}) soil minus C evolved from unamended soil (C_{control}), which is representative of the decomposition of background SOM; this assumption neglects any potential priming effects from the addition of plant material (Kuzyakov et al., 2000). The percentage of C remaining

$$\%C_{\text{remaining}} = \left[\left(C_{\text{initial}} - C_{\text{evolved}}\right)/C_{\text{initial}}\right]100 \quad [2]$$

was calculated as a fraction of the initial C (C_{initial}) added in residue after subtracting the C evolved as CO_2 (C_{evolved}). A double exponential function was used to describe decomposition biologically and mathematically (Wieder and Lang, 1982):

$$C_t = C_a \exp(-k_a t) + (100 - C_a)\exp(-k_p t) \quad [3]$$

This model assumes that litter can be partitioned into two pools; a rapidly decomposing or active fraction (C_a) and a slowly decomposing fraction (100 – C_a) for plant litter, where the percentage of C remaining at time t is C_t, C_a is the percentage of C remaining in the active fraction, k_a (% C d^{-1}) is the decomposition rate for C_a, and k_p (% C d^{-1}) is the decomposition rate of (100 – C_a). The percentage of C remaining cannot exceed 100 or decline below zero. This double exponential model does not consider any possible transformation of labile into more recalcitrant material, which may occur through microbial activity (Wieder and Lang, 1982). Half-lives were calculated with

$$t_{1/2} = \frac{0.693}{k_t} \quad [4]$$

where t (day) and k_t corresponds to either k_a or k_p.

Soil Nitrogen Mineralization

Total N, NO_3^-–N, NH_4^+–N, and total C were determined on soil removed from the second jar at 0, 15, 31, 66, 94, and 120 d after experiment initiation. Soil concentration of total N and total C were measured using a LECO CN-2000 (LECO Corp.). Ammonium N and NO_3^--N were extracted from dried soil with 1 *M* KCl using a 1 g:10 mL soil/solution ratio; the procedure was modified from (Mulvaney, 1996). Their concentrations were measured using an Alpkem Autoanalyzer (Pulse Instruments Ltd., Saskatoon, SK) by standard colorimetric Berthelot (NH_4^+) and Griess–Ilosvay (NO_3^-, following Cd reduction to NO_2^-) methods as described by Mulvaney (1996).

Statistical Analysis

Statistical analyses were performed using SAS/STAT software release 9.1 (SAS Institute, 2002). Statistical differences among crops and plant organs (within crops) were determined using a generalized linear model (Proc GLM), $P \leq 0.05$ and LSMEANS, which allows mean comparisons even when data points are missing.

Decomposition kinetics were estimated with Proc NLIN using a two-component nonlinear model as described above (Wieder and Lang, 1982). Stepwise multiple regressions (Proc REG) and Pearson correlation coefficients (Proc CORR) were used to investigate the relationship between plant biochemical constituents and decomposition. Nitrogen mineralization kinetics was estimated with a linear regression, which estimates an average rate of mineralization.

RESULTS

Composition

Plant quality varied among species and organs within species (Table 1). Carbon concentration ranged from 340 to 470 g kg^{-1}, while N ranged from 4.0 to 44 g kg^{-1}, resulting in C/N ratios ranging from 10 to 110. The amount of soluble carbohydrates (sucrose, glucose, fructose, and starch) varied among species and organs. Starch concentration in the alfalfa roots was as much as two orders of magnitude greater than in the roots of other species, which reflects the carbohydrate storage function of these roots. Hemicellulose and cellulose, primary cell wall material, were the most prevalent plant component in all organs and species. Total lignin (AI lignin plus AS lignin) concentration ranged from 65 g kg^{-1} (alfalfa leaf) to 212 g kg^{-1} (soybean root) and the lignin/N ratio ranged from 1.5 g kg^{-1} (alfalfa leaf) to 40 g kg^{-1} (soybean stem). Leaves differed in total lignin content and chemical composition of lignin present. Leaves consistently had a lower concentration of AI lignin but about 1.6-fold greater concentration of AS lignin than stem or roots of the same species. Acid-insoluble ash probably included soil contamination and mineral constituents of the sample, and thus included a measure of nonplant material. Roots from alfalfa, soybean, and corn, and leaves from cuphea and switchgrass had the greatest concentrations of AI ash (Table 1). Corn leaves were also high in AI ash. It can be difficult to remove all adhering soil from soil-grown roots. Sticky glandular hairs on cuphea leaves and hirsute leaves on corn and switchgrass make it difficult to remove all soil material from plant tissue.

Decomposition

Consumption of organic materials (e.g., plant tissue) and subsequent respiratory release of CO_2 by microorganisms was used as an indicator of decomposition. During 498 d of incubation, CO_2 emission ranged from 106 to 123 mg CO_2–C per sample jar, which corresponded to 0.52 to 0.60 kg CO_2–C kg^{-1} plant tissue added. The initial amount of C added to the soil and the net amount of C evolved provided an estimate of the C remaining in the soil from the plant tissue using Eq. [2]. This method overestimated the actual plant C remaining, due to conversion of plant C into microbial biomass C (Paul and Clark, 1996). The percentage of C remaining after 498 d varied significantly among species ($P \leq 0.0001$) and among organs ($P \leq 0.003$). Averaged across organs, alfalfa and switchgrass had about 13% less C remaining than soybean, corn, or cuphea (Table 2). Within species, the percentage of C remaining varied significantly among organs only for alfalfa and corn, where roots had more C remaining than their aboveground counterparts.

Decomposition kinetics (Table 2) were estimated from nonlinear regression of the percentage of C remaining with time (Fig. 1). The active fraction (C_a) represented 25 to 37% of the C in the plant material (Table 2). Alfalfa leaves had the most rapid decay, losing

Table 1. Concentration of C, N, sucrose (SUC), glucose (GLU), fructose (FRU), starch (STR), hemicellulose (HC), cellulose (CEL), acid-insoluble lignin (AIL), acid-soluble lignin (ASL), and acid-insoluble ash (AIA) from field-grown corn (Pioneer 3893), soybean (NK S14-M7), and cuphea collected at maturity, alfalfa (Wrangler) collected at the third cutting, and switchgrass (Sunburst) collected in late August. Alfalfa and switchgrass were collected during their second growing season (*n* = 4).

Species	Organ	C	N	SUC	GLU	FRU	STR	HC	CEL	AIL	ASL	AIA
		g kg^{-1} plant material										
Alfalfa	leaves	454a‡	44.0a	12.8b	5.60b	4.69b	48.7b	177c	133b	55.3c	9.54a	0.63b
	stems	448ab	21.2b	24.4b	14.7a	9.62a	6.50b	200ab	415a	117a	6.41b	2.75b
	roots	433b	24.0b	45.2a	0.66c	0.14c	114a	239a	421a	89.9b	4.89b	10.2a
Soybean	leaves	439a	15.8a	6.69a	7.28b	8.44b	9.73a	245a	207b	107c	6.68a	2.13a
	stems	468a	4.36c	6.00a	15.6a	14.5a	3.71ab	289a	526a	168b	4.78b	1.44a
	roots	467b	7.48b	2.65a	4.45b	6.02b	1.01b	308a	586a	207a	4.97b	6.82a
Cuphea	leaves	384b	26.3a	2.40a	14.0a	11.4a	18.7a	141c	55c	108b	16.8a	93.4a
	stems	435a	9.30b	3.13a	8.13b	6.29b	1.63b	230b	519a	157a	6.91b	26.2b
	roots	432a	13.6b	0.97b	10.3ab	4.09b	2.18b	261a	309b	179a	10.4ab	12.3c
Corn	leaves	416b	13.6a	19.0b	6.21b	6.64b	2.11a	461a	340b	91.4b	6.31a	76.8b
	stems	458a	5.86c	83.8a	22.5a	24.0a	1.48ab	375ab	457a	108a	5.69b	5.97c
	roots	343c	9.09b	7.52b	6.52b	6.02b	0.53b	281c	342b	102ab	6.55a	158a
Switchgrass	leaves	445c	12.6a	28.7a	2.51c	0.58b	4.08a	498b	418ab	89.1c	6.55a	29.21a
	stems	452b	4.05c	28.6a	14.3a	7.45a	8.77a	646a	517a	123b	4.36b	12.3b
	roots	465a	7.09b	13.6b	7.60b	8.76a	4.08a	549b	334b	161a	4.46b	11.0b
Crop (C)		†	†	†	**	†	†	†	†	†	†	†
Organ (O)		†	†	†	†	†	†	*	†	†	†	†
C · O		†	†	†	†	†	†	*	†	**	***	†
$LSD_{0.05}$ among crops		15.6	2.64	10.0	4.33	4.38	17.9	71	90	22	2.79	8.07

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† Significant at the 0.0001 probability level.

‡Values in a column within a crop followed by a different letter are different at P ≤ 0.05.

50% of their C within the 498-d incubation. Decomposition rates for the active fraction for alfalfa leaves and roots were substantially faster than for other plants and respective organs; therefore, the half-lives for the active fraction of alfalfa leaves followed by roots were the shortest (Table 2). For the active fraction in other crops, leaves had the shortest half-lives and half-lives for stems and roots were similar. Half-lives for the passive fractions were lowest for alfalfa followed by switchgrass; however, dynamics among plant organs varied within crops. Calculated k_p values were inversely related to time, such that apparent half-lives increased (data not shown). The composition of the substrate becomes increasingly more recalcitrant as microbes consume the more readily decomposable material. Therefore, when comparing kinetics values among studies it is important to note the duration of the experiment.

Correlation coefficients between plant components and decomposition kinetics were determined (Table 3). Across all crops, k_a was significantly correlated with the majority of plant components measured. High positive and significant correlations of k_a were observed with starch and initial N concentration. High negative and significant correlations were observed between k_a and AI lignin, total lignin, and the lignin/N ratio. The k_p and C_a were significantly and negatively correlated with AI ash and initial C or N concentration, although the correlation coefficients were low. Stepwise multiple regressions supported the correlation findings between decomposition kinetics and compositional factors (Table 4).

Nitrogen Mineralization

During the first 15 d, all organs and tissues had net N mineralization except switchgrass leaves and stems, where there was a decrease in NO_3^- concentration before N mineralization began to increase dramatically (Fig. 2). The total N mineralized after adding alfalfa leaf tissue was 50 to 60% more than observed for the other crops during the first 90 d (Fig. 2), which is consistent with the large concentration of N in alfalfa leaves (Table 1).

The highest rate of mineralization was observed for alfalfa leaves (Table 5). Mineralization of switchgrass materials was generally faster than all other crop tissues except alfalfa leaves; however, rates of mineralization were similar among organs. Rates of mineralization were similar among the remaining crops, where rates were typically highest for leaves and similar for stem and root materials.

DISCUSSION

To understand compositional control of decomposition kinetics, we used controlled laboratory studies and examined relationships via stepwise multiple regression among five crops partitioned into leaf, stem, and root organs. This technique indicated initial N, starch, total lignin, and AI ash concentrations were the four best predictors of k_a, model r^2 = 0.83, with initial N concentration as the single best predictor (partial r^2 = 0.72, Table 4). A four-component model (r^2 = 0.43) was identified for k_p, with AI ash, hemicellulose, and initial N concentrations and C/N ratio being the best predictors. The best model for C_a-based biochemical composition had an r^2 = 0.32, and included AI ash, AI lignin, and lignin/N ratio.

The addition of organic material into the soil can result in net N mineralization or N immobilization. Materials that have low N or a high C/N ratio are expected to result initially in N immobilization. A general rule of thumb is that a C/N ratio >20 will result initially

Table 2. Observed percentage of residue C remaining after 498 d and kinetic coefficients calculated from a double exponential decomposition model (Eq. [3]; Wieder and Lang, 1982) after incubating plant tissue in soil for 498 d at 25°C and 60% water-filled pore space. Values are means ± standard error of the estimate (n = 4).

Crop	Organ	Observed C remaining	C_a†	k_a‡	k_p§	Half-life¶ k_a	Half-life k_p
		%	%	% C $d^{-1} \times 10^2$	% C $d^{-1} \times 10^4$	——d——	
Alfalfa	leaf	50.8b#	37.1 ± 1.7	17.6 ± 2.8	5.47 ± 1.3	3.9	1270
	stem	55.4ab	31.5 ± 1.5	9.7 ± 1.1	5.39 ± 1.0	7.1	1290
	root	60.8a	29.3 ± 1.0	13.8 ± 1.5	3.64 ± 0.7	5.0	1910
Soybean	leaf	65.7a	25.0 ± 0.6	8.5 ± 0.5	3.29 ± 0.3	8.2	2110
	stem	60.5a	32.8 ± 1.4	3.2 ± 3.2	2.35 ± 0.7	21.6	2950
	root	64.2a	27.7 ± 1.2	3.2 ± 0.3	2.67 ± 0.6	21.6	2600
Cuphea	leaf	67.9a	25.4 ± 1.1	8.8 ± 1.0	2.34 ± 0.6	7.9	2960
	stem	62.4a	31.2 ± 1.1	4.5 ± 0.3	2.50 ± 0.6	15.3	2770
	root	68.3a	24.4 ± 1.1	5.2 ± 5.2	3.40 ± 0.6	13.2	2040
Corn	leaf	62.7b	27.9 ± 0.7	8.8 ± 0.5	3.21 ± 0.4	7.9	2160
	stem	60.4b	31.7 ± 1.3	5.8 ± 0.5	2.73 ± 0.7	12.0	2540
	root	73.6a	20.6 ± 1.6	4.0 ± 0.6	1.58 ± 0.7	17.4	4390
Switchgrass	leaf	56.4a	32.5 ± 1.1	7.2 ± 0.5	4.17 ± 0.7	9.7	1660
	stem	56.8a	32.6 ± 1.7	5.7 ± 0.6	3.91 ± 1.0	12.1	1770
	root	58.8a	26.9 ± 1.3	3.2 ± 0.3	4.77 ± 0.6	22.0	1450

† C_a is the %C-remaining in the rapidly decomposing plant litter.

‡ k_a is the decomposition rate for C_a, which represents the rapidly decomposing plant litter.

§ k_p is the decomposition rate of (100 - C_a), which represents the slow or passive litter fraction.

¶ Half-life = 0.693/k.

Values with different letters within crop are different $P \leq 0.05$.

in net immobilization (Tisdall et al., 1986). Therefore, a least some immobilization was likely, as a majority of plant tissues had C/N ratios in excess of 20 except for alfalfa leaves, stems, and roots, and cuphea leaves (Table 1). Release of organic N through mineralization is regulated by the C/N ratio; microbes do not assimilate N from organic sources until substrate N reaches a critical concentration (Paul and Clark, 1996). Availability of C often controls microbial N assimilation since N mineralization occurs only after significant decomposition of crop residues (Stevenson and van Kessel, 1996). Nitrogen mineralization is also an indicator of decomposition; therefore, the rates of C and N mineralization are related. Results of stepwise regression among N-mineralization parameters and C-mineralization kinetics indicated the average rate of N mineralization (slope from linear regression) was related to k_a (r^2 = 0.42, $P \leq 0.0009$, data not shown). Stepwise regression did not identify any significant models among N-mineralization parameters and k_p (data not shown).

Ghidey and Alberts (1993) compared buried shoot and buried root residue of corn and soybean. They found faster decay rates for buried shoot residue than for root material in both years of a 2-yr study. Buried soybean materials decomposed faster than corn in the first year. Ghidey and Alberts (1993) attempted to link their findings to higher C/N ratios in the more slowly decomposing material; however, their measurements showed a substantially higher C/N ratio in soybean roots than corn roots, even though soybean roots decomposed faster than the corn roots. Similarly, Moretto et al. (2001) showed substantially lower mass loss of leaf material with a substantially higher C/N ratio, but the C/N ratio in roots was not as different and did not contribute to as drastically a different mass loss among materials. They discovered

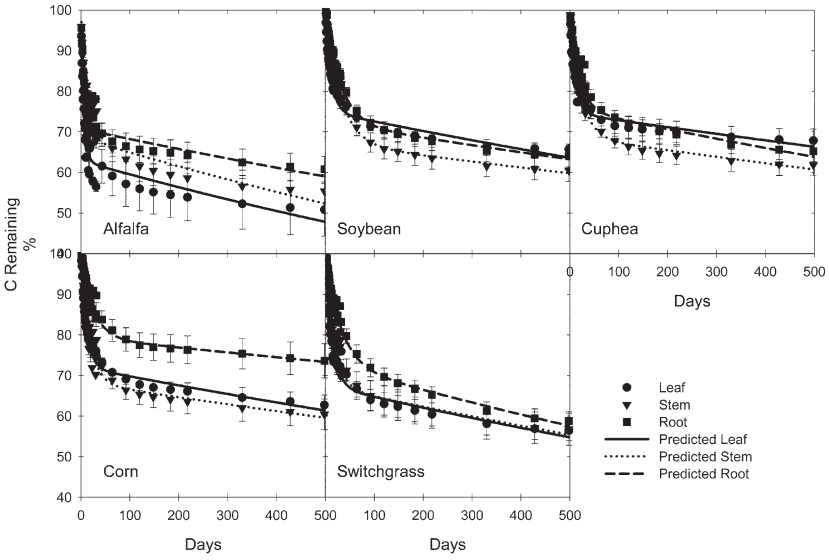

Fig. 1. Percentage of plant C remaining based on cumulative CO_2 flux and initial C input from plant tissue. Plant tissue was incubated in soil for 498 d at 25°C and 60% water-filled pore space. Vertical bars are SE, n = 4. Predicted lines calculated using two-pool, double exponential model (Wieder and Lang, 1982): $C_t = C_a\exp(-k_a t) + (100 - C_a)\exp(-k_p t)$, where k_a is the decomposition rate for C_a, which represents the rapidly decomposing or active plant litter, k_p is the decomposition rate of (100 − C_a), which represents the slowly decomposing plant litter, and C_a is the percentage of C remaining in the active litter fraction, which assumes that adding plant tissue did not alter the decomposition of soil organic matter present in the soil.

Table 3. Pearson correlation coefficients among the concentration of compositional factors and kinetic coefficient from a two-component, double exponential decomposition kinetics model (Wieder and Lang, 1982) calculated after incubating plant tissue in soil for 498 d at 25°C and 60% water-filled pore space.

	Pearson correlation coefficients		
Composition factor of plant tissue	k_a†	k_p‡	C_a§
Sucrose	0.15	0.09	0.21
Glucose	−0.28*	−0.16	0.04
Fructose	−0.30*	−0.18	0.02
Soluble sugars	−0.01	−0.002	0.17
Starch	0.69*	0.23	0.16
Hemicellulose	−0.36*	0.16	0.11
Cellulose	−0.47*	−0.12	0.14
Acid-insoluble lignin	−0.67*	0.21	−0.15
Acid-soluble lignin	0.27*	−0.05	−0.14
Acid-insoluble ash	−0.15	−0.36*	−0.46*
Initial C	−0.11*	−0.25	−0.27*
Initial N	0.84*	0.34*	0.17
C/N ratio	−0.57*	−0.19	0.15
Total lignin	−0.65*	−0.22	−0.17
Lignin/N ratio	−0.66*	−0.24	0.07

* Coefficient is significant at $P \leq 0.05$.

† k_a is the decomposition rate for Ca, which represents the rapidly decomposing plant litter.

‡ k_p is the decomposition rate of (100 – Ca), which represents the slow or passive litter fraction.

§ C_a is the percentage of C remaining in the rapidly decomposing plant litter.

a significant negative correlation between C/N ratio and mass loss. Moretto et al. (2001) also found significant correlations between mass loss and lignin, N, P, lignin/N and lignin/P contents, for both leaf and root material. In the present study, materials with a low C/N ratio or a low lignin/N (such as alfalfa, and leaf material of other crops) had faster decomposition rates (both k_a and k_p) than material with high ratios.

Under the controlled conditions in this study, >50% of the residue C still remained after 498 d of incubation. Field and laboratory incubations exceeding a year are uncommon; however, several field studies indicate >50% mass loss in <1 yr. For example, Burgess et al. (2002) found that 30 to 40% of corn stover in litterbags decomposed after 193 d. Schomberg et al. (1994) found that about 55% of sorghum [*Sorghum bicolor* (L.) Moench] and wheat (*Triticum aestivum* L.) decomposed in buried litterbags in 169 and 116 d, respectively. In several studies (Broder and Wagner, 1988; Burgess et al., 2002; Buyanovsky and Wagner, 1997; Stott and Martin, 1990), 30% of residue remained after 1 yr and as little as 10% remained after 2 yr. In many of these studies, residue was not partitioned into its constituent parts: leaves, stems, and roots. Composition of the input probably had an effect on the observed decomposition kinetics. Blenis et al. (1999) separated canola (*Brassica* spp.) parts and showed 45 to 55% decomposition of stem and only 30 to 40% decomposition of roots in approximately 300 d. A decomposition study of bunchgrasses (*Poaceae* family) in Argentina showed similar results in some species for separated root and leaf material after 16 mo of field incubation where >65% of the material remained; however, after 21 mo of incubation, roots were more decomposed than leaf litter (Moretto et al., 2001). Ghidey and Alberts (1993) examined decomposition of residue on the surface, buried shoot residue, and buried root materials of five crop species and found 35 to 60, 70 to 80, and 45 to 75% mass loss, respectively, in the first year. Although it is apparent that temperature has an effect on litter decomposition (Katterer et al., 1998), it is likely that our data do not conform to the findings of field incubations, in part due to differences in method. Our results were based on C loss and calculating the percentage of C remaining vs. directly measuring mass loss; our method also assumed that the rate of decomposition of SOM already present was not changed by the incorporation of fresh plant material. It should also be noted that mass loss in field studies with litterbags can be a result of material falling out of the bag rather than from being decomposed. Additionally, field studies would have a more diverse decomposing community, which may have been excluded by drying and sieving the soil used in the laboratory studies, and might be why we observed slower decomposition than some field studies. The plant tissue was not sterilized; therefore, the microbial numbers or species introduced with the plant tissue could have been different among organs and species.

Table 4. Summary of stepwise multiple regression of plant compositional factors and two-component double exponential model decomposition kinetics calculated after incubating plant tissue in soil for 498 d at 25°C and 60% water-filled pore space.

Dependent variable	Independent variable	Partial r^2	Model r^2	*P*
k_a†	N concentration	0.72	0.72	0.0001
	starch	0.06	0.78	0.0005
	total lignin	0.03	0.81	0.006
	acid-insoluble ash	0.02	0.83	0.02
k_p‡	acid-insoluble ash	0.13	0.13	0.006
	hemicellulose	0.11	0.36	0.006
	N concentration	0.07	0.42	0.02
	C/N ratio	0.03	0.43	0.14
C_a§	acid-insoluble ash	0.20	0.20	0.001
	acid-insoluble lignin	0.08	0.27	0.02
	lignin/N	0.04	0.32	0.08

† k_a is the decomposition rate for C_a, which represents the rapidly decomposing plant litter.

‡ k_p is the decomposition rate of (100 - Ca), which represents the slow or passively decomposing plant litter.

§ C_a is the percentage of C remaining from the rapidly decomposing plant litter.

Potential Implications of Substrate Quality for Carbon Dynamics

The amount of C stored in soil is a function of total inputs and the rate of biomass decay and SOM turnover, provided C is not lost due to leaching or erosion. A strategy for increasing soil C is to modify the C quality of residue to decrease the rate of decay, which may promote the transition of C into the SOM fraction, which is resistant to decomposition (e.g., humic fraction), while maintaining or increasing C inputs. Within a given set of physiochemical environment and management factors, residue quality may influence the conversion into SOM. In this study, the effect of chemical composition of the plant tissue on its decay was studied; initial plant mineralization is an early step in the process of converting fresh C inputs to recalcitrant SOM. Residue composition also influences the microbial community and change in the community as decomposition progresses influences the rate of decomposition (Broder and Wagner, 1988).

Understanding how root composition compares with aboveground composition may help explain the differen-

tial contribution of root C to SOC compared with shoot C. The passive component ($100 - C_a$) of corn root tissue in this experiment had the longest half-life of more than a decade, calculated from k_p, while corn leaves and stems had half-lives of 6 to 7 yr (Table 3). This may partially explain why corn roots make such an important contribution to SOC; they contribute as much as threefold more than aboveground C inputs (Allmaras et al., 2004; Wilts et al., 2004). Our observation of different decomposition rates for shoot and root material is consistent with Hooker et al. (2005), who attributed a difference in the contribution to SOC to different cycling rates between shoot and root material.

Understanding why roots (at least of corn) contribute more to SOC than aboveground parts requires knowing respective decay kinetics, total biomass, residue placement, and rhizosphere dynamics. Tissue with slow decomposition will make little impact in building soil C if there is minimal biomass. Several isotopic studies have shown that root material originating from exudates and necromass contribute substantially to the retention of C in the SOM pools (Gale and Cambardella, 2000; Kisselle et al., 2001; Puget and Drinkwater, 2001). Carbon cycle models need to include above- and belowground biomass as well as rhizodeposition to estimate accurately C movement from shoot to root and root to soil pools (Edwards et al., 2004; Johnson et al., 2006).

Modeling the kinetics of decomposition of both plant residues and SOM typically has involved efforts to separate fast from slow decomposing pools. The DAISY model originally presented by Hansen et al. (1991) used water solubility to differentiate plant parts. The CENTURY model uses inputs for N and lignin concentration (Parton, 1996), EPIC separates plant residue into three pools (metabolic, structural, and passive; Izaurralde et al., 2006), and CQESTR uses a constant rate based on the N content of the plant biomass (Rickman et al., 2001). Müller et al. (2003) indicated that C/N ratio and cellulose content could be better predictors for partitioning plant materials. Results of our study support the use of N and lignin components for the separation of fast and slow decomposing pools.

CONCLUSIONS

Our study examined the decomposition dynamics of five selected crops with varying composition under controlled temperature and moisture regimes. Residue materials were partitioned into leaf, stem, and root organs to give a clearer indication of compositional control on decomposition and eventually allow better calculation of the contribution of plant materials to C sequestration. Rate constants are a function of the incubation period, thus making direct comparison among separate experiments difficult when using simple, first-order kinetic models. Chemical recalcitrance appears to slow root decomposition; this was especially noted in corn roots. Such chemical recalcitrance to decay may partially explain why roots have been found to contribute more C to the SOC pool than residues. Results of our study also support the use of N and lignin components for the separation of fast- and slow-decomposing pools in litter turnover models. This information could be used to refine existing models and it adds to our knowledge and understanding of composition and decomposition of crop species.

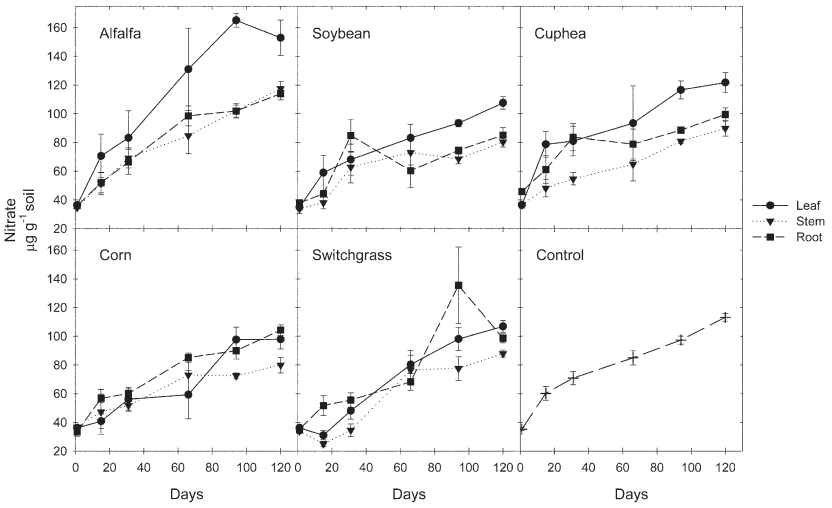

Fig. 2. Concentration of NO_3^- in soil measured 0, 15, 31, 66, 94, and 120 d after incubating plant tissue in soil at 25°C and 60% water-filled pore space to estimate N mineralization. Vertical bars are SE, *n* = 4.

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Table 5. Nitrogen mineralization rates estimated by linear regression from NO_3^- concentration in soil after inoculating and incubating plant tissue in soil for 0, 15, 31, 66, 94, and 120 d at 25°C and 60% water-filled pore space. The slope represents the average rate of mineralization.

Crop	Organ	Intercept	Slope	r^2
		mg kg^{-1}	mg kg^{-1} d^{-1}	
Alfalfa	leaf	37.7	1.14	0.77
Alfalfa	stem	45.0	0.62	0.56
Alfalfa	root	40.2	0.67	0.88
Soybean	leaf	39.2	0.60	0.80
Soybean	stem	38.6	0.36	0.52
Soybean	root	46.4	0.32	0.35
Cuphea	leaf	53.2	0.61	0.61
Cuphea	stem	38.2	0.44	0.72
Cuphea	root	55.1	0.37	0.46
Corn	leaf	33.7	0.57	0.73
Corn	stem	35.3	0.39	0.69
Corn	root	41.2	0.56	0.88
Switchgrass	leaf	26.7	0.71	0.85
Switchgrass	stem	23.9	0.79	0.50
Switchgrass	root	36.1	0.65	0.52

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