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Variation in root architecture among switchgrass cultivars impacts root decomposition rates

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ABSTRACT

Roots regulate soil carbon (C) input, but fine root decomposition rates and root impacts on soil organic C turnover (SOC) are uncertain. This uncertainty is, partly, caused by the heterogeneity of root systems, which vary in diameter distributions and tissue chemistry. Here, we evaluated how root diameter distributions affect root and SOC decomposition. Roots from eight *Panicum virgatum* (switchgrass) cultivars were analyzed for root diameter size-class distribution and C:N ratio. Roots from each cultivar were mixed with C_3 soil according to five root diameter treatments: (1) 0–0.5 mm, (2) 0.5–1 mm, (3) 1–2.5 mm, (4) a 1:1:1 mixture of roots from each diameter size class, and (5) a mixture combining diameter classes in proportions representing measured size distributions for each cultivar. All treatments were incubated for 90 days under laboratory conditions. Respired CO_2 was measured throughout and the microbial community structure was measured at termination of the experiment. Carbon-13 isotope techniques were used to partition respiration into root-derived C versus native SOC-derived C. Results indicated: (1) specific root length differed among the cultivars, (2) root decomposition rates within the three size classes varied by cultivar, but were not correlated with cultivar differences in root C:N ratios, (3) root diameter size class affected root and SOC decomposition, and (4) mixing roots of different diameters did not lead to synergistic increases in decomposition. We conclude that intraspecific variation in root architecture is significant and that fine root diameter size class distribution is an important trait for shaping decomposition processes.

1. Introduction

Soils store more carbon (C) than vegetation and the atmosphere combined, and plant roots are an important conduit of C input to soils (Norby and Jackson, 2000; Kong and Six, 2010). Root-derived soil C drives microbial activity and thus the rate at which C cycles between plants, soils and the atmosphere, making roots an important component of the global C cycle (Lal, 2004). Fine roots, defined as roots smaller than 2 mm in diameter (Fan and Guo, 2010), are the most important component of soil C input (Rasse et al., 2005; Joslin et al., 2006), but there is much uncertainty about fine root impacts on soil C cycling, because of uncertainty about their decomposition rates (Silver and Miya, 2001; Langley and Hungate, 2003), and about the impact of fine root decomposition on soil organic C (SOC) decomposition. This uncertainty may be related to the wide range of fine root diameters co-located within a root system, which may affect root and SOC decomposition rates differently.

Tissue quality alone does not predict root decomposition rates particularly well, and it appears that we have a rudimentary understanding of the root characteristics that regulate decomposition rates. Tissue quality, as defined by C:N or lignin:N ratios, does not always control decomposition rates of root tissues in the same way as leaf tissues (McClaugherty et al., 1984; Lohmus and Ivask, 1995; Fan and Guo, 2010), and other chemical tissue characteristics such as cellulose:lignin:N ratio (Fog, 1988; Entry and Backman, 1995), calcium and phosphorous concentrations (Silver and Miya, 2001) or total non-structural carbohydrates (Fan and Guo, 2010) may be more important in driving root decomposition rates (Silver and Miya, 2001). Moreover, a root system is composed of a heterogeneous assembly of fine roots with a wide variety of diameters, which vary in tissue quality (McClaugherty et al., 1984; Lohmus and Ivask, 1995; Fan and Guo, 2010) and decompose collectively, but

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studies on root decomposition have been conducted with roots of one diameter size class decomposing individually, which assumes that roots of a single size class decompose as a homogeneous subset of the total root system. This approach may not paint a complete picture of decomposition rates, since roots of different diameters decompose simultaneously (Guo et al., 2008) and together affect the microbial community and root and SOC decomposition processes.

Simultaneous decomposition of roots with a variety of diameters and thus chemical characteristics may alter overall root decomposition rates in less predictable ways, much like non-additive patterns in the abundance and activity of decomposers are frequently reported when litter of different species decompose together (Blair et al., 1990; Briones and Ineson, 1996; Wardle et al., 1997; Anderson and Hetherington, 1999; De Graaff et al., 2011). Indeed, synergistic patterns in decomposition rates, where mass loss exceeded expected decay by >20%, are common in litter mixing studies with aboveground plant material (Gartner and Cardon, 2004). The positive correlation between decomposition rates and litter chemical diversity may be explained by priming (Kuzyakov et al., 2000; Meier and Bowman, 2008), which is defined as the stimulation of overall decomposition rates by the addition of labile substrates, such as root exudates or litter of high quality (Dalenberg and Jager, 1989; Kuzyakov et al., 2007). Because root quality varies among fine roots with different diameters (McClaugherty et al., 1984; Lohmus and Ivask, 1995; Fan and Guo, 2010), mixing fine roots with a variety of diameters may lead to non-additive increases in decomposition rates.

In addition, the heterogeneous assembly of fine roots with different diameters in root systems may affect the rate of SOC decomposition. Previous research shows that the supply of easily decomposable litter (such as fine roots) and easily available organic substrates to soil may result in positive (Dalenberg and Jager, 1989; Hamer and Marschner, 2002, 2005; Kuzyakov et al., 2007) or negative (Kuzyakov and Bol, 2006; Blagodatskaya et al., 2007) priming of SOC. For example, in the presence of roots, SOC decomposition can decrease by as much as 30% or increase by up to 300% (Dormaar, 1990; Cheng et al., 2003; Cheng and Kuzyakov, 2005). The observed variation in the magnitude and direction of the priming of SOC caused by root decomposition and root exudation may be related to the characteristics of the fine root component of root systems (De Deyn et al., 2008). To the best of our knowledge, no study yet has linked fine root diameter size-class distribution to the rate of SOC decomposition.

With this study we set out to evaluate how differences in diameter size-class distribution among root systems affect root and SOC decomposition rates. We hypothesized that very fine roots within a root system decompose faster than coarser roots and that a relatively high abundance of very fine roots in root systems increases overall root and SOC decomposition rates. We used root systems from eight different *Panicum virgatum* (hereafter: switchgrass) cultivars, which were expected, based on preliminary data from a greenhouse study, to exhibit significant intraspecific variation in root architectures (R.M. Miller, Argonne National Laboratory, unpublished data). Root systems were analyzed for root diameter size-class distribution and were incubated in a uniform soil under controlled laboratory conditions for 90 days. We established five root treatments across the cultivars: (1) roots of 0–0.5 mm diameter, (2) roots of 0.5–1 mm diameter, (3) roots of 1–2.5 mm diameter, (4) a 1:1:1 mixture of the three root diameter size classes, and (5) a mixture combining the roots with the three diameter size classes in proportions representing the measured diameter size-class distributions for each cultivar. Because roots with an isotopic ^{13}C signature of approximately $-12‰$ were incubated in soil with a ^{13}C signature of approximately $-26‰$, we were able to differentiate respiration derived from root C versus native SOC.

2. Methods

2.1. Sampling protocol

In October 2009, we collected soils and roots from eight *P. virgatum* L. (hereafter: switchgrass) cultivars grown in monoculture at the U.S. Department of Energy National Environmental Research Park at Fermilab in Batavia, IL, USA. The sampled cultivars were: (1) Alamo, (2) Blackwell, (3) Carthage, (4) Cave-in-Rock, (5) Forestburg, (6) Kanlow, (7) Southlow, and (8) Sunburst. The experimental plots (88°13′47″W, 41°50′29″N) were planted in June 2008, on soils that were under a stand of Eurasian pasture grasses for 36 years. Monocultures of three of the switchgrass cultivars originating from different latitudes (Kanlow, Cave-in-Rock, Southlow) were grown in the large (20 × 36 m) replicated plots ($n = 3$) of the primary experimental area. In addition, replicated field trials of the other switchgrass ecotypes used in this study were established in adjacent smaller plots (3 × 2 m; $n = 4$ [Blackwell, Forestburg, Sunburst] and 2 × 1 m; $n = 3$ [Alamo, Carthage]). None of the sampled plots were fertilized. Using a 4.8-cm diameter soil corer, we collected soil cores from each of three replicate field plots to a depth of 15 cm from on top of the crown and directly next to the crown of individual plants for each cultivar. The soil cores were placed in individual polyethylene bags, shipped overnight on ice to Oak Ridge National Laboratory, and kept at 6 °C until further processing. Roots were carefully washed from the soil cores over stacked sieves (2 mm and 53 μm) within 7 days of sampling, after which they were kept at 6 °C.

2.2. Separation of roots by diameter size class

Roots from each plant of each cultivar ($n = 3$ field replicates; roots pooled from on-crown and next-to-crown cores for each plant) were analyzed for root diameter size-class distribution using WinRhizo (http://www.regentinstruments.com/products/rhizo/Rhizo.html). Roots were submerged in deionized water and floated in acrylic trays (20 × 25 cm) on a scanner. The scanner was acquired from WinRhizo and allows the roots to be lit from above and below while being scanned, thereby reducing shadows on the root image. Roots were arranged using plastic forceps and care was taken that roots did not overlap. Roots were scanned at a resolution of 200 dpi and the threshold for root diameter size class separation was set at 0.5 mm, allowing us to separate roots into 3 different diameter size classes: 0–0.5 mm; 0.5–1 mm; 1–2.5 mm. After scanning, we used small scissors to physically separate roots into the three diameter size classes. Roots within each diameter size class were then rescanned to verify the accuracy of the physical separations. Subsequently, the roots were dried (70 °C) and cut by hand into segments of 5 mm (0.5–1 mm and 1–2.5 mm diameter size classes) or 2 mm (0–0.5 mm diameter size class). The roots were cut into different sizes, because fine roots, which were attached to the coarser roots were often much shorter than the coarser roots. As a result, we predicted that these end up in soil in smaller fragments when they turnover than coarser roots. Subsamples were ground and analyzed for total C concentrations, total N concentrations, and stable C isotope ratios ($^{13}C/^{12}C$) using an Integra-CN, continuous flow, isotope ratio mass spectrometer (serCon Ltd, Crewe, United Kingdom) coupled with a LECO CN-2000 elemental analyzer (LECO Incorporated, St. Joseph, MI).

2.3. Root incubation

Soil for the incubation experiment was collected from the Walker Branch watershed, located in the U.S. Department of Energy Oak Ridge Reservation near Oak Ridge, TN, USA (35°58′N,

84°17″W). The soil series was Fullerton silt loam, which is classified as a Typic Paleudult. Soil C content was 2941 ± 127 g m^{-2}, soil N content was 133 ± 7 g m^{-2}, and soil pH is was 4.2–4.6 (Garten et al., 2008). Dominant plant species were chestnut oak (34%), red oak (23%) and dogwood (14%). The Walker Branch watershed site is described in detail elsewhere (Johnson et al., 2007). Soils were collected to a depth of 15 cm by using a 4.8-cm diameter soil corer. Immediately upon sampling, the individual soil cores were composited, sieved to 2 mm, and visible roots >2 mm in length were removed. Soils were stored at 6 °C for approximately 2 weeks.

The dried and segmented switchgrass roots were mixed with the soil and incubated for 90 days at 20 °C, and CO_2 efflux from the soil was measured throughout the experiment. For each cultivar, we established five root treatments: 20 g of soil (dry weight) was amended with 0.2 g (dry weight) of (1) roots in the 0–0.5 mm diameter size class, (2) roots in the 0.5–1 mm diameter size class, (3) roots in the 1–2.5 mm diameter size class, (4) a mixture of roots from each of the diameter size classes in a 1:1:1 ratio by mass (g dry weight), or (5) a "realistic" mixture of roots from each of the diameter size classes. For each cultivar, the realistic mixture was composed of the average proportions of roots in the 0–0.5 mm, 0.5–1 mm and 1–2.5 mm diameter size classes, as determined by mass (g dry weight) of roots within each size class. All root treatment × cultivar combinations were incubated in triplicate. In addition, triplicates of unamended soils (control soils) were incubated to account for CO_2 evolution from the preexisting soil C, and blank jars (three) containing no soil were included to determine the background levels of CO_2 and its ^{13}C-isotopic composition. Soil water-holding capacity was determined by the difference in weight for soils at saturation and at oven dry (100 °C), and water was added on days 1 and 15 to obtain 60% saturation.

Specimen cups holding the soil with root additions were placed in sealed 1 L Mason jars, and 5 mL of water was added to the bottom of the jar to maintain humidity (e.g. De Graaff et al., 2010). A septum in the jar lid allowed gas samples to be removed from the headspace with a 10 mL syringe. CO_2 samples were collected in 12 mL exetainers (Labco limited, Buckinghamshire, UK) for storage until analysis. Soil CO_2 evolution was measured on days 1, 3, 7, 15, 30, 60 and 90 of the incubation. Following each gas sampling, the caps were removed and the jars were flushed with air for 30 min to avoid toxic CO_2 build-up in the jars.

2.4. CO_2 and ^{13}C-isotope analyses

The natural difference in $\delta^{13}C$ signature between switchgrass roots and forest soil allowed us to partition total CO_2 respiration rates into CO_2 derived from root decomposition versus CO_2 derived from the decomposition of SOC. We collected a subsample of all root diameter size classes from each of the cultivars prior to the incubation. The average ^{13}C signature of these roots was −12.4 ± 0.21‰.

The concentration of CO_2 and its PDB–^{13}C signature were determined at the University of California-Davis Stable Isotope Facility using a continuous flow, isotope ratio mass spectrometer (PDZ Europa TGII trace gas analyzer and Geo 20–20 isotope ratio mass spectrometer, Cheshire UK). Carbon mineralization data were expressed on a soil oven-dry (100 °C) basis.

Results of the C-isotope analyses are expressed in δ units (‰). The $\delta^{13}C$ values were determined in relation to Vienna-Pee Dee Belemnite as follows:

$$\delta^{13}C = \left(\left(R_{sample}/R_{standard}\right) - 1\right)*1000 \quad (1)$$

To calculate the amount of CO_2–C derived from the root litter incubated in soil, the following mass balance was used (Denef et al., 2001):

$$Q_{sb} = Q_{control} - Q_{bla} \quad (2)$$

$$\delta^{13}C_{sb} = \left(\left(Q_{control}*\delta^{13}C_{control}\right) - \left(Q_{bla}*\delta^{13}C_{bla}\right)\right)/Q_{sb} \quad (3)$$

$$Q_{sc} = \left(\left(Q_{tc}*\left(\delta^{13}C_{tc} - \delta^{13}C_{rootC}\right)\right) - \left(Q_{bla}*\left(\delta^{13}C_{bla} - \delta^{13}C_{rootC}\right)\right)\right)/\left(\delta^{13}C_{sb} - \delta^{13}C_{rootC}\right) \quad (4)$$

$$Q_{rootC} = Q_{tc} - Q_{sc} - Q_{bla} \quad (5)$$

$$\text{Priming} = Q_{sc} - Q_{sb} \quad (6)$$

where $Q_{control}$ is the measured total amount of C respired from the control soil including the blanks, and $\delta^{13}C_{control}$ is its measured isotopic composition; Q_{bla} is the total amount of measured C from the blank jars, and $\delta^{13}C_{bla}$ is its measured isotopic composition; Q_{tc} is the measured total amount of C respired from soils amended with the litter added and including the blanks, and $\delta^{13}C_{tc}$ is its measured isotopic composition; Q_{sb} is the total amount of C respired from the control soil minus the C derived from the blanks (Equation (2)) and $\delta^{13}C_{sb}$ is its isotopic composition (Equation (3)); Q_{sc} is the total amount of C respired from soils amended with the roots minus the blanks and root-derived C (Equation (4)); Q_{rootC} is the total amount of C respired from the roots, and $\delta^{13}C_{rootC}$ is its isotopic composition (Equation (5)). The priming effect of SOC was quantified for each treatment and cultivar combination by subtracting Q_{sc} from Q_{sb} (Equation (6)).

2.5. Quantification of bacterial and fungal gene copy numbers

At the conclusion of the incubations, the soil in each container was mixed, and a 5-g subsample was collected and frozen (−80 °C) for DNA extraction and to assess the relative abundance of fungi and bacteria. Microbial DNA was extracted from 0.25 g of soil using the PowerSoil®-htp 96 Well Soil DNA Isolation Kit (MO BIO Laboratories, Inc. Carlsbad, CA, USA) in concert with a 96 well plate shaker, using a plate adapter set (MOBIO Laboratories, Inc. Carlsbad, CA, USA). After extraction, DNA concentration and purity were determined with nano-drop using the ND-1000 Spectrophotometer (NanoDrop Technologies, Inc., Wilmington, DE, USA).

Quantitative PCR runs were performed as described by De Graaff et al. (2010) and Castro et al. (2010). The primers for 16S rRNA bacterial genes were EUB338 (Lane, 1991) and Eub518 (Muyzer et al., 1993), and primers for fungal rRNA genes were nu-SSU-1196F and nu-SSU-1536R (Borneman and Hartin, 2000). Samples were analyzed in duplicate with triplicate standard curves. We tested 1:10 DNA dilutions in selected samples, did not observe inhibition, and obtained similar results. Standard curves were prepared using known amounts of DNA extracted from pure cultures carried out concomitantly with experimental samples and exhibited a linear relationship between the log of the rRNA–gene copy number and the calculated threshold (Ct) value ($R^2 > 0.99$). *Escherichia coli* was used for bacterial standards (circa 180 bp amplicon), and *Saccharomyces cerevisiae* was used for fungal standards (circa 340 bp amplicon). Amplification efficiencies ranged from 1.6 to 1.8, which are consistent with other reported values (*e.g.*, Fierer et al., 2005; Castro et al., 2010).

2.6. Statistical analysis

To assess differences in root diameter size-class distributions and specific root lengths among cultivars, one-way analysis of

variance (ANOVA) comparisons were made using the Univariate GLM in SPSS Statistics 17.0, with cultivar-types as fixed effects. To evaluate differences among cultivars and root diameter size classes in C:N ratios, fungal:bacterial rRNA gene copy ratios, and CO_2 respiration rates, two-way ANOVA's were conducted with treatments (i.e., cultivar and root diameter size class) as fixed effects, using the Univariate GLM in SPSS Statistics 17.0. For all ANOVAs, means were compared by the Tukey test, after confirmation that the ANOVA was significant. The level of significance was $P \leq 0.05$.

To assess if mixing root tissue composed of multiple diameter size classes resulted in non-additive higher decomposition rates, we compared differences in respiration rates between the predicted respiration rates calculated from the decomposition of individual root diameter size classes (hereafter referred to as 'predicted') and observed respiration rates for the mix of root diameter size classes (hereafter referred to as 'observed'). Predicted respiration was calculated for each cultivar throughout the incubations by using the following methods (Blair et al., 1990; Wardle et al., 1997):

$$\text{Expected respiration}(1{:}\ 1{:}\ 1\ \text{mix}) = (S1_t + S2_t + S3_t)/3$$

$$\text{Expected respiration}(\text{realistic mix}) = (S1_t{*}A1) + (S2_t{*}A2) + (S3_t{*}A3)/100$$

where $S1_t$, $S2_t$, and $S3_t$ are the average respired CO_2–C for each of the individual root diameter size classes for a given cultivar at each measurement time (t) and A1, A2, and A3 are the average % abundance (by dry weight) of each diameter size class measured in the root system of that cultivar. We performed a linear regression with the 'predicted' and 'observed' respiration data across measurement times and tested whether the regression lines were different from a 1:1 line. In addition, we tested whether the slopes of the regression lines differed from each other using ANCOVA in SPSS. The level of significance was $P \leq 0.05$.

3. Results

3.1. Differences in root architecture among switchgrass cultivars

Specific root length (cm root/g dry weight) varied significantly among cultivars, with up to a 150% difference between the cultivar with the lowest and highest specific root lengths (Fig. 1). Specifically, Alamo had a significantly lower specific root length (i.e., generally coarser root systems), than Carthage and Forestburg (i.e., generally more fibrous root systems) (Fig. 1). To better understand how specific root structures differed among cultivars, we measured the relative abundance of roots (on root length basis) in three distinct diameter size classes (i.e. 0–0.5 mm, 0.5–1 mm and 1–2.5 mm) for the root systems of each cultivar (Table 1). The fraction of root length relative to total length in the 1–2.5 mm size class differed significantly between Carthage and Alamo cultivars, where 7% versus 20% of total root length was comprised of roots in the 1–2.5 mm diameter size class, respectively ($P \leq 0.05$) (Table 1). Conversely, in the 0–0.5 mm diameter size class, relative root lengths ranged from 67% (Alamo) to 83% (Carthage), and this difference was marginally significant ($P = 0.62$) (Table 1).

3.2. Cultivar and root diameter impacts on root quality

Root quality was significantly different among cultivars within each of the root diameter size classes (Table 2; $P \leq 0.001$). Carbon to N ratios ranged from 40 to 61 in roots of the 0–0.5 mm diameter size class, from 45 to 92 in the roots of the 0.5–1 mm diameter size class, and from 46 to 102 in roots of the 1–2.5 mm diameter size class (Table 2). We also found differences among cultivars in fungal-bacterial rRNA gene copy ratios at termination of the incubation study, but only in soils amended with roots within the 0–0.5 mm diameter size class (Table 2). When averaged across all cultivars, C:N ratios were narrower for roots in the 0–0.5 mm root diameter size class than for roots in the 0.5–1 mm and 1–2.5 mm size classes (Table 2; $P \leq 0.05$). Similarly, fungal:bacterial rRNA gene copy ratios were lower in soils amended with roots in the 0–0.5 mm root diameter size class than in soils amended with roots in the greatest diameter size class when averaged across all cultivars (Table 2, $P \leq 0.05$).

3.3. Cultivar and root diameter distribution impacts on root decomposition rates

Cultivar affected root + soil-derived and root-derived CO_2 respiration rates (Fig. 2a–f), but not SOC decomposition rates (data not shown). The differences among cultivars in CO_2 respiration rates were greatest on day three of the incubation for all diameter size classes. However, on many days (within the first 60 days of the incubation) cultivars ranked differently with respect to the magnitude of CO_2 respiration rates within the distinct diameter size classes. For example, in the 0–0.5 mm and 0.5–1 mm roots, Forestburg and Cave-in-Rock roots decomposed fastest and Alamo and Southlow roots decomposed slowest (Fig. 2a, b, d and e $P \leq 0.05$). Whereas, in the 1–2.5 mm roots Cave-in-Rock roots decomposed at a greater rate than Carthage and Sunburst roots (Fig. 2c, and f

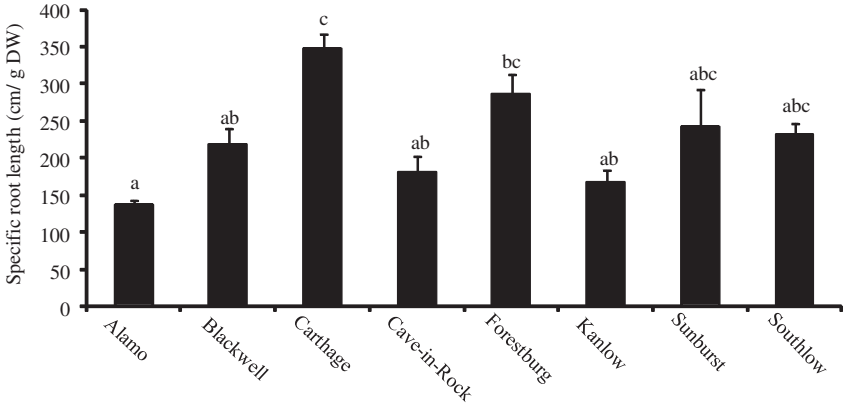

Fig. 1. Specific root lengths (cm/g dry weight) of eight different *Panicum virgatum* cultivars. Values are means ± SE ($n = 3$). Different letters show statistically significant differences among cultivars ($P \leq 0.05$).

Table 1
The fraction of root length relative to total root length in 0–0.5 mm, 0.5–1 mm and 1–2.5 mm diameter size classes for each of the *Panicum virgatum* cultivars. Different letters after numbers indicate significant differences ($P < 0.05$) among cultivars within each root diameter size class. Values are means of three replicate plants per cultivar ± SE ($n = 3$).

Fraction of root length in each of the root diameter size classes, relative to total root length ($l\,l^{-1}$)			
Cultivar	0–0.5 mm	0.5–1 mm	1–2.5 mm
Alamo	0.67 ± 0.01^{a}	0.12 ± 0.01^{a}	0.20 ± 0.01^{b}
Blackwell	0.72 ± 0.02^{a}	0.13 ± 0.01^{a}	0.15 ± 0.02^{ab}
Carthage	0.83 ± 0.00^{a}	0.10 ± 0.00^{a}	0.07 ± 0.00^{a}
Cave-in-Rock	0.69 ± 0.05^{a}	0.12 ± 0.01^{a}	0.19 ± 0.03^{ab}
Forestburg	0.75 ± 0.01^{a}	0.16 ± 0.03^{a}	0.09 ± 0.01^{ab}
Kanlow	0.73 ± 0.04^{a}	0.11 ± 0.01^{a}	0.16 ± 0.04^{ab}
Southlow	0.71 ± 0.04^{a}	0.17 ± 0.01^{a}	0.12 ± 0.04^{ab}
Sunburst	0.75 ± 0.01^{a}	0.12 ± 0.02^{a}	0.13 ± 0.01^{ab}

$P \leq 0.05$). Regression analyses showed that these differences in decomposition among cultivars were not related to differences in specific root length, root C:N ratios or the soil microbial community composition (data not shown).

The microcosms used for the experiment had been used in ^{13}C enrichment studies before, and were thoroughly acid washed prior to use. Yet, some of the microcosms containing soils with 0–0.5 mm diameter size class roots from Alamo, Cave-in-Rock, Carthage, and Southlow consistently experienced ^{13}C isotopic contamination (enrichment) during the incubation experiment. Therefore, we could not calculate root-derived respiration for these cultivars in the 0–0.5 mm root diameter size class, and these cultivars were not included in any of the statistics for root derived respiration. In addition, soil + root derived ^{13}C values on day 30 were generally lower than the ^{13}C values of the root material added to soil, thus these data were omitted from analyses as well. The $\delta^{13}C$–CO_2 values of the included data fell within the expected range of values between −26‰ and −12.4‰.

To assess the impact of root diameter distribution on decomposition rates, we determined how roots in the three diameter size classes differentially affected total, root-derived, and SOC-derived respiration by averaging respiration rates across cultivars. Respiration rates from soil + roots and roots only in the finest size class were significantly greater than those with roots in the coarser diameter size classes on day one of the incubation. On days 7 and 15, respiration from soil + roots in the finest and coarsest diameter size classes exceeded respiration of roots in the 0.5–1 mm size class, and decomposition of the coarsest roots was greater relative to that of the finest roots on day 30 of the incubation (Fig. 3a, b; $P \leq 0.05$), after which decomposition rates converged.

On day one of the incubation, roots in the 1–2.5 mm size class had a positive effect on respiration of SOC, whereas roots in the 0–0.5 mm and 0.5–1 mm size classes had a negative effect on SOC respiration ($P \leq 0.001$), (Fig. 3c). Positive decomposition of SOC was caused by roots in each of the size classes on days three, seven and fifteen of the incubation, where roots in the 1–2.5 mm size class caused greater priming effects than the roots in the other size classes. The finest roots caused the smallest priming effects during the first seven days of the incubation (Fig. 3c; $P \leq 0.05$). The total percent of C positively primed over the entire duration of the incubation experiment was greatest when roots in the 0.5–1 mm and 1–2.5 mm diameter size class were incubated (Fig. 4). In contrast, roots in the 0–0.5 mm size class did not significantly impact total SOC decomposition rates (Fig. 4).

We found that re-combining the three root size classes in either a 1:1:1 mixture or in realistic ratios representing the size distribution of roots for each cultivar produced total respiration rates that were similar to those predicted from the incubations of individual root size classes (Fig. 5a, b). The slopes of the regressions were 0.69 ± 0.03 for the 1:1:1 mixture of roots, 0.75 ± 0.01 for the mixture of root diameter size classes in realistic ratios and 0.71 ± 0.05 when the 1:1:1 mixture was regressed on the realistic mixture, and these slopes did not differ significantly from each other ($P = 0.64$).

4. Discussion

With this study, we asked whether differences in fine root diameter distribution of eight switchgrass cultivars can affect root decomposition rates and/or SOC decomposition. The study led to four main results: (1) specific root length and C:N ratio differed among root systems of the cultivars, (2) root decomposition rates within the three size classes varied by cultivar, but these differences were not explained by cultivar differences in root quality, (3) the finest roots decomposed faster than the coarsest roots, only on day one of the experiment, whereas the coarsest roots decomposed fastest after approximately one month of incubation, and SOC decomposition was stimulated most strongly by the coarsest roots, and (4) mixing roots of different diameters did not alter overall root decomposition rates.

4.1. Cultivar impacts on specific root length and decomposition rates

The root systems of the switchgrass cultivars were characterized by significantly different architectures. The 150% difference in specific root length (cm/g dry weight) between cultivars with the lowest and highest specific root lengths demonstrated the existence of a wide range in average root diameters among the cultivars. Similar differences in root architecture among these cultivars have been observed before in a pot experiment (R.M. Miller, unpublished data). Our analysis of root diameter size-class distributions confirmed this and corroborates other studies reporting

Table 2
C:N ratios of three diameter size classes of *Panicum virgatum* roots and fungal:bacterial rRNA gene copy number ratios in soils amended with three diameter size classes of *Panicum virgatum* roots at day 90 of the incubation. Different letters after numbers indicate significant differences ($P < 0.05$) among cultivars within each root diameter size class. Values are means of three replicate plants per cultivar ± SE ($n = 3$).

Cultivar	C:N ratio			Fungal–bacterial rRNA gene copy number ratio		
	0–0.5 mm	0.5–1 mm	1–2.5 mm	0–0.5 mm	0.5–1 mm	1–2.5 mm
Alamo	49.25 ± 11.24^{ab}	87.13 ± 1.89^{c}	80.22 ± 13.1^{abc}	0.08 ± 0.003^{a}	0.13 ± 0.003^{a}	0.11 ± 0.01^{a}
Blackwell	49.17 ± 0.88^{ab}	79.5 ± 2.55^{bc}	78.54 ± 0.88^{abc}	0.16 ± 0.01^{c}	0.14 ± 0.02^{a}	0.20 ± 0.005^{a}
Carthage	53.63 ± 2.43^{ab}	91.95 ± 5.86^{c}	102.26 ± 1.05^{c}	0.10 ± 0.01^{a}	0.13 ± 0.002^{a}	0.18 ± 0.02^{a}
Cave-in-Rock	60.77 ± 1.81^{b}	85.63 ± 5.06^{c}	91.09 ± 6.77^{bc}	0.11 ± 0.01^{abc}	0.11 ± 0.02^{a}	0.17 ± 0.02^{a}
Forestburg	39.51 ± 4.35^{a}	44.92 ± 2.43^{a}	46.12 ± 3.06^{a}	0.15 ± 0.01^{bc}	0.13 ± 0.03^{a}	0.14 ± 0.05^{a}
Kanlow	42.88 ± 2.36^{ab}	48.14 ± 4.20^{ab}	58.32 ± 2.35^{ab}	0.12 ± 0.01^{abc}	0.11 ± 0.01^{a}	0.18 ± 0.03^{a}
Southlow	43.74 ± 0.44^{ab}	60.86 ± 5.41^{ab}	60.98 ± 14.21^{ab}	0.10 ± 0.01^{ab}	0.14 ± 0.03^{a}	0.11 ± 0.02^{a}
Sunburst	46.56 ± 3.45^{ab}	57.14 ± 5.58^{ab}	50.97 ± 4.6^{a}	0.11 ± 0.01^{abc}	0.16 ± 0.02^{a}	0.16 ± 0.005^{a}

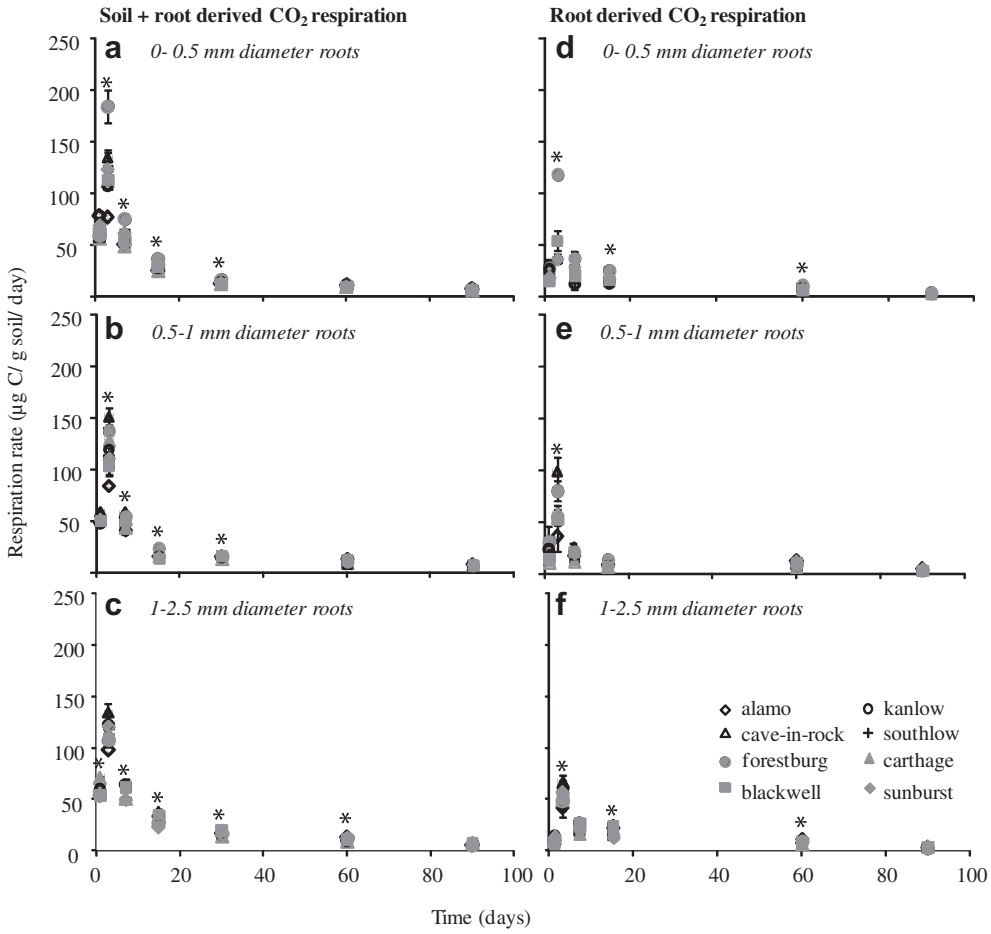

Fig. 2. Microbial respiration rates from soils amended with dried roots from eight *Panicum virgatum* cultivars. Roots from each cultivar were separated into three root diameter size classes (0–0.5 mm, 0.5–1 mm and 1–2.5 mm) and were incubated separately. Soil + root-derived respiration with (Fig. 3a) 0–0.5 mm diameter roots; (Fig. 3b) 0.5–1 mm diameter roots; (Fig. 3c) 1–2.5 mm in diameter roots; and root-derived respiration of (Fig. 3d) 0–0.5 mm diameter roots; (Fig. 3e) 0.5–1 mm diameter roots; and (Fig. 3f) 1–2.5 mm diameter roots. Values are means ± SE ($n = 3$). One asterisk signifies a statistically significant difference among cultivars at the $P \leq 0.05$ level and two asterisks signify a statistically significant difference among cultivars at the $P \leq 0.01$ level.

that root architecture varies by plant genotype or cultivar (Jackson, 1995; Fischer et al., 2006). In addition, root C:N ratios differed among cultivars within each of the three diameter size classes. These results are comparable with studies that have demonstrated intra-specific variability in leaf litter quality (Dungey et al., 2000; Treseder and Vitousek, 2001; Schweitzer et al., 2004; Lecerf and Chauvet, 2008). Finally, we found that both fungal:bacterial rRNA gene copy number ratios differed significantly among cultivars at the end of the incubation in soils amended with roots in the 0–0.5 mm size class, reconfirming that genotypic variation within a plant species can affect soil communities (Dungey et al., 2000; Schweitzer et al., 2008). However, intraspecific differences in root tissue quality and associated soil microbial communities within specific root diameter size classes have, to our knowledge, not been shown before.

Differences in the structure and quality of root systems among cultivars and their impact on belowground micro-organisms can exert important effects on belowground C dynamics (Hendrickson and Robinson, 1984; Hendricks et al., 1993; Hirsch et al., 2003; Phillips et al., 2003; Schweitzer et al., 2004; Lecerf and Chauvet, 2008). This study indicates that genetic variability within plant species can lead to differences in fibrous root decomposition rates, and most notably, to differences in decomposition of fibrous roots separated into three narrow diameter size classes (i.e., 0–0.5 mm, 0.5–1 mm and 1–2.5 mm). However, we were unable to detect a statistically significant difference among cultivars on SOC decomposition. The impact of intraspecific variability in roots on belowground cycling of C should be considered as a potentially important driver of differences in ecosystem C dynamics among cultivars of switchgrass. Namely, as roots intermingle directly with the soil, they could have greater direct impacts on soil processes than aboveground litter, and therefore intraspecific variability in roots might especially affect ecosystem processes (Rasse et al., 2005; Kong and Six, 2010). We hypothesized that intraspecific differences in root C:N ratios and in soil microbial communities would correlate with specific cultivar root decomposition rates, but we did not find evidence for correlations between root C:N ratios or microbial communities and root decomposition rates. As a result, we are uncertain about the mechanisms that caused different root decomposition rates among cultivars.

4.2. Root diameter size class distribution impacts on decomposition rates

On average, root-derived respiration rates were greater for the finest roots (0–0.5 mm diameter) than for larger diameter roots on day one of the incubation, whereas on day 30 the coarsest roots had greater decomposition rates, and on day 60 the decomposition rates of each of the roots with different diameters converged. Others have found that fine roots decomposed slower than coarser

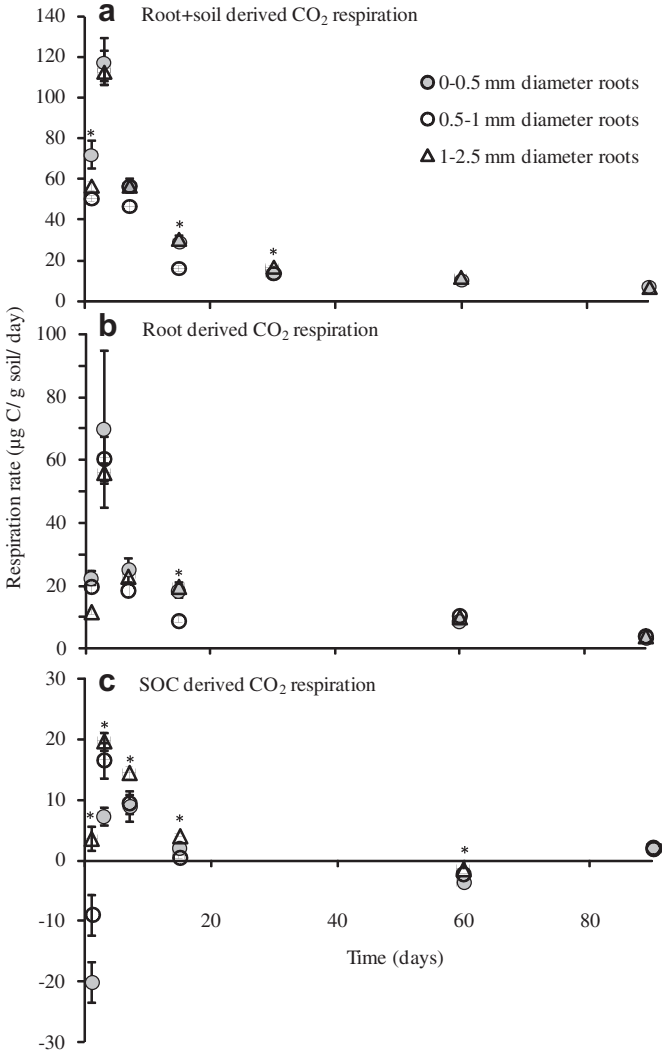

Fig. 3. Microbial respiration rates of soil + roots and its partitioning into respiration derived from roots and soil organic carbon (SOC) over a 90-day incubation of soils amended with *Panicum virgatum* roots of three root diameter size classes (i.e. 0–0.5 mm, 0.5–1 mm and 1–2.5 mm) and averaged across the cultivars included in the ^{13}C calculations. (Fig. 4a) measured soil + root respiration rates; (Fig. 4b) calculated root-derived respiration rates and (Fig. 4c) calculated SOC-derived respiration rates. Values are means ± SE ($n = 8$ for the 0.5–1 mm and 1–2.5 mm diameter size classes, and n = 4 for the 0–0.5 mm diameter size classes). One asterisk signifies a statistically significant difference among cultivars at the $P \leq 0.05$ level and two asterisks signify a statistically significant difference among cultivars at the $P \leq 0.01$ level.

roots (McClaugherty et al., 1984; Lohmus and Ivask, 1995; King et al., 1997; Fan and Guo, 2010) in studies where mass loss was determined over periods of weeks (McClaugherty et al., 1984; Fan and Guo, 2010) or months using litterbags (Lohmus and Ivask, 1995; King et al., 1997). Our measurements of microbial respiration across shorter time intervals allowed for a sensitive evaluation of decomposition dynamics, and in the very short-term, our data indicate that the lower C:N ratio of the finest roots relative to coarser roots leads to greater decomposition rates of roots in the 0–0.5 mm size class. We cut the roots of different diameter size classes into different lengths prior to the incubation (i.e. 2 mm for the finest roots and 5 mm for the coarser roots) and this may have also sped up decomposition rates of the finest roots relative to coarser roots on day one of the incubation. The greater fungal:bacterial ratio in soils amended with the coarsest roots, compared to soils with the finest roots suggests that a greater amount of easily

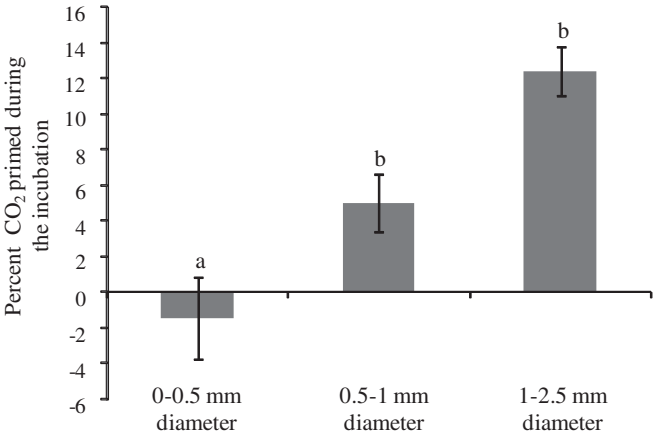

Fig. 4. The total percentage of soil organic carbon (SOC) respiration (i.e. priming) relative to total C respiration over a 90-day incubation of soils amended with *Panicum virgatum* roots of three root diameter size classes (i.e. 0–0.5 mm, 0.5–1 mm and 1–2.5 mm), and averaged across the cultivars included in the ^{13}C calculations. Values are means ± SE ($n = 8$ for the 0.5–1 mm and 1–2.5 mm diameter size classes, and n = 4 for the 0–0.5 mm diameter size classes). Different letters show statistically significant differences among cultivars ($P \leq 0.05$).

decomposable C is also present in the finest roots compared to the coarsest roots in the longer term.

Cultivar had no significant effect on SOC decomposition, but when averaged across cultivars, root diameter size class differentially affected priming of SOC. Decomposition of roots in the 0–0.5 and 0.5–1 mm size class led to a reduction in SOC decomposition on day one, indicating that these roots were preferentially used by

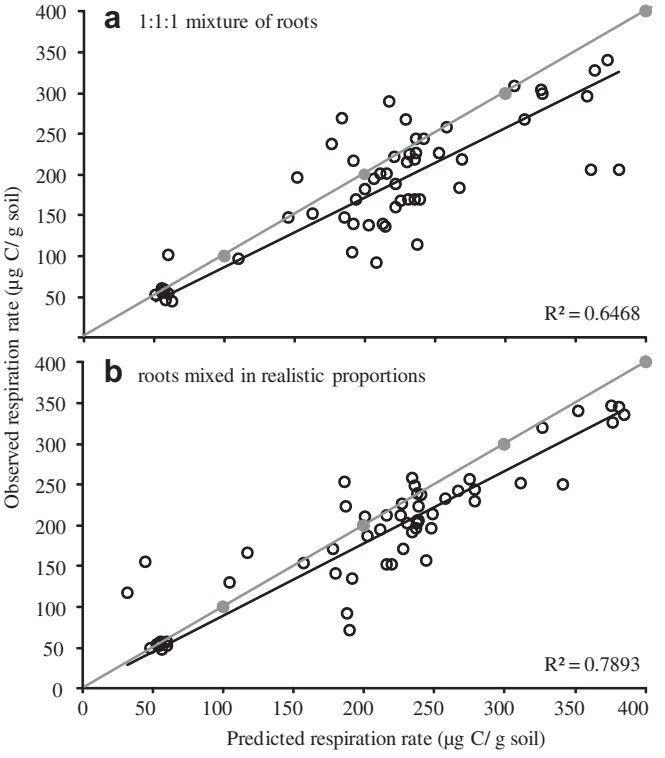

Fig. 5. Difference between 'predicted' respiration rates (weighted average of decomposition of individual root diameter size classes (i.e. 0–0.5 mm, 0.5–1 mm and 1–2.5 mm)) and observed respiration rates of roots of the three diameter size classes decomposed in a mixture: (a) when roots were mixed in a 1:1:1 ratio across time compared to a 1:1 line (in gray); (b) when roots were mixed in a realistic proportions across time compared to a 1:1 line (in gray).

soil microbes, but did not stimulate SOC decomposition. On days three, seven and fifteen of the incubation all roots positively promoted SOC decomposition, but overall roots in the 1–2.5 mm size class stimulated SOC decomposition rates more than the finer roots. The finest roots in the switchgrass root systems were predominantly first order roots, which should turnover frequently (Wells and Eissenstat, 2001; Tierney and Fahey, 2002; Matamala et al., 2003; Guo et al., 2008). Thus, under field conditions, we might expect a steady supply of these fine roots to soil. The differential impacts of root diameter size class on SOC decomposition rates suggest that root architecture may be an important trait for predicting soil C sequestration, and support the idea that a mechanistic framework, based on plant traits that drive soil C inputs and outputs would be helpful for understanding soil C sequestration (De Deyn et al., 2008).

The most labile roots in a root system may prime decomposition of more recalcitrant roots, leading to synergistic effects on total root system decomposition rates. However, this phenomenon has never been examined even though roots of different diameter size classes turnover simultaneously in soil (Guo et al., 2008). First, to assess whether a mixture of roots of different diameter size classes enhanced root decomposition in a non-additive way, we decomposed a 1:1:1 ratio mixture of the three root diameter size classes. Second, to test whether the distribution of root size classes in a root system (i.e. root architecture) affects overall root decomposition rates, we decomposed roots of the three diameter size classes mixed in realistic proportions. However, neither mixture altered overall root decomposition rates. Apparently, differences in decomposition among roots from different diameter size classes were too subtle to induce priming effects. A similar effect in aboveground litter mixtures has been observed by Hoorens et al. (2002) and Meier and Bowman (2008). Our data suggest that inputs of the finest roots relative to coarser roots are important to root and SOC decomposition rates, but these root inputs are not likely to stimulate decomposition rates beyond additive predicted values.

In our incubation study, we used non-living roots; hence, root exudates were not considered. Root exudates released from live roots can induce positive priming effects of up to 300% (Cheng et al., 2003). By using non-living roots we assessed the possible effect of root turnover on priming of SOC and we expect that live roots would have induced greater priming effects. We also expect that a greater proportion of very fine roots in a living root system (i.e. greater specific root length) would enhance the surface area of roots actively releasing exudates, and thus living roots with a high specific root length may induce priming of SOC to a greater extent than living roots with a lower specific root length.

4.3. Conclusion

We conclude that genetic variability among switchgrass cultivars shapes root architecture, root C:N ratios, root and SOC decomposition rates and soil microbial communities. Subtle cultivar differences in root decomposition rates within root diameter size classes could not be explained by root C:N ratios or by shifts in the soil microbial community. Different diameter roots affected SOC decomposition differentially, suggesting that the relative abundance of roots of different diameter size classes is a plant trait that can significantly influence SOC decomposition processes. Given that climate and atmospheric changes may alter the relative abundance of roots of different diameters (Meier and Leuschner, 2008; Iversen, 2010) and their turnover rates (Meier and Leuschner, 2009), our findings suggest shifts in root diameter size classes are likely to impact net soil C sequestration.

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