

# Root Traits and Carbon Input in Field-Grown Sweet Pearl Millet, Sweet Sorghum, and Grain Corn

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## ABSTRACT

Little information exists on root morphological characteristics of agricultural crops under field conditions, which can be a major determinant of plant N uptake efficiency and C input to soil. Sweet pearl millet [*Pennisetum glaucum* (L.) R.BR.] and sweet sorghum [*Sorghum bicolor* (L.) Moench] are envisioned as energy crops in eastern Canada, to complement corn starch ethanol. The aims of this study were to characterize and compare root biomass and root traits of field-grown sweet pearl millet, sweet sorghum, and grain corn (*Zea mays* L.), and to estimate their annual C input to soil. At two sites in eastern Canada, root samples recovered from 30-cm deep soil cores in sandy loams were weighed and scanned. Image analysis was performed with the WinRhizo software. Roots and shoots were analyzed for C concentration. Estimated C input to soil at harvest was higher for corn (243 g C m<sup>-2</sup>) than for sorghum and millet (197 and 131 g C m<sup>-2</sup>, respectively). In contrast, millet and sorghum had the greatest specific root lengths (83, 39, and 22 m g<sup>-1</sup> for millet, sorghum, and corn, respectively), and a larger contribution of very fine roots (<0.5 mm diam.) to the total root surface (60–63% for millet and sorghum, and 45–55% for corn). The longer and finer roots of millet and sorghum could contribute to their high N uptake efficiency. However, compared to grain corn, their lower C input to soil needs to be recognized to ensure a balanced C budget.

THE POTENTIAL to grow sweet pearl millet and sweet sorghum as energy crops has recently been investigated in eastern Canada (Bouchard et al., 2011; Leblanc et al., 2012; Crépeau et al., 2013; Dos Passos Bernardes et al., 2015; Thivierge et al., 2015a), as these annual grasses could complement or replace corn starch for ethanol production. Both species produced high dry matter and water-soluble carbohydrate yields with low N requirements (78–91 kg N ha<sup>-1</sup>) (Leblanc et al., 2012; Thivierge et al., 2015a). Using <sup>15</sup>N-labeled fertilizer, Thivierge et al. (2015b) demonstrated that sweet pearl millet and sweet sorghum could recover 54 to 82% of the applied mineral N, which is higher than values generally reported for corn (28–60%) in eastern Canada (Reddy and Reddy, 1993; Liang and MacKenzie, 1994; Tran et al., 1997; Stevens et al., 2005; Nyiraneza et al., 2010).

The high efficiency of sweet pearl millet and sweet sorghum to recover applied fertilizer N, also termed N uptake efficiency, could be related to specific traits of their rooting system. Indeed, the crop's capacity to compete for soil N relies on root morphological characteristics, such as root diameter, length, and surface (Eissenstat, 1992; Oikeh et al., 1999; Wang et al., 2005; Cantarel et al., 2015), the finest roots being predominantly involved in nutrient absorption (Eissenstat, 1992; Pallant et al., 1993; Jackson et al., 1997; Craine et al., 2003). Since studying root morphology is time-consuming and labor intensive (Dowdy et al., 1995; Nickel et al., 1995; Costa et al., 2002; Monti and Zatta, 2009), little information exists on root morphological characteristics of agricultural crops, particularly under field conditions. Indeed, most studies were performed with potted soils or hydroponic systems, in which altered environmental conditions induce modifications to root traits (Mengel and Barber, 1974; Böhm, 1979; Darrah, 1993; Useche and Shipley, 2010).

Besides their role in nutrient uptake, roots constitute a major source of C for soil (Rasse et al., 2005), and root biomass might be a good indicator of crop C input to soil (Monti and Zatta, 2009). In addition to the root biomass itself, C input

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**Abbreviations:** BS, Boreal Shield ecozone; C<sub>E</sub>, carbon from extra-root material; CEC, cation exchange capacity; CHU, corn heat unit; C<sub>P</sub>, carbon from agricultural product; C<sub>R</sub>, carbon from roots; C<sub>S</sub>, carbon from stover; DM, dry matter; HI, harvest index; MWP, Mixedwood Plains ecozone; RLD, root length density; SRL, specific root length; SEM, standard error of the means; SOC, soil organic carbon; S/R, shoot to root ratio.

Published in Agron. J. 108:459–471 (2016)

doi:10.2134/agronj2015.0291

Received 18 June 2015

Accepted 2 Nov. 2015

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also arises from root exudation and root turnover during the growing season (Buyanovsky and Wagner, 1986; Balesdent and Balabane, 1996; Bolinder et al., 1997, 1999). It has been demonstrated that a larger proportion of root-derived C (root and extra-root) is retained in soil organic matter than shoot-derived C (Balesdent and Balabane, 1996; Bolinder et al., 1999; Rasse et al., 2005; Kätterer et al., 2011). In grain corn, root biomass contributes from 1.5 to 3.4 Mg C ha<sup>-1</sup> yr<sup>-1</sup> to soil (Buyanovsky and Wagner, 1986; Balesdent and Balabane, 1996; Qian and Doran, 1996; Johnson et al., 2006; Chang et al., 2014). By including extra-root C, the average contribution to soil C was estimated to 4.0 Mg C ha<sup>-1</sup> yr<sup>-1</sup> for grain corn and 1.7 Mg C ha<sup>-1</sup> yr<sup>-1</sup> for grain sorghum in the United States (Johnson et al., 2006).

Grain corn contributes to soil an additional 3.2 to 4.2 Mg C ha<sup>-1</sup> yr<sup>-1</sup> through corn stover and cobs (Balesdent and Balabane, 1996; Zan et al., 2001; Sainju et al., 2005a; Johnson et al., 2006; Chang et al., 2014), when considering that approximately 50% of the aboveground fixed C remains in the field at harvest as crop residues (Whitman et al., 2011). By contrast, the harvest of sweet pearl millet or sweet sorghum implies the almost complete removal of aboveground biomass, since it is harvested as would be corn silage. Consequently, concerns about soil C and nutrient budgets for sorghum and sweet sorghum have been raised by some authors (Doran et al., 1984; Prother and Staggenborg, 2010; Han et al., 2011). Annual C inputs from the rooting systems of sweet pearl millet and sweet sorghum must be estimated to determine how it may compensate for the removal of aboveground biomass.

This study aimed at (i) determining the root biomass and C input of grain corn, sweet pearl millet, and sweet sorghum at harvest, and at (ii) gaining knowledge of root traits in these species (root diameter, length, and surface) at the flowering stage, which could provide insights to their high N uptake efficiency. The main hypotheses tested were that: (i) grain corn has a greater root biomass and a greater C input to soil than sweet pearl millet and sweet sorghum, at harvest, and that (ii) sweet pearl millet and sweet sorghum have a greater root length density (RLD), a greater specific root length (SRL), and a greater proportion of the total root surface accounted for by very fine roots (<0.5 mm in diameter) than grain corn, at flowering.

## METHODOLOGY

### Sites and Species Description

This study was performed at two experimental sites located in two different ecozones of Canada (ESWG, 1995). The first site, located at Sainte-Anne-de-Bellevue (Québec, Canada,

45°26' N, 73°56' W), is part of the Mixedwood Plains ecozone (hereafter identified as MWP site) and generally accumulates 2901 to 3100 corn heat units (CHU) during the growing season (Atlas agroclimatique du Québec, 2012). Corn heat units are a climatic index, calculated daily as per Brown and Bootsma (1993):

$$\text{CHU} = [1.8(T_{\min} - 4.4) + 3.33(T_{\max} - 10) - 0.084(T_{\max} - 10)^2]/2$$

where  $T_{\min}$  is the daily minimum temperature, in Celsius, and is set at 4.4°C if it is less than 4.4°C; and  $T_{\max}$  is the daily maximum temperature, in Celsius, and is set at 10°C if it is less than 10°C. At a specific location, CHU accumulation is the sum of daily CHU during the growing season. The second site, located at Saint-Augustin-de-Desmaures (Québec, Canada, 46°44' N, 71°31' W), accumulates 2501 to 2700 CHU during the growing season (Atlas agroclimatique du Québec, 2012) and is part of the Boreal Shield ecozone (hereafter identified as BS site). Soil types were a St. Bernard sandy loam (coarse-loamy, mixed, nonacid, calcareous, frigid Eutrochrept) at the MWP site, and a St. Antoine sandy loam (fine-loamy, mixed, acid, frigid Haplorthod) at the BS site. Selected soil characteristics are detailed in Table 1. The mean annual air temperature (1981–2010) at MWP and BS sites are 6.8 and 4.2°C, respectively, and the mean annual precipitation is 1000 and 1190 mm (Environment Canada, 2015). Daily air temperature and rainfall for each growing season are indicated in Fig. 1.

At both sites, sweet pearl millet hybrid CSSPM7 (AERC Inc., Delhi, ON, Canada), sweet sorghum hybrid CSSH45 (AERC Inc., Delhi, ON, Canada), and grain corn were grown for two successive growing seasons (2011 and 2012). Different grain corn hybrids were chosen for each site: hybrid DKC 43-27, 2800 CHU (Dekalb, Monsanto Canada Inc., Winnipeg, MA, Canada), was sown at the MWP site, and hybrid 39D97, 2350 CHU (Pioneer, DuPont, Chatham, ON, Canada), at the BS site. Corn hybrids were resistant to glyphosate [N-(phosphonomethyl)glycine] and glufosinate [(RS)-2-Amino-4-(hydroxy(methyl)phosphonoyl)butanoic acid], and to the European corn borer (*Ostrinia nubilalis*). Corn seeds also received a systemic insecticide treatment with thiamethoxam {3-[(2-Chloro-1,3-thiazol-5-yl)methyl]-5-methyl-N-nitro-1,3,5-oxadiazinan-4-imine}. For the two consecutive growing seasons, crops were grown on different plots in adjacent fields. The previous crops were spring barley (*Hordeum vulgare* L.) for both years at BS, and corn in 2011 and oat (*Avena sativa* L.) in 2012 at MWP. No irrigation was used.

Table 1. Selected soil characteristics of the 0- to 0.2-m layer at the two experimental sites.

Site	Year	Sand	Clay	SOC†	CEC†	pH‡	P§	K§
		g kg <sup>-1</sup>			mol <sub>c</sub> kg <sup>-1</sup>		kg ha <sup>-1</sup>	
Mixedwood Plains	2011	620	190	12.8	14.7	6.4	172	193
	2012	620	150	18.0	12.9	6.6	192	204
Boreal Shield	2011	560¶	210	19.1	16.7	6.6	434	352
	2012	560¶	210	16.2	20.0	6.7	356	504

† SOC, soil organic carbon content, determined by dry combustion; CEC, cation exchange capacity.

‡ pH, 1:1 soil/water ratio.

§ Mehlich-3 available P and K.

¶ Soil texture at the Boreal Shield site was determined once in 2010. All the other soil characteristics were determined every year at both sites.

## Experimental Set-Up and Crop Management

A completely randomized design with four replications was set at each site, with species as the only factor. Plots of sweet pearl millet and sweet sorghum included seven 5-m rows at MWP (area of 6.3 m<sup>2</sup>), and nine 6-m rows (area of 9.7 m<sup>2</sup>) at BS. Row spacing was 0.18 m. Plots of grain corn included four 5-m rows at MWP (area of 15.2 m<sup>2</sup>), and four 6-m rows (area of 18.2 m<sup>2</sup>) at BS. Row spacing was 0.76 m.

Seedbed preparation consisted of moldboard plowing in the fall, harrowing in the spring to stimulate weed germination, and a final harrowing to kill weeds before seeding. The seeding rate was 10 kg ha<sup>-1</sup> of pure live seeds for sweet pearl millet and sweet sorghum, and 80,000 grains ha<sup>-1</sup> for corn at both sites. Seeding was performed at a depth of 2.5 cm for sweet pearl millet and sweet sorghum, as soon as soil temperature reached 12°C (AERC, 2014), using a Wintersteiger plot seeder (Wintersteiger, Salt Lake City, UT), and at a depth of 5 cm for corn, as soon as

soil temperature reached 10°C (FADQ, 2013), using a NG Plus mounted four-row planter (Monosem Inc., Edwardsville, KS).

Calcium ammonium nitrate (27–0–0) was applied to sweet pearl millet and sweet sorghum plots at a rate of 80 kg N ha<sup>-1</sup>, from which 40 kg N ha<sup>-1</sup> were broadcast and incorporated into the top 5 cm of soil with a harrow before seeding, and 40 kg N ha<sup>-1</sup> were sidedressed at the four-leaf stage. This N rate had been found to maximize water-soluble carbohydrate yield at both sites in sweet pearl millet (Leblanc et al., 2012; Thivierge et al., 2015a) and in sweet sorghum (Thivierge et al., 2015a). In grain corn, calcium ammonium nitrate (27–0–0) was applied at a total rate of 150 kg N ha<sup>-1</sup> at the MWP site and 120 kg N ha<sup>-1</sup> at the BS site, according to local recommendations (CRAAQ, 2010); 50 kg N ha<sup>-1</sup> at the MWP site and 30 kg N ha<sup>-1</sup> at the BS site were applied at planting with the seeder, whereas the rest (100 kg N ha<sup>-1</sup> at the MWP site and 90 kg N ha<sup>-1</sup> at the BS site) was sidedressed at the four-leaf stage.

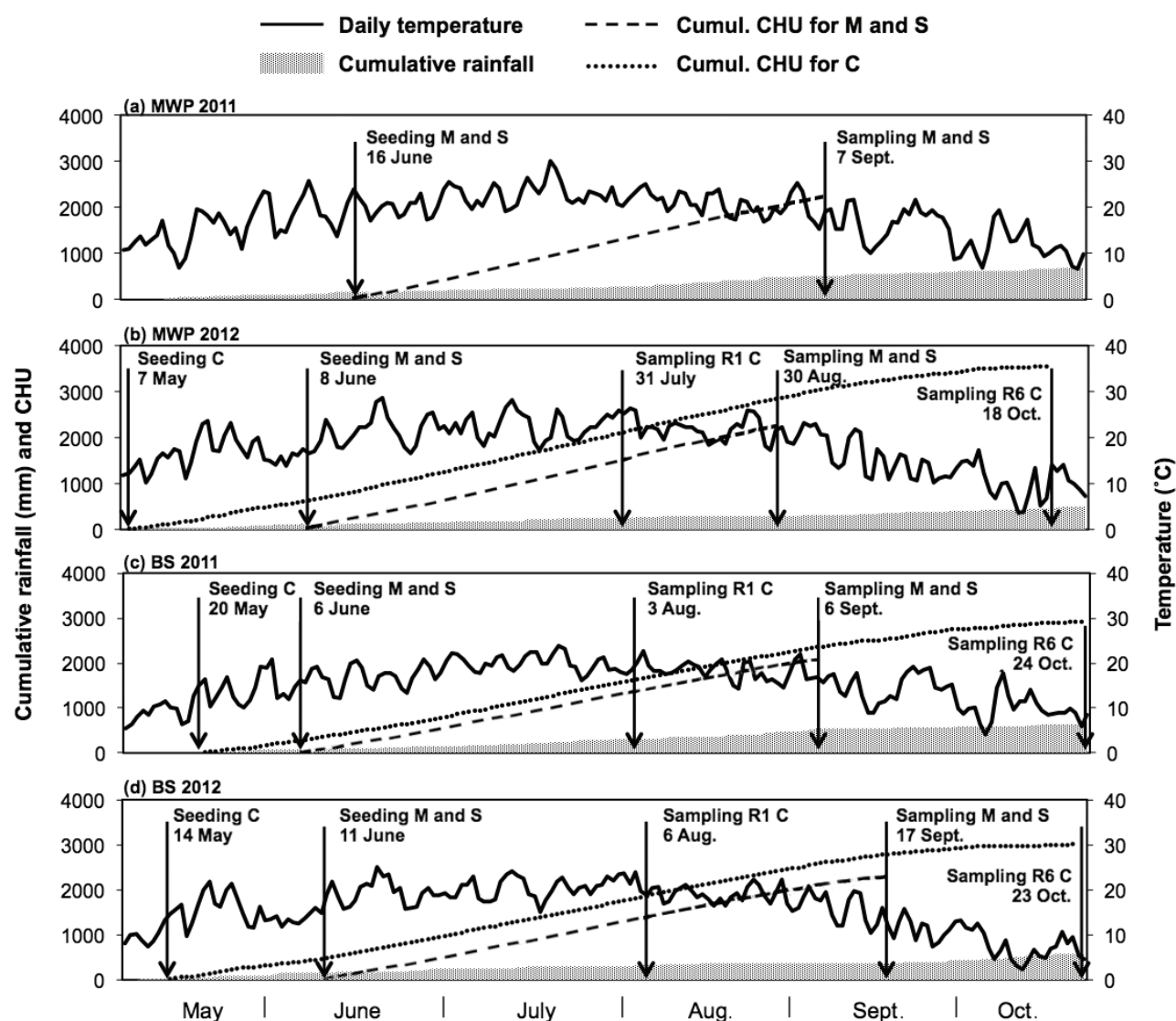


Fig. 1. Daily average air temperatures (°C), cumulative rainfall (mm), and cumulative corn heat units (CHU) from seeding to harvest for each species, for 2011 and 2012, at (a, b) the Mixedwood Plains (MWP) and (c, d) the Boreal Shield (BS) sites. Arrows indicate seeding and root sampling dates for grain corn (C) at two growth stages (R1 and R6), and for sweet pearl millet (M), and sweet sorghum (S). A mistake with the application of herbicide in 2011 at the MWP site destroyed grain corn. Therefore, only millet and sorghum CHU are depicted in Fig. 1a. For the MWP site, air temperature and rainfall were retrieved from the Pierre Elliott Trudeau airport weather station, located at approximately 15 km from the experimental field (45°28' N, 73°45' W). Air temperature and rainfall were monitored onsite at the BS site.



Phosphorus (triple superphosphate, 0–46–0) and potassium (potassium chloride, 0–0–60) were applied at seeding for the three species, based on soil analyses and local recommendations (CRAAQ, 2010). Therefore, for sweet pearl millet and sweet sorghum, 40 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> and 60 kg K<sub>2</sub>O ha<sup>-1</sup> were applied each year at the MWP site, whereas 20 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> and 40 kg K<sub>2</sub>O ha<sup>-1</sup> were applied at the BS site in 2011, and 40 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> and 60 kg K<sub>2</sub>O ha<sup>-1</sup> in 2012. For grain corn, 50 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> and 75 kg K<sub>2</sub>O ha<sup>-1</sup> were applied each year at the MWP site, whereas 40 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> and 40 kg K<sub>2</sub>O ha<sup>-1</sup> were applied each year at the BS site.

In sweet pearl millet and sweet sorghum, bentazone [3-isopropyl-1H-2.1.3-benzothiadiazin-4(3H)-one 2.2-dioxide] was applied at a rate of 1.08 kg a.i. ha<sup>-1</sup> between the three- and five-leaf growth stages to suppress dicotyledonous weeds. Hand weeding was necessary in sweet sorghum plots at the 8- to 10-leaf stage at both sites, whereas the dense crop cover of sweet pearl millet repressed most of the weeds and no weeding was necessary. In corn, glyphosate was applied at a rate of 0.89 kg a.i. ha<sup>-1</sup> between the four- and six-leaf stages.

### Plant and Root Sampling and Analyses

Roots were sampled at pre-determined growth stages for each species. Growth stages were identified as per Vanderlip (1993) for sweet pearl millet and sweet sorghum, and Ritchie et al. (1992) for corn. The stage was considered to be reached when 50% or more of the plants in the plot were at or beyond that stage (Ritchie et al., 1992; Vanderlip, 1993).

Corn root sampling was done at two growth stages (Fig. 1). The first sampling was done at the beginning of the reproductive stage (stage R1, silking, 75–85 d after seeding), as it was demonstrated that the root system is at its maximum length at this stage (Foth, 1962; Mengel and Barber, 1974; Wiesler and Horst, 1994). The second root sampling was done at physiological maturity (stage R6, 157–162 d after seeding; Ritchie et al., 1992), and the aboveground biomass (grains and stover) of corn was harvested at this date on two center rows of 5 m in length. A mistake with the herbicide application in 2011 at the MWP site destroyed corn and therefore, results for grain corn at the MWP site are those of the four replications of 2012 only. At the two root sampling dates for corn, six soil cores per plot were taken using an 8-cm diam. stainless steel auger to a depth of 30 cm: two cores on the row (R) (on a plant cut at 2-cm stubble height; CRAAQ, 2010), two cores in the middle of the inter-row (IR), and two in an intermediate position (IP). The values from the three sampling positions were averaged [(R + IR + IP)/3], as per Bolinder et al. (1997). As the plants were cut at 2-cm stubble height, which was the closer to the soil surface that it was possible to get, most parts of the crown and adventitious roots were not included as root biomass.

For sweet pearl millet and sweet sorghum, roots were sampled only once (Fig. 1), at the half-blooming stage (Stage 6; Vanderlip 1993), as root length is at its maximum at that stage in grain sorghum (Robertson et al., 1993; Pritchard et al., 2006). Half blooming was reached on 75% of the plants at the MWP site (approximately 83 d after seeding; Fig. 1) and on 50% of the plants at the BS site (approximately 95 d after seeding; Fig. 1), and this was the farthest growth stage possible to reach during the two growing seasons to avoid lodging

problems. Six soil cores (0–30-cm depth) per plot were taken for root sampling: three on the row (R) (on a plant cut at 2-cm stubble height; CRAAQ, 2010) and three between rows (BR) (Moroke et al., 2005; Sainju et al., 2005b). The values from the two sampling positions were averaged [(R + BR)/2], as per Buyanovsky and Wagner (1986). Aboveground biomass of sweet pearl millet and sweet sorghum was harvested on five center rows of 3.5 m in length.

Fresh aboveground biomass from all three species was weighed. A 500-g subsample was dried at 55°C until constant weight for determination of dry matter (DM) concentration, ground (0.15 mm), and analyzed for total N and C concentrations by dry combustion (LECO CNS-1000, Leco Corp., St. Joseph, MI). Corn stover and grains were analyzed separately.

Each soil core was divided into two layers: 0 to 15 and 15 to 30 cm. Each 15-cm soil core was individually soaked in 500 mL of sodium hexametaphosphate solution (100 g L<sup>-1</sup>) for 16 h to disperse soil aggregates (Bolinder et al., 1997, 2002; Moroke et al., 2005). Separation of roots from soil was performed using a hydropneumatic elutriation washing machine (Smucker et al., 1982) connected onto a 760-μm sieve (Böhm, 1979; Bolinder et al., 1997, 2002). Residual sediments were inspected for roots before disposal. Roots were then transferred onto a 250-μm sieve and gently washed with water to remove any remaining mineral particles. Roots were conserved in a methanol solution (10% v/v) at 4°C for a maximum of 7 d (Dowdy et al., 1995). On the day of analysis, they were transferred onto a 250-μm sieve, rinsed with water, and stained by soaking 2 h in a 0.5 g L<sup>-1</sup> Neutral Red (3-Amino-7-dimethylamino-2-methylphenazine hydrochloride, Basic Red 5, Toluylen red) solution (Sigma-Aldrich Co., St. Louis, MO). Finally, roots were separated from remaining non-root debris by flotation (Bolinder et al., 1997, 2002).

Clean roots from sweet pearl millet, sweet sorghum, and corn (stage R1 only) were carefully placed on a 30 by 40-cm plastic plate, and covered with water until all roots were immersed (Dowdy et al., 1995; Costa et al., 2002; Monti and Zatta, 2009). Roots were scanned (Epson Expression 10000XL, Epson Canada, Markham, ON) at a 300 dots per inch (dpi) resolution (Bauhus and Messier 1999; Costa et al., 2002). Image analysis was performed using the WinRhizo software (Regent Instruments Inc., Québec, QC). After preliminary tests, a length-to-diameter ratio of 6:1 was settled as a threshold to distinguish root from non-root materials, and to reject the latter. The image analysis system separated roots according to their diameter, in 40 classes from 0- to 4-mm diam., with 0.1-mm increments. For each class, the outputs resulting from the image analysis were root length and root surface. As in Böhm (1979), very fine roots were defined as roots with less than 0.5 mm in diameter, but excluding root hair. With a 300 dpi resolution, the minimum root diameter that the WinRhizo software could detect was of 0.085 mm. For this reason, root hair, with 0.003 to 0.007 mm of diameter (Manske and Vlek, 2002), were not accounted for. For each soil layer (0–15 and 15–30 cm of depth), the results from the six soil cores per plot were averaged (Bolinder et al., 1997).

Finally, all root samples, including those from stage R6 of corn, were dried at 50°C until constant weight. For each plot and sampling stage, roots from the same soil layer were pooled,

ground (ball mixer-mill MM400, Retsch, Germany), and divided into two subsamples. Total N and C concentrations were determined by dry combustion (LECO CNS-1000, Leco Corp., St. Joseph, MI) on the first subsample; ash content was determined on the second subsample by heating root biomass to 600°C until constant weight using a thermogravimetric analyzer (TGA701, Leco Corp., St. Joseph, MI). Root biomass was expressed on an ash-free dry mass basis (Kätterer and Andrén, 1999; Bolinder et al., 2002).

## Calculations and Statistical Analyses

The harvest index (HI) for grain corn was calculated as the ratio of grain yield to total aboveground yield [dry grain / (dry grain + cob + stover + most of the crown)] (Hay, 1995). The shoot/root ratio (S/R ratio) for all species was obtained by dividing the total dry aboveground biomass (dry grain + cob + stover + most of the crown) by the total dry root biomass (0–30 cm, ash-free) at harvest (Bolinder et al., 1997). Root biomass did not include any extra-root material (i.e., root turnover and root exudates) but included a small part of the crown and adventitious roots, as plants were cut at 2-cm stubble height.

The total C fixed by crops at harvest, also termed net primary productivity, was calculated as per Bolinder et al. (2007):

$$\text{Total C fixed} = C_P + C_S + C_R + C_E$$

where  $C_P$  is the measured C content of agricultural product (all aboveground biomass for sweet pearl millet and sweet sorghum, and only grain for corn),  $C_S$  is the measured C content from stover (only applied to corn),  $C_R$  is the measured C content of roots, and  $C_E$  is the estimated C content derived from extra-root materials (root turnover and exudates). In the present study, extra-root C was assumed to be equivalent to 65% of  $C_R$  at harvest, on an annual basis (Bolinder et al., 2007, 2012). This is a conservative estimation, as many authors assumed that extra-root C was equivalent to 100% of  $C_R$ , or even more (Keith et al., 1986; Johansson, 1992; Swinnen et al., 1995; Rasse et al., 2005; Chang et al., 2014).

Bolinder et al. (1999) considered that 5% of silage corn aboveground biomass is left as stubble after harvest. Since harvest height of sweet pearl millet and sweet sorghum is similar to that of silage corn, we considered 5% of  $C_P$  to remain in the field at harvest, and 5% of  $C_S$  in the scenario where corn stover is harvested. The C input from sweet pearl millet and sweet sorghum at harvest was calculated as:

$$\text{C input from sweet pearl millet and sweet sorghum} = (0.05 \times C_P) + C_R + C_E$$

The C input from grain corn at harvest was calculated for two possible scenarios:

$$\begin{aligned} \text{C input from corn with stover exported} \\ = (0.05 \times C_S) + C_R + C_E \end{aligned}$$

$$\begin{aligned} \text{C input from corn with stover remaining} \\ \text{in the field} = C_S + C_R + C_E \end{aligned}$$

Root length density (RLD) was calculated as the total root length per unit of soil volume, and expressed as  $\text{cm cm}^{-3}$  (Dowdy et al., 1995; Oikeh et al., 1999). The specific root length (SRL) was taken as the ratio of root length to root biomass (Useche and Shipley, 2010) and expressed as  $\text{m g}^{-1}$ .

The uptake efficiency of the root absorbing surface was not measured. Darrah (1993) and Bindraban et al. (2015) showed that the efficiency of uptake per unit surface area of root varies in time for plants grown in soil and depends on soil conditions as N availability, N form ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ), pH, and interactions with other nutrients. Here, we assumed that over the growing season this parameter did not differ among species and was mainly driven by soil conditions.

Data were statistically analyzed separately for each site. Replications and years were considered random effects, whereas crop species was considered a fixed effect. All data were subjected to analysis of variance using the MIXED procedure in SAS (SAS Institute, 2003) for the dependent variables: aboveground biomass, root biomass, S/R ratio, RLD, SRL,  $C_P$ ,  $C_S$ ,  $C_R$ ,  $C_E$ , total fixed C, and C input. Data normality was verified using the UNIVARIATE procedure, and the Shapiro–Wilk test (Shapiro and Wilk, 1965) was used to determine whether the residuals were normally distributed. The homogeneity of variance was verified visually with graphics of residuals. Standard error of the means (SEM) is reported. Single-df contrasts were used to compare corn grain vs. sweet pearl millet and sweet sorghum, and to compare sweet pearl millet vs. sweet sorghum. Statistical significance was postulated at  $P \leq 0.05$ .

## RESULTS

### Biomass Partitioning in Plants and Carbon Input at Harvest

At the MWP site, total aboveground biomass at harvest (including stover and grains for corn) was similar among species, and averaged  $1779 \text{ g m}^{-2}$  (Table 2). At the BS site, the aboveground biomass of sweet pearl millet and sweet sorghum (average of  $1318 \text{ g m}^{-2}$ ) was lower than corn ( $1552 \text{ g m}^{-2}$ ). Harvest index for corn varied from 0.43 to 0.54 at the MWP site, and from 0.42 to 0.50 at the BS site. Average C concentrations of corn grains, cob, stover, and roots were 45.6, 47.4, 46.2, and 43.1% at MWP, respectively, and 45.6, 48.1, 47.3, and 41.2% at BS. The N concentrations of corn grains, cob, stover, and roots were 1.3, 0.7, 0.7, and 1.6% at MWP, respectively, and 1.2, 0.8, 0.9, and 1.5% at BS. For sweet pearl millet, average C concentrations of aboveground biomass and roots were 46.0 and 43.1% at MWP, and 45.8 and 43.5% at BS, while N concentrations were 0.8 and 1.9% at MWP, and 1.1 and 1.9% at BS. Finally, for sweet sorghum, average C concentrations of aboveground biomass and roots were 46.2 and 41.4% at MWP, and 45.8 and 42.9% at BS, while N concentrations were 0.8 and 1.8% at MWP, and 1.0 and 1.5% at BS.

Root biomass at harvest in the top soil layer (0–15 cm) was greater for corn than for sweet pearl millet and sweet sorghum ( $323$  vs.  $167 \text{ g m}^{-2}$ , averaged between sites), and greater for sweet sorghum than for sweet pearl millet ( $216$  vs.  $119 \text{ g m}^{-2}$ , averaged between sites; Table 2). For the 15- to 30-cm soil layer, corn still had the greatest root biomass at both sites, whereas there was no difference between sweet pearl millet and sweet sorghum. For all crop species, 87 to 93% of the total

**Table 2.** Aboveground biomass, root biomass (0–30-cm depth) and shoot to root ratio at harvest for sweet pearl millet, sweet sorghum, and grain corn grown on sandy loam soils at the Mixedwood Plains and the Boreal Shield sites (average of 2011 and 2012 at each site).

Site	Mixedwood Plains				Boreal Shield			
Variable	Aboveground dry biomass‡	Root dry biomass†		Shoot/root† ratio	Aboveground dry biomass‡	Root dry biomass†		Shoot/root† ratio
		0–15 cm	15–30 cm			0–15 cm	15–30 cm	
		g m <sup>-2</sup>				g m <sup>-2</sup>		
Species								
Sweet pearl millet	1683	111	16.9	13.2	1340	126	11.4	9.8
Sweet sorghum	1900	212	16.5	8.3	1296	219	13.4	5.6
Grain corn§	1754	325	30.7	4.9	1552	320	25.8	4.5
SEM¶	117.2	23.8	3.30	1.11	83.4	24.8	5.11	1.38
				<i>P</i> values				
Fixed effects								
Species	0.206	<0.001	0.003	<0.001	0.018	<0.001	0.022	0.001
Contrasts								
Corn vs. millet and sorghum	0.185	<0.001	0.001	<0.001	0.006	<0.001	0.019	<0.001
Millet vs. sorghum	0.170	<0.001	0.871	<0.001	0.603	0.002	0.136	0.009

† At harvest, ash-free. Root dry biomass did not include any extra-root material (i.e., root turnover and root exudates) but included a small part of the crown and adventitious roots, as plants were cut at 2-cm stubble height.

‡ Includes grains and stover in the case of corn.

§ A mistake with the application of herbicide in 2011 at the MWP site destroyed the grain corn. Therefore, data for grain corn at the MWP site are those of the four replications of 2012 only.

¶ SEM, standard error of means.

root biomass (0–30-cm depth) was found in the 0- to 15-cm soil layer at the MWP site, and 92 to 94% at the BS site. At both sites, the S/R ratio was the highest in sweet pearl millet, intermediate in sweet sorghum, and the lowest in grain corn (Table 2).

At the MWP site, there was no significant difference among species for the total amount of C fixed (average of 977 g C m<sup>-2</sup>) and for the amount of C found in the aboveground biomass (average of 818 g C m<sup>-2</sup>; Table 3). At the BS site, the values were similar between sweet pearl millet and sweet sorghum (average of 732 g m<sup>-2</sup> of total C fixed and 601 g m<sup>-2</sup> of aboveground C), but greater in corn (941 and 724 g C m<sup>-2</sup>, respectively; Table 3). This is in accordance with the greater aboveground dry matter yield reported for corn at the BS site (Table 2).

At both sites, the amount of C fixed into the root biomass at harvest in the 0- to 15-cm soil layer was greater for corn than for sweet sorghum and sweet pearl millet (127 vs. 71 g m<sup>-2</sup>, averaged between sites), and greater for sweet sorghum than for sweet pearl millet (92 vs. 51 g m<sup>-2</sup>, averaged between sites; Table 3). Similar trends were found in the 15- to 30-cm soil layer, except that the amount of C fixed into the root biomass was similar between sweet sorghum and sweet pearl millet. The estimated C input to the soil at the end of the growing season was greater with corn than with the other two species at both sites, even in the scenario where corn stover would be exported with the grains (244, 198, and 131 g C m<sup>-2</sup> for corn, sweet sorghum, and sweet pearl millet, respectively, averaged between sites; Table 3).

### Root Traits at Flowering

At the beginning of the reproductive stage, when root traits were measured, root biomass in the 0- to 15-cm soil layer differed among species at both sites and was greater for corn than for sweet sorghum and sweet pearl millet, and greater for sweet sorghum than for sweet pearl millet (Table 4). In contrast, root length density (RLD) in the 0- to 15-cm soil layer was greater for sweet pearl millet and sweet sorghum (8.9 cm cm<sup>-3</sup>,

averaged between species and sites) than for corn (5.1 cm cm<sup>-3</sup>, averaged between sites) at both sites, and was also greater for sweet pearl millet than for sweet sorghum at the BS site (Table 4). In the 15- to 30-cm layer, RLD was also higher for sweet pearl millet and sweet sorghum (average of 4.4 cm cm<sup>-3</sup>) than for corn (2.8 cm cm<sup>-3</sup>) at the MWP site, but was similar among species at the BS site (average of 3.4 cm cm<sup>-3</sup>). Specific root length (SRL), the ratio of root length to root dry mass, differed among species in the 0- to 30-cm soil layer at both sites (Table 4). Sweet pearl millet had the highest SRL (83 m g<sup>-1</sup> averaged between sites), followed by sweet sorghum (39 m g<sup>-1</sup>) and by corn (22 m g<sup>-1</sup>).

The total root surface (0–30-cm soil depth) was subdivided based on its distribution among root diameter classes ranging from <0.5 to 4 mm diam. (Fig. 2). At both sites, very fine roots (<0.5 mm diam.) accounted for a larger proportion of the total root surface in sweet pearl millet and sweet sorghum (60% to 63%) than in corn (45% to 55%). At the MWP site, all the larger root diameter classes (>0.5 mm) accounted for a greater proportion of total root surface in corn than in sweet pearl millet and sweet sorghum (Fig. 2a). The same differences were also observed for root diameter classes 0.5 to 1.0, 1.0 to 1.5, 3.0 to 3.5, and 3.5 to 4.0 mm at the BS site (Fig. 2b). Averaged across the three species, 68% of the total root surface (0–30-cm depth) was found in the top 15 cm of soil, at both sites.

## DISCUSSION

### Biomass Partitioning in Plants and Carbon Input at Harvest

The higher S/R ratios found in sweet pearl millet and sweet sorghum than in corn (Table 2) revealed dissimilarities in resource allocation between these species. Indeed, proportionally less resource was allocated to the rooting system of sweet pearl millet and sweet sorghum than corn. The S/R ratios measured for corn are in the range of values reported from a literature review by Bolinder et al. (2007), with a mean of 5.6.

Table 3. Carbon partitioning and estimated annual C input to the soil (0–30-cm depth) at harvest for sweet pearl millet, sweet sorghum, and grain corn grown on sandy loam soils at the Mixedwood Plains and the Boreal Shield sites (average of 2011 and 2012 at each site).

Variable	Mixedwood Plains										Boreal Shield				
	Site														
	Root biomass $C_R^\dagger$					C input to soil									
	Aboveground biomass $^\ddagger$ ( $C_P + C_S$ )	0–15 cm	15–30 cm	Extra-root $C_E^\ddagger$	Total C fixed $^\ddagger$	Corn stover left in field $^\S$	Corn stover exported $^\P$	Aboveground biomass $^\ddagger$ ( $C_P + C_S$ )	0–15 cm	15–30 cm	Extra-root $C_E^\ddagger$	Total C fixed $^\ddagger$	Corn stover left in field $^\S$	Corn stover exported $^\P$	C input to soil
g C m $^{-2}$															
Species															
Sweet pearl millet	864	48	7.1	36	955	134	134	609	54	5.0	39	706	128	128	
Sweet sorghum	803	88	6.5	62	961	199	199	592	95	5.5	65	758	196	196	
Grain corn#	786	132	11.7	94	1016	682	250	724	121	9.3	86	941	608	237	
SEM $^{\dagger\dagger}$	57.2	9.8	1.29	6.7	73.8	25.2	20.2	38.5	8.3	1.65	5.5	37.7	22.3	13.0	
<i>P</i> values															
Fixed effects															
Species	0.328	<0.001	0.007	<0.001	0.700	<0.001	<0.001	0.008	<0.001	0.040	<0.001	<0.001	<0.001	<0.001	
Contrasts															
Corn vs. millet and sorghum	0.371	<0.001	0.002	<0.001	0.421	<0.001	0.002	0.002	<0.001	0.024	<0.001	<0.001	<0.001	<0.001	
Millet vs. sorghum	0.204	<0.001	0.575	<0.001	0.908	0.009	0.003	0.679	<0.001	0.308	<0.001	0.190	0.004	<0.001	

$^\dagger$   $C_P$ , measured C content from agricultural product (all aboveground biomass for sweet pearl millet and sweet sorghum, and only grain for corn);  $C_S$ , measured C content from stover (only applied to corn);  $C_R$ , measured C content of roots;  $C_E$ , estimated C content from extra-root material (assuming that the equivalent of 65% of the C from root biomass is released as extra-root C, e.g., Bolinder et al., 2007).

$^\ddagger$  Total C fixed =  $C_P + C_S + C_R + C_E$ .

$^\S$  C input from corn (stover left in field):  $C_S + C_R + C_E$ .

$^\P$  C input from corn (stover exported):  $0.05 C_S + C_R + C_E$ .

# A mistake with the application of herbicide in 2011 at the MWP site destroyed grain corn. Therefore, data for grain corn at the MWP site are those of 2012 only.

$^{\dagger\dagger}$  SEM, standard error of means.



**Table 4.** Root dry biomass, root length density, and specific root length at the flowering stage for sweet pearl millet, sweet sorghum, and grain corn grown on sandy loam soils at the Mixedwood Plains (MWP) and the Boreal Shield (BS) sites (average of 2011 and 2012 at each site).

Site	Mixedwood Plains					Boreal Shield				
	Total root dry biomass		Root length density		Specific root length	Total root dry biomass		Root length density		Specific root length
Variable	0–15 cm	15–30 cm	0–15 cm	15–30 cm	0–30 cm	0–15 cm	15–30 cm	0–15 cm	15–30 cm	0–30 cm
Units†	g m <sup>-2</sup>		cm cm <sup>-3</sup>		m g <sup>-1</sup>	g m <sup>-2</sup>		cm cm <sup>-3</sup>		m g <sup>-1</sup>
Species‡										
Sweet pearl millet	220	33.6	9.7	4.3	84.4	250	22.7	10.7	3.6	81.1
Sweet sorghum	421	32.7	9.0	4.4	46.1	437	26.6	6.3	3.2	31.2
Grain corn§	629	40.4	5.4	2.8	18.1	470	27.9	4.8	3.4	25.0
SEM¶	48.0	5.92	0.62	0.38	5.03	41.7	3.69	0.48	0.24	6.17
<i>P</i> values										
Fixed effects										
Species	<0.001	0.445	<0.001	<0.001	<0.001	<0.001	0.360	<0.001	0.170	<0.001
Contrasts										
Corn vs. millet and sorghum	<0.001	0.219	<0.001	<0.001	<0.001	0.003	0.339	<0.001	0.963	<0.001
Millet vs. sorghum	<0.001	0.846	0.120	0.876	<0.001	<0.001	0.289	<0.001	0.064	<0.001

† Units: g m<sup>-2</sup>, g of root dry mass (ash-free) per m<sup>2</sup> of soil; cm cm<sup>-3</sup>, cm of root length per cm<sup>3</sup> of soil volume; m g<sup>-1</sup>, m of root length per g of root biomass (ash-free).

‡ At flowering (at stage 6, mid-bloom, for sweet pearl millet and sweet sorghum; at stage R1, silking, for grain corn), ash-free.

§ A mistake with the application of herbicide in 2011 at the MWP site destroyed grain corn. Therefore, data for grain corn at the MWP site are those of 2012 only.

¶ SEM, standard error of means.

We were not able to find S/R values at flowering or at harvest for sweet pearl millet and sweet sorghum in the literature. However, in Kansas, Piper and Kulakow (1994) measured a S/R ratio of 11.7 at harvest for grain sorghum, although no indication about the root sampling depth was given. The S/R ratio provides an estimate of the partitioning of photosynthates between roots and shoots. This partitioning may vary according to various stress factors, such as decreased soil fertility or water stress (Amos and Walters, 2006). The S/R ratio also depends strongly on root sampling protocol (Bolinder et al., 2007), and therefore must be interpreted with care. The S/R ratios >1 measured for corn, sweet pearl millet, and sweet sorghum grown in eastern Canada indicated that these annual crops invested the majority of their resources in the aboveground biomass. This contrasts with perennial crops that invest more in their root system, as indicated by S/R ratios ranging from 0.44 to 0.86 in eastern Canada, for established perennial forage grasses (Bolinder et al., 2002).

The proportion of the total root biomass (0–30-cm depth) found in the 0- to 15-cm soil layer (87–94% among sites and species, Table 2) is close to the value of 85% reported by Crozier and King (1993) for grain corn in North Carolina. By contrast, this proportion was of 70% for small-grain cereals (Bolinder et al., 1997) and 61% for perennial grasses on the establishment year (Bolinder et al., 2002). The presence of a part of the crown and adventitious roots at or near the soil surface in corn, sweet sorghum, and sweet pearl millet might explain the larger proportion of root biomass found in the top 15 cm of soil when compared to small-grain cereals or perennial grasses. It stands to reason that corn, sweet pearl millet, and sweet sorghum grew roots deeper than 30 cm. Indeed, Chang et al. (2014) measured 895 kg ha<sup>-1</sup> of corn root biomass between 30- and 75-cm depth in South Dakota. For sorghum, Sainju et al. (2005a) found

160 kg ha<sup>-1</sup> of root biomass between 30- and 120-cm depth in Georgia, and Stone et al. (2001) counted roots down to 1.8 m in Kansas, but without measuring the biomass. Therefore, the 0- to 30-cm sampling depth in the present study likely resulted in an underestimation of total root biomass and C input. However, in the above cited studies (Sainju et al., 2005a; Chang et al., 2014), 81 to 83% of the root biomass found in the 0- to 60-cm soil layer was present in the top 30 cm, suggesting that our underestimation was reasonable. We therefore assume that the differences that we observed between species would still be significant with a deeper sampling depth.

The aboveground C measured at harvest for corn (Table 3) was similar to values reported in eastern Canada (715 g C m<sup>-2</sup>; Zan et al., 2001), in northern France (730 g C m<sup>-2</sup>; Balesdent and Balabane, 1996) and in Georgia (638 g C m<sup>-2</sup>; Sainju et al., 2005a). Such values could not be found in the literature for sweet pearl millet or sweet sorghum, but a literature review from Johnson et al. (2006) reported an average value of 281.4 g C m<sup>-2</sup> for grain sorghum in the United States. This is much lower than the aboveground biomass C measured in the present study for sweet sorghum and sweet pearl millet (Table 3). The total amount of root C in corn was similar to estimates reported in France (152 g C m<sup>-2</sup> in the 0–35-cm soil layer; Balesdent and Balabane, 1996), while greater values were reported in Nebraska (308 g C m<sup>-2</sup> in the 0- to 70-cm soil layer; Qian and Doran, 1996) and Missouri (154–340 g C m<sup>-2</sup> in the 0–50-cm soil layer; Buyanovsky and Wagner, 1986). Deeper soil samples and greater corn yields in those studies likely explain the larger estimates of C inputs from roots.

Even in the scenario where corn stover would be exported with the grains, estimates of C input to soil from corn at the end of the growing season remained significantly greater than that of the two other species (Table 3), and was above the average annual C



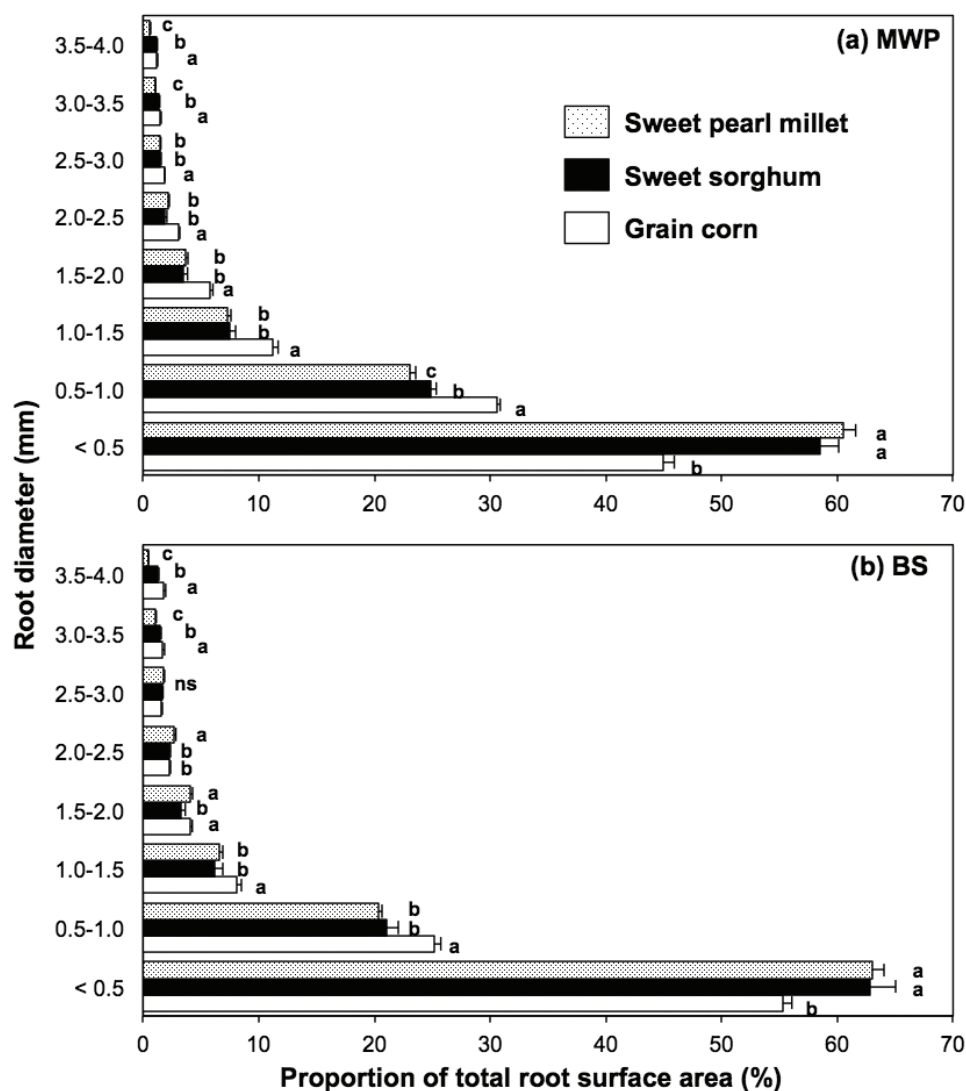


Fig. 2. Diameter distribution (<4 mm diam.) of total root surface (0–30-cm depth) at the flowering stage for sweet pearl millet, sweet sorghum, and grain corn grown at (a) the Mixedwood Plains and at (b) the Boreal Shield sites. Values are averaged for 2011 and 2012 at each site. A mistake with the application of herbicide in 2011 at the MWP site destroyed grain corn. Therefore, data for grain corn at the MWP site (Fig. 2a) are those of 2012 only. Error bars indicate +1 standard error.

input of 206 g C m<sup>-2</sup> reported by Bolinder et al. (1999) for silage corn in eastern Canada. The C input from sweet pearl millet and sweet sorghum was in the range of that reported for small-grain cereals (107–205 g C m<sup>-2</sup>) when straw is exported with the grains (Swinnen et al., 1995; Bolinder et al., 1997). Therefore, the concern raised by some authors about the possible loss of soil organic matter and soil fertility levels with complete aboveground crop residue removal under sorghum or sweet sorghum could be legitimate (Doran et al., 1984; Proffeter and Staggenborg, 2010; Han et al., 2011). Our results for C input do not allow predicting and quantifying the direct impact of these crops on SOC and soil organic matter, since many other factors would need to be taken into account (Monti and Zatta, 2009). However, it has been demonstrated that changes in soil organic matter in agroecosystems are positively correlated with C inputs, everything else being equal (Larson et al., 1972; Rasmussen et al., 1980). Therefore, considering the present results, it is reasonable to argue that the capacity to maintain soil organic matter content would be greater with corn than with sweet sorghum and sweet pearl millet, and greater with sweet sorghum than sweet pearl millet.

### Root Traits at Flowering

According to Berntson et al. (1995), Lemaire et al. (1996), and Bonifas and Lindquist (2009), there would be three ways for crops to improve their N uptake: they can increase the amount of biomass they allocate to roots, modify their root morphological characteristics, or increase the N uptake efficiency of the root absorbing surface. The latter aspect was not investigated here, and was assumed to be similar among the three species. Since root biomass of sweet pearl millet and sweet sorghum for the 30-cm deep soil layer and their root-derived C at harvest were significantly smaller than in corn, their previously reported high N uptake efficiency (Thivierge et al., 2015b) clearly cannot be attributed to a larger allocation of resources to roots. However, differences in root morphological traits among sweet pearl millet, sweet sorghum, and corn could provide insights in this matter.

The RLD measured for grain corn (Table 4) are in the range of values reported in the literature at the silking stage, which vary from 2.2 to 6.1 cm cm<sup>-3</sup> (Mengel and Barber, 1974; Wiesler and Horst, 1994; Nickel et al., 1995; Oikeh et al.,

1999) for the top 15 to 30 cm of soil. For grain sorghum in the top 10 cm of soil, RLD reached  $3.2 \text{ cm cm}^{-3}$  under dry-land conditions and reduced soil tillage (Moroke et al., 2005), and  $5.1 \text{ cm cm}^{-3}$  under non-limiting water conditions (Salih et al., 1999).

Specific root length (SRL) is a widely used indicator of the ability of crops to compete for belowground nutrients (Eissenstat, 1992; Farley and Fitter, 1999; Cantarel et al., 2015). The SRL values measured for grain corn (Table 4) are in the range of values reported elsewhere: 19 to  $24 \text{ m g}^{-1}$  (Oikeh et al., 1999) and 25 to  $39 \text{ m g}^{-1}$  (Barber, 1971). Kätterer and André (1999) reported a SRL of  $60 \text{ m g}^{-1}$  for field-grown reed canarygrass (*Phalaris arundinacea* L.) at harvest. Extreme values ranging from 110 to  $135 \text{ m g}^{-1}$  for grain sorghum and from 71 to  $120 \text{ m g}^{-1}$  for pearl millet were reported by Okamoto and Okada (2004), but they were measured 21 d after sowing in a pot experiment; young root systems are typically characterized by higher SRL (Fitter, 2002). Our results indicate that even though sweet pearl millet and sweet sorghum allocated less C to their root system than corn (Table 3), they produced longer root systems (Table 4), which likely increased their competitiveness for nutrients. Moreover, Bonifas and Lindquist (2009) observed that a smaller allocation of resources to roots along with a high SRL may allow for greater investment of resources to the aboveground biomass. This could explain the high aboveground DM yield of sweet pearl millet and sweet sorghum observed in the present study.

By definition, plants with a high SRL produce more root length per unit of invested C (Eissenstat, 1992; Farley and Fitter, 1999). Fast-growing species are generally characterized by a high SRL (Craine et al., 2003; Cantarel et al., 2015), which provides an advantage in nutrient uptake since the root system of these species show more plasticity (Eissenstat, 1992; Farley and Fitter, 1999). Studying European grasslands, Cantarel et al. (2015) found that grass species characterized by a high SRL depleted soil N rapidly, which resulted in low soil nitrification rates. The high SRL values measured in the present experiment for sweet pearl millet and sweet sorghum (Table 4) could explain the efficient uptake of fertilizer N reported in previous studies (Thivierge et al., 2015a, 2015b). Interestingly, Thivierge et al. (2015a, 2015b) reported similar N uptake efficiencies for sweet sorghum and sweet pearl millet, even though SRL in sweet pearl millet is about two to three times greater than in sweet sorghum. This difference could be related to the stronger ability of sorghum roots to secrete nitrification inhibitors (Zakir et al., 2008; Subbarao et al., 2013; Tesfamariam et al., 2014) that likely helped in competing for soil N and may have compensated for the lower SRL. Sweet pearl millet also appears to have this ability, but to a much lesser extent (Subbarao et al., 2007).

Wang et al. (2005) found that root surface was positively correlated with N uptake in corn. Since nutrients enter the plant mainly through the finest roots (Eissenstat, 1992; Pallant et al., 1993; Jackson et al., 1997; Craine et al., 2003), the root surface accounted for by the finest roots is of great interest. The fact that very fine roots ( $<0.5 \text{ mm}$  diam.) accounted for a larger proportion of the total root surface in sweet pearl millet and sweet sorghum than in corn (Fig. 2) could be related to their differences in N uptake efficiency. Fine-rooted species are highly responsive and can exhibit more plasticity to acquire nutrients, which are generally heterogeneously distributed in

soil (Farley and Fitter, 1999). It must be highlighted here that the proportion of the total root surface (0–30-cm depth) found in the top 15 cm of soil at flowering (68% averaged across species and sites) was lower than the proportion of total root biomass found in the same layer (92% averaged across species and sites). Assuming this pattern of partitioning of root biomass and root surface applies to deeper soil layers, restricting soil sampling to the top 30 cm could result in a greater underestimation of total root surface than total root biomass.

Besides their specific function in N uptake, very fine roots could also play a key role in soil C sequestration. Indeed, fine roots can introduce C into small interstices of the soil matrix where it could be physically protected from microbial degradation, enhancing its persistence (Balesdent and Balabane, 1996; Rasse et al., 2005). Thus, not only biomass but also morphological characteristics of roots should be taken into account when assessing C input from roots.

## CONCLUSION

This study showed that root biomass and estimated C input to soil at harvest were higher for grain corn than for sweet sorghum and sweet pearl millet. In this regard, the possible decline in soil organic matter under sweet pearl millet and sweet sorghum is a legitimate concern. On the other hand, the root morphological characteristics in sweet pearl millet and sweet sorghum clearly differed from those in grain corn, with a greater specific root length, and a higher proportion of total root surface accounted for by the finest roots. These characteristics could explain the high aboveground biomass yield measured in the present study for sweet pearl millet and sweet sorghum, despite a relatively small root biomass, and the high N uptake efficiency reported in previous studies. The relationships between nutrient uptake, crop productivity, and root morphological characteristics warrant further investigation, especially pertaining to the roots in deeper soil layers, which may contribute to aboveground biomass production and nutrient uptake, particularly under conditions of water stress.

## ACKNOWLEDGMENTS

The senior author gratefully acknowledges the support of the Natural Sciences and Engineering Research Council of Canada (NSERC) for a fellowship. The work was financially supported by the Programme de soutien à l'innovation en agroalimentaire (PSIA) of the Ministère de l'agriculture, des pêcheries et de l'alimentation du Québec (MAPAQ). The authors express their gratitude to Dr. Martin A. Bolinder for his timely comments on an earlier version of this article. They also warmly thank Annie Bréard for statistical advice, and Valérie Bélanger, Marie-Eve Bernard, Amélie Desilets Roy, Johanne Tremblay, Gabriel Lévesque, Stephan Pouleur, Christine Juge, and Jessy Caron for their advice and assistance during field and laboratory work.

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