



Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Research Paper

Root biomass in cereals, catch crops and weeds can be reliably estimated without considering aboveground biomass



Teng Hu^{a,*}, Peter Sørensen^a, Ellen Margrethe Wahlström^a, Ngonidzashé Chirinda^b, Behzad Sharif^a, Xiaoxi Li^a, Jørgen Eivind Olesen^a

^a Department of Agroecology, Aarhus University, Blichers Allé 20, Tjele, DK 8830, Denmark

^b Centro Internacional de Agricultura Tropical (CIAT), A. A. 6713, Cali, Colombia

ARTICLE INFO

Keywords:

Organic farming
Shoot biomass
Root biomass
Root:shoot ratio
Allometric root estimation

ABSTRACT

Reliable information on belowground plant biomass is essential to estimate belowground carbon inputs to soils. Estimations of belowground plant biomass are often based on a fixed allometric relationship of plant biomass between aboveground and belowground parts. However, environmental and management factors may affect this allometric relationship making such estimates uncertain and biased. Therefore, we aimed to explore how root biomass for typical cereal crops, catch crops and weeds could most reliably be estimated. Published and unpublished data on aboveground and root biomass (corrected to 0–25 cm depth) of cereal crops (wheat and barley), catch crops and weeds were collected from studies in Denmark. Leave one out cross validation was used to determine the model that could best estimate root biomass.

Root biomass varied with year, farming system (organic versus conventional) and cereal species. Shoot and root biomass of catch crops were higher than for weeds (sampled in late autumn), and farming system significantly affected root biomass of catch crops and weeds. The use of fixed root biomass based on the most influential factors (farming system and species) provided the lowest error of prediction for estimation of root biomass, compared with the use of fixed allometric relations, such as root/shoot ratio. For cereal crops, the average root dry matter in organic farming systems was 218 g m^{-2} (243 and 193 g m^{-2} for wheat and barley, respectively), but in conventional systems only 139 g m^{-2} (142 and 129 g m^{-2} for wheat and barley, respectively). For catch crops and weeds, the root dry matter in organic farming systems were around 127 and 35 g m^{-2} , and in conventional farming systems 75 and 28 g m^{-2} , respectively.

In conclusion, the present analysis indicates that root biomass in cereals, catch crops and weeds can be reliably estimated without considering aboveground biomass, and it may be better estimated using fixed values based on species and farming systems than using fixed allometric ratios.

1. Introduction

Soil fertility in agricultural systems is sustained through inputs of organic matter from plant residues and from applied manure and compost (Lal, 2004a,b). These inputs contribute to carbon (C) storage and sequestration in soils, which in some cases may help to mitigate other greenhouse gas emissions (Powlson et al., 2011). The plant inputs of C from both aboveground and belowground components are generally calculated from their plant biomass by multiplying with specific transfer (humification) coefficients (Chirinda et al., 2012; Kätterer et al., 2011). However, unlike aboveground plant biomass, root biomass is difficult to sample and quantify. The C originating from roots can represent an important source for soil C storage (Warembourg and Paul, 1977), not least because they may contribute more to stable soil organic

C (SOC) pools than aboveground inputs (Kätterer et al., 2011). Such considerations suffer from the fact that the amount of belowground C inputs is mostly not well quantified under field conditions (Smucker, 1984; Taylor, 1986). The difficulties in measuring belowground C inputs means that other approaches have to be taken to estimate this component. Therefore, simple estimation methods have been proposed for estimating belowground C inputs, and these are used for accounting purposes and in many cases also for soil C modelling (Keel et al., 2017).

Allometric estimation of root C inputs, where a certain (often constant) proportion of plant dry biomass is allocated to the root, is a commonly used method, for instance in national inventories of soil C changes (Johnson et al., 2006). Estimating root biomass using fixed allometric ratios is based on the assumption that for specific species and environmental conditions, growth of roots and shoots are closely associated

* Corresponding author.

E-mail address: huteng@agro.au.dk (T. Hu).

<http://dx.doi.org/10.1016/j.agee.2017.09.024>

Received 29 June 2017; Received in revised form 21 September 2017; Accepted 24 September 2017

Available online 05 October 2017

0167-8809/© 2017 Elsevier B.V. All rights reserved.

(Pearsall, 1927; Poorter and Nagel, 2000). This assumes that the biomass allocated to roots is proportional to shoot biomass with a ratio determined by plant species and environmental conditions. As a consequence, the proportion is often a key parameter to estimate root biomass of crops under similar conditions. However, the ratio between the root and aboveground biomass varies between species and depends on environmental conditions (Bolinder et al., 1997, 2007; Campbell et al., 2000).

Many studies have shown that the proportion of the net primary productivity that is allocated to the belowground part is sensitive to the environmental conditions, e.g. nutrient and water availability and tillage (Hodge et al., 2000; Muñoz-Romero et al., 2009). Increasing N application will increase the growth of shoots, while N fertilisation has little effect on root biomass (Jenkinson, 1981; Anderson, 1988; Huggins and Fuchs, 1997). Thus shoots and roots respond differently to particular environmental conditions. Even though the allometric ratio has been shown to vary considerably (Johnson et al., 2006; Gyldenkerne et al., 2007), it is widely used to estimate root biomass, e.g. in models of soil carbon inputs (Kätterer et al., 2011; Berti et al., 2016). Although there is some evidence showing that root biomass seem to be constant for a certain species in a particular environment rather than varying if estimated from shoot biomass using a fixed allometric relationship (Chirinda et al., 2012), this assumption has not been thoroughly tested.

Given the large uncertainties in current methods for estimating root C inputs, our objective was to compare methods for root biomass estimation, in particular the fixed allometric functions versus fixed root biomass. In this analysis we also explore which environmental and management factors affected shoot and root biomass of cereals, catch crops and weeds.

2. Methodology

Published and unpublished shoot and root biomass data from several field experiments in Denmark were collected. Mean values of each treatment were used to obtain statistically equal weight between

treatments, and the data covered both cereal crops (Table 1) and catch crops and weeds (Table 2).

2.1. Cereals

2.1.1. Description of experiments

Data for cereal crops (winter and spring wheat (*Triticum aestivum* L.) and spring barley (*Hordeum vulgare* L.)) was collected from studies conducted at Foulum (56°30'N, 09°35'E) in western Denmark. Organic and conventional farming systems at Foulum showed no overall differences in topsoil (0–25 cm) properties, which was loamy sand soil (Typic Hapludult) with clay content of 88 g kg⁻¹. The soil pH was 6.5. Organic matter content was 38 g kg⁻¹. Soil bulk density was 1.42 g cm⁻³. Average annual temperature and precipitation during 1961–1990 were 7.3 °C and 704 mm. More information on soil properties was provided by Olesen et al. (2000).

Data from 2008 and 2010 were sampled in a long-term crop rotation experiment initiated in 1997 (Olesen et al., 2000). Briefly, the experiment included two rotation systems, one inorganic fertiliser-based conventional system and one organically managed system in two replicates. All treatments were ploughed (Table 1). More information on field management is given in Chirinda et al. (2012).

Data from 2013 and 2014 were sampled in a field experiment established in 2002 under conventional management with four replicates. Generally, there were two factors: nitrogen fertiliser rates and tillage (ploughing and no tillage) (Table 1). In 2013, nitrogen rates were 50 and 250 kg N ha⁻¹, while in 2014 they were 65 and 265 kg N ha⁻¹ for the same sub-plots. More details on the experiment are given in Munkholm et al. (2008) and Hansen et al. (2011).

The mean climatic conditions during the spring period (March to May) are shown for these experimental years in Table 3. The potential evapotranspiration was calculated using a modified Makkink method (Hansen, 1984) using temperature and global radiation as determining variables.

Table 1
Shoot dry matter at maturity and root dry matter at anthesis in field studies with cereals at Foulum, Denmark.

Species	Shoot (Maturity) (g m ⁻²)	Root (Anthesis) (g m ⁻²)	Sampling depth (cm)	Root corrected to 0–25 cm g m ⁻²	Root/(Shoot + Root) 0–25 cm	Year	Seeding time	Farming system	N applied (kg ha ⁻¹)	Tillage	Reference	
Wheat	1907	204	30	194	0.09	2008	Autumn	Conventional	165	Ploughed	Chirinda et al. (2012)	
	838	213		203	0.19			Organic	0			
	1271	249		236	0.16				102			
	1145	291		277	0.19				108			
	1482	251		239	0.14				108			
	1124	156	30	148	0.12	2010	Spring	Conventional	110			
	1350	187		177	0.12				110			
	1093	322		306	0.22			Organic	102			
	1171	211		201	0.15				102			
	1175	116	20	124	0.10			2013	Autumn			Conventional
	1571	86		92	0.06		250					
	1226	123		131	0.10		50			No-tillage		
	1613	99		106	0.06		250					
	1283	154	20	165	0.11	2014				Conventional	65	Ploughed
	1673	148		159	0.09				265			
1266	128		137	0.10				65	No-tillage			
1614	120		129	0.07				265				
Barley	1135	153	30	146	0.11	2008	Spring	Conventional	130	Ploughed	Chirinda et al. (2012)	
	965	238		226	0.19			Organic	0			
	772	200		190	0.20			57				
	1043	236		224	0.18			57				
	1271	240		228	0.15			57				
	1267	140	30	133	0.09	2010		Conventional	120			
	1251	113		108	0.08				120			
	982	162		154	0.14			Organic	62			
	987	142		135	0.12				62			

Table 2
Shoot and root dry matter measured in fields with catch crops and weeds in Denmark.

Species	Shoot (g m ⁻²)	Root (g m ⁻²)	Sampling depth (cm)	Root corrected to 0–25 cm g m ⁻²	Root/ (Shoot + Root) 0–25 cm	Location	Sampling procedure	Farming system	Legume based or not ^a	Sowing time ^b	Reference
Fodder radish	170	130	18	147	0.46	Foulum	Excavation	Organic	NL	Autumn	Li et al. (2015)
Perennial ryegrass	130	130		147	0.53				LB	Spring	
Red clover	190	140		158	0.45					Spring	
Ryegrass/clover mix	190	120		135	0.42					Spring	
Winter vetch	170	120		135	0.44					Autumn	
Ryegrass/clover mix	207	153	30	143	0.41	Foulum	Soil cores	Organic	LB	Spring	Chirinda et al. (2012)
Fodder radish	271	144	20	135	0.33					Spring	
Fodder radish	470	90	20	98	0.17	Aarslev	Excavation	Organic	NL	Autumn	Thorup-Kristensen (2001)
Winter rape	400	140		152	0.28					Autumn	
Phacelia	420	50		54	0.11					Autumn	
Rye	210	100		108	0.34					Autumn	
Oats	310	70		76	0.20					Autumn	
Italian ryegrass	350	190		206	0.37					Autumn	
Malva sylvestris	360	200		217	0.38					Autumn	
Agrostemma githago	530	100		108	0.17					Autumn	
Rye/vetch mix.	330	140		152	0.32				LB	Autumn	
Winter vetch	370	60		65	0.15					Autumn	
Fodder radish	200	72	20	78	0.30	Foulum	Excavation	Conventional	NL	Spring	Mutegi et al. (2011)
Fodder radish	219	108		117	0.35					Spring	
Fodder radish	267	46	20	50	0.16	Flakkebjerg	Soil cores	Conventional	NL	Autumn	Unpublished
Radish/Rye mix	629	81	20	87	0.12	Foulum	Excavation	Conventional	NL	Spring	Unpublished
Radish/Ry/Vetch mix	184	41		44	0.19					Spring	
Radish/Ry/Vetch mix	565	96		104	0.16			Organic	LB	Spring	
Chicory/clover mix	85	63		69	0.45					Spring	
Weeds	85	78	30	73	0.46	Foulum	Soil cores	Conventional	–	–	Chirinda et al. (2012)
Weeds	53	78		73	0.58			Organic			
Weeds	262	4	20	4	0.02	Foulum	Excavation	Conventional	-	-	Unpublished
	47	8		8	0.15						
	208	8		9	0.04			Organic			
	45	22		24	0.34						

^a NL, non-legume; LB, legume-based.

^b Spring, catch crops were undersown in preceding cereal crops; Autumn, catch crops were sown after harvest of the cereals.

Table 3
Climatic conditions during spring (March to May) at Foulum during the experimental years.

Year	Mean temperature (°C)	Mean daily global radiation (MJ m ⁻²)	Precipitation (mm)	Potential evapotranspiration (mm)
2008	7.4	15.0	134	209
2010	5.4	12.9	106	169
2013	5.3	14.6	85	188
2014	8.5	13.5	157	191

2.1.2. Measurements

Shoot biomass was sampled at maturity, and root biomass was sampled at anthesis as this is the growth stage expected to have maximum root biomass. Plant samples of aboveground biomass were taken by cutting plants at 1–2 cm height within two 0.5 m² frames. Samples were oven dried at 60 °C for 48 h for dry matter (DM). Three soil cores (5 cm diameter) were collected within the rows and three between the rows for root biomass. Root sampling reached 30 cm depth in 2008 and 2010, and 20 cm in 2013 and 2014. Samples to 60 cm depth were also taken in 2008, 2013 and 2014. The root samples were washed out using

tap water and collected on a sieve with a mesh size of 0.425 mm. Samples were oven dried at 70 °C for 48 h and weighed for dry matter. A part of the root sample was heated at 650 °C for five hours to determine the ash content, and final root dry matter was expressed as ash-free dry matter (Chirinda et al., 2012).

2.2. Catch crops and weeds

2.2.1. Description of experiments

Data on catch crops (fodder radish (*Raphanus sativus* L.), perennial ryegrass (*Lolium perenne* L.), red clover (*Trifolium pratense* L.), white clover (*Trifolium repens* L.), winter vetch (*Vicia villosa* Roth.), winter rape (*Brassica napus* L.), phacelia (*Phacelia tanacetifolia* Benth.), rye (*Secale cereale* L.), oats (*Avena sativa* L.), Italian ryegrass (*Lolium multiflorum* Lam.), *Malva sylvestris* L., *Agrostemma githago* L. and chicory (*Cichorium intybus* L.)) were collected from Mutegi et al. (2011) in four replicates, Chirinda et al. (2012) in two replicates, Li et al. (2015) in three replicates sampled at Foulum (56°30'N, 09°35'E), from Thorup-Kristensen (2001) in three replicates at Aarslev (55°18'N, 10°27'E), and from Wahlström et al. (2015) in four replicates at Flakkebjerg (55°19'N, 11°23'E) (Table 2). Topsoil (0–25 cm depth) at Foulum is described above for cereals crops. Topsoil of the same depth at Aarslev and Flakkebjerg were both classified as sandy loam (Typic Agrudalf) with

clay content of 147 g kg^{-1} at both sites, and pH 7.0 and 7.4, respectively (Thorup-Kristensen, 2001; Olesen et al., 2000). The average annual temperature and precipitation were $8.1 \text{ }^\circ\text{C}$ and 719 mm (during 1986–1998) at Aarslev (Mueller and Thorup-Kristensen, 2001), and $7.8 \text{ }^\circ\text{C}$ and 626 mm (during 1961–1990) at Flakkebjerg (Olesen et al., 2000).

Published data from Foulum (Chirinda et al., 2012; Li et al., 2015) was sampled from cropping systems under organic farming, except for weeds sampled in the inorganic fertiliser-based rotation system in Chirinda et al. (2012). The data from Li et al. (2015) included two legume-based catch crops. Data from Aarslev was from a cropping system with vegetables under organic farming, where catch crops were sown after the harvest of green pea crops. Two of the treatments included legume-based catch crops with winter vetch (Thorup-Kristensen, 2001). The data from Flakkebjerg were from fodder radish sown after the harvest of spring barley in a conventionally managed cropping system (Wahlström et al., 2015).

2.2.2. Measurements

At Foulum, Mutege et al. (2011) sampled fodder radish in December by clipping the aboveground biomass at the soil surface from four subplots of 0.64 m^2 , and by extracting root from three soil cores in each replicate to 100 cm depth. Samples were then sub-divided at 20 cm , 35 cm and 60 cm depths. Chirinda et al. (2012) used the method for cereal crops also to measure catch crops in early November. Li et al. (2015) sampled catch crop roots in small frames ($35 \times 24 \text{ cm}$) down to 18 cm . The area covered two rows of catch crops. The root washing procedure was the same as in Chirinda et al. (2012). At Aarslev, aboveground parts of catch crops were sampled in 1 m^2 just below ground level, and roots were washed out from two excavated soil blocks of $30 \times 12 \text{ cm}^2$ area and 20 cm depth in November (Thorup-Kristensen, 2001). Only visibly live roots were retained. At Flakkebjerg, aboveground parts of catch crops were sampled at soil surface in two 0.25 m^2 areas in November, and roots were sampled from three soil cores (8.6 cm diameter) vertically down to 100 cm depth, and subdivided at 20 cm , 35 cm , 55 cm and 80 cm depths (Wahlström et al., 2015).

To supplement these data, additional data were collected from catch crops and weeds sampled in December 2014 in the aforementioned long-term organic crop rotation experiment at Foulum (Olesen et al., 2000) in two replicates. Three types of catch crops following potato and spring wheat were sampled for shoot and root biomass. These catch crops were mixtures of species, i.e. fodder radish + rye, fodder radish + rye + vetch, chicory + perennial ryegrass + red clover + white clover. Also sampling was made in plots without catch crops, but with weeds. Shoots were separated on the basis of species, while roots were analysed as a pooled sample. A square of 0.5 m^2 was used for sampling of aboveground material in each plot. Inside the 0.5 m^2 square, an area of $35 \times 24 \text{ cm}^2$ was chosen from within and from midway between crop rows. Aboveground plants inside the $35 \times 24 \text{ cm}^2$ area were cut with scissors at the soil surface and collected in a plastic bag, whilst the remaining sample inside the 0.5 m^2 was collected in a second bag. Each sample was separated according to species groups and dry matter was determined after oven drying at $60 \text{ }^\circ\text{C}$ for 42 h . Belowground biomass was determined for the $35 \times 24 \text{ cm}^2$ area to a depth of 20 cm in each plot. The soil samples were stored at $2 \text{ }^\circ\text{C}$ before root washing.

The roots were first separated from the soil by passing through a 1-cm sieve. Large visible roots and those retained on the 1 cm sieve were collected, termed 'large roots'. The bulk soil passing the 1 cm sieve was mixed and subdivided into a subsample of $350\text{--}450 \text{ g}$, which was washed on a 0.425 mm sieve. The roots collected on this sieve are termed 'small roots' (Rasmussen et al., 2010). Roots were further washed with tap water to remove minerals and collected on a set of sieves with mesh sizes of 2 mm , 1 mm and 0.425 mm . Subsequently, the collected roots and debris were placed in a tray, where white living roots were separated from dead organic matter (including decayed roots) based on colour and physical appearance (Muñoz-Romero et al., 2009). Living

roots were oven-dried at $60 \text{ }^\circ\text{C}$ for 42 h and weighed. A part of each root sample was heated at $650 \text{ }^\circ\text{C}$ for five hours to determine the ash content, and final root dry matter was expressed as ash-free dry matter (Chirinda et al., 2012).

2.3. Root biomass depth correction

Different farming systems and N managements showed little impact on vertical root biomass distribution of either cereal crops or catch crops and weeds (See Supplementary materials Table S1 in the online version at DOI: [10.1016/j.agee.2017.09.024](https://doi.org/10.1016/j.agee.2017.09.024)), and similar results were also reported in Hirte et al. (2017). Since roots were sampled to different depths in the various studies, we applied two different functions for the depth correction, one for cereals (Eq. (1)) and another for catch crops and weeds (Eq. (2)). This choice was based on previous studies and on available data. This was as far as possible validated against root biomass data from different depths reported in Supplementary material. Root dry matter measurements of cereal crops were converted to 25 cm depth according to the Michaelis-Menten function of root distribution with depth (z ; cm) as used in Kätterer et al. (2011) for root depth distribution of small-grain cereals in southern Sweden.

$$\text{Rm}(z) = [z(z_{50} + z_r)]/[z_r(z_{50} + z)] \quad (1)$$

$\text{Rm}(z)$ is the fraction of total root mass to the soil depth of z (cm), z_r is maximum root depth (z_r was set at 150 cm), z_{50} is the depth of 50% of the root mass (z_{50} was for cereals in Sweden set at 10 cm). This means that 76, 80 and 91% of the roots are allocated to 25 cm , 30 cm and 60 cm soil depth, respectively. In this function, 88% of root biomass in $0\text{--}60 \text{ cm}$ depth was estimated for $0\text{--}30 \text{ cm}$ depth, which was close to the root vertical distribution of cereals in years 2008 and 2014 (Table S1).

Roots of fodder radish sampled in Flakkebjerg were classified into 5 depths: $0\text{--}20$, $20\text{--}35$, $35\text{--}55$, $55\text{--}80$ and $80\text{--}100 \text{ cm}$ (Wahlström et al., 2015). Within 100 cm depth, recoverable root dry matter of catch crops in different depths was well described as (See Fig. S1 in the online version at DOI: [10.1016/j.agee.2017.09.024](https://doi.org/10.1016/j.agee.2017.09.024)):

$$\text{Rm}(z) = 0.1926 z^{0.3641} \quad (2)$$

According to Eq. (2), in soil depths of 25 , 30 and 60 cm , root dry matter accounted for 62, 66 and 86%, respectively, of total root biomass in the upper 100 cm soil. This meant that 78% of the root present in $0\text{--}60 \text{ cm}$ depth was recovered in $0\text{--}30 \text{ cm}$ layer. This corresponded well to the root distribution observed for catch crops (with mainly ryegrass) and weeds, where the proportion of recoverable root biomass from 0 to 30 cm depth compared to biomass in $0\text{--}60 \text{ cm}$ was between 68 and 77% (Chirinda et al., 2012). Thus, the equation was assumed suitable and was used to convert root dry matter of catch crops and weeds from the measured depths to $0\text{--}25 \text{ cm}$ depth.

2.4. Data analysis

The MIXED procedure of SAS (SAS Institute, 1996) was used to test which factors influence crop shoot, root and the allometric ratios (root/shoot, shoot/root, shoot/(shoot + root) and root/(shoot + root) ratio): year, species (wheat or barley), seeding time (spring or autumn), tillage (ploughing or no tillage), farming system (organic or conventional management) and nitrogen fertilisation rate, where shoot biomass, root biomass and nitrogen fertilisation rate were used as continuous variables and other variables were categorical. We thus assumed that allometric ratios would depend on plant type and management. These allometric functions essentially assume linear relations of root biomass to either shoot or total biomass. For catch crops and weeds the following factors were considered: location, catch crops or weeds, legume based or non-legume based catch crops, undersowing catch crops or sowing these after

Table 4
Factors affecting shoot, root biomass and their allometric ratios, and comparison of methods for estimating root biomass using cross-validation (LOOCV) for cereals, N = 26.

Target variables	P values for influential factors ^a						LOOCV for root estimation methods based on most influential factors in	
	Year	Species	Seeding time ^b	Farming system	Nitrogen	Tillage	MBE _p (g m ⁻²)	RMSE _p (g m ⁻²)
Shoot			0.0205		< 0.0001			
Shoot of cereal crops		–	0.0205		< 0.0001			
Root	0.0154	0.0022		0.0013			Root estimation by fixed root amount	
Root ignoring year	–	0.0347		< 0.0001			0.0	33.3
Root of cereal crops		–		< 0.0001			–0.3	37.6
Root (Species)	–	0.7850	–	–	–	–	0.0	39.8
Root (Species, seeding time)	–	0.2831	0.2248	–	–	–	0.0	57.8
								59.7
Root/shoot ratio				< 0.0001			Root estimation by root/shoot ratio	
Root/shoot ratio of cereal crops		–		< 0.0001			3.4	42.7
Root/shoot ratio (Species)	–	0.3504	–	–	–	–	3.4	42.7
Root/shoot ratio (Species, seeding time)	–	0.7196	0.1702	–	–	–	10.2	78.1
							9.2	77.0
Shoot/root ratio	0.0008	0.0023	0.0222	0.0018	< 0.0001		Root estimation by shoot/root ratio	
Shoot/root ratio ignoring year	–			0.0002	0.0005		2.0	42.6
Shoot/root ratio of cereal crops	0.0090	–		0.0064	0.0001		–3.5	43.4
Shoot/root ratio (Species)	–	0.2242	–	–	–	–	–1.0	45.5
Shoot/root ratio (Species, seeding time)	–	0.7495	0.1099	–	–	–	–17.6	75.4
							–15.5	73.4
Shoot/all or root/all ratio	0.0366	0.0047	0.0166	0.0001	0.0155		Root estimation by shoot/all or root/all ratio	
Shoot/all or root/all ratio ignoring year	–			< 0.0001	0.0309		1.7	38.2
Shoot/all or root/all ratio of cereal crops		–		< 0.0001	0.0309		0.5	38.5
Shoot/all or root/all ratio (Species)	–	0.3239	–	–	–	–	0.5	38.5
Shoot/all or root/all ratio (Species, seeding time)	–	0.7325	0.1616	–	–	–	6.3	77.1
							5.7	75.9

^a Factors with ‘–’ were not included in the statistical analysis for influential factors. Blank cells were items included in the statistical analysis, but not statistically significant (p > 0.05). Factors shown in p values were used for leave one out cross validation (LOOCV). Factors in brackets mean the only factors considered for LOOCV.

^b Seeded in spring or autumn.

harvest of the main crop, and farming system. A manual procedure with backward elimination was used to remove variables that did not contribute significantly based on the Akaike Information Criterion (AIC). The best model was thus selected according to the lowest AIC and significant (P < 0.05) effect of independent variables.

Different approaches (allometric functions and various determining factors) for estimating root biomass were tested by leave one out cross validation (LOOCV) based on mean bias error (MBE) and root mean squared error (RMSE). The models chosen for testing were based on the selected models using the stepwise procedure described above. Specific equations are shown as below:

$$MBE_p = \frac{\sum_{i=1}^n (P_i - O_i)}{n} \tag{3}$$

$$RMSE_p = \sqrt{\frac{\sum_{i=1}^n (P_i - O_i)^2}{n}} \tag{4}$$

where MBE_p and RMSE_p means MBE and RMSE of prediction for the selected models for LOOCV with total population of samples as n, P_i is the predicted root dry biomass of sample i through the selected model trained by all other samples, and O_i is the observed root dry biomass of sample i.

3. Results

3.1. Factors affecting shoot and root biomass

Shoot biomass of cereals was strongly influenced by the quantity of nitrogen applied in mineral fertiliser or manure. The shoot biomass varied between spring and winter cereals, while root biomass varied between years and depended on farming system (organic or conventional) and cereal crop species (Table 4). Thus shoot and root dry biomass was not closely associated, but influenced by different factors. In addition, the different allometric ratios responded differently to

Table 5
Mean root dry biomass (to 25 cm depth) measured in cereals, catch crops and weeds at Foulum, Denmark (data from Tables 1 and 2).

	Farming system	Species	Root biomass ^a (g m ⁻²)	N
Cereals	Organic	Wheat	243 ± 41	6
		Barley	193 ± 40	6
		Cereals	218 ± 47	12
	Conventional	Wheat	142 ± 30	11
		Barley	129 ± 19	3
		Cereals	139 ± 28	14
Catch crops and weeds	Organic	Catch crops	127 ± 44	19
		Weeds	35 ± 34	3
	Conventional	Catch crops	75 ± 29	5
		Weeds	28 ± 38	3

^a Mean ± S.D.

determining factors. Root/shoot ratio was sensitive to the type of farming system, while shoot/root ratio, shoot/all and root/all were influenced by several factors, i.e. year, species, sowing time, farming system and nitrogen rate. Therefore, the most reliable estimates of root biomass depend on farming system and species with higher root biomass in organic compared with conventional systems (Table 5).

When pooling data over all years and cereal species, the root biomass only responded significantly to farming system, whereas shoot/root ratio as well as shoot/all and root/all ratios depended mostly on farming system and nitrogen rate.

There were significant differences between catch crops and weeds for both shoot and root biomass (Table 6). Root biomass was affected by type of farming system. Root/shoot ratio depended on location and farming system, while shoot/root ratio varied between catch crops and weeds. Shoot/all or root/all ratios were not significantly affected by any factors.

Table 6
Factors affecting shoot, root biomass and their allometric ratios, and comparison of methods for estimating root biomass of catch crops and weeds using cross-validation (LOOCV).

Target variables	P Value for influential factors ^a				Test for root estimation methods based on most influential factors in LOOCV			
	Location	Farming system	CC or not ^b	LB or not ^c	Undersown or not ^d	MBE _p (g m ⁻²)	RMSE _p (g m ⁻²)	N
Shoot			0.0062					
Root		0.0347	0.0009			Root estimation by fixed root amount		
Root (CC or not, Farming system)	–	0.0347	0.0009	–	–	0.2	43.0	30
Root (CC or not, LB or not)	–	–	–	0.6430	–	0.2	43.0	30
						0.0	46.3	30
						Root estimation by root/shoot ratio		
Root/shoot ratio	0.0294	0.0138				20.8	87.8	29
Root/shoot ratio (CC or not, Farming system)	–	0.0885	0.5707	–	–	30.3	90.5	30
Root/shoot ratio (CC or not, LB or not)	–	–	–	0.2133	–	29.3	92.2	30
						Root estimation by shoot/root ratio		
Shoot/root ratio			0.0116			–18.5	67.2	30
Shoot/root ratio (CC or not, Farming system)	–	0.2819	0.0279	–	–	5.7	80.9	30
Shoot/root ratio (CC or not, LB or not)	–	–	–	0.2196	–	–15.9	71.8	30
						Root estimation by shoot/all or root/all ratio		
Shoot/all; root/all ratio						11.7	76.6	30
Shoot/all; root/all ratio (CC or not, Farming system)	–	0.1060	0.9298	–	–	17.2	80.9	30
Shoot/all or root/all ratio (CC or not, LB or not)	–	–	–	0.1796	–	15.5	83.5	30

^a Factors with ‘–’ were not included in statistical analysis for influential factors. Blank cells were items included in the statistical analysis, but not statistically significant ($p > 0.05$). Factors shown in p values were used for leave one out cross validation (LOOCV). Factors in brackets mean the only factors considered for LOOCV.

^b CC or not means catch crops or weeds.

^c LB or not means legume based or non-legume based catch crops.

^d Undersown or not means undersowing or not undersowing catch crops.

3.2. Root estimation methods

Different methods for estimating root biomass were tested by cross validation and evaluated in terms of MBE_p and RMSE_p using cross validation (Table 4). The most reliable predictions of soil root biomass were obtained for cereals using fixed root amount with mean biomass values depending on year, farming system and species giving an RMSE_p of only 33 g m⁻² (Table 4). The second best method was using fixed root biomass depending on farming system and cereal species with RMSE_p of 38 g m⁻². Fixed root estimation which only considered farming system provided the simplest estimation, but with a RMSE_p of 40 g m⁻². Grouping data according to species, or species and sowing time (autumn or spring) reduced the performance of root biomass prediction (i.e. higher RMSE_p of the cross-validation). Estimation of root biomass based on shoot biomass with allometric relations according to root/shoot, shoot/root or even shoot/all (root/all) ratio showed either poorer prediction performance and/or was more complex than using fixed root biomass.

Table 7
Root biomass estimated by least square means (0–25 cm). Same data as used in Table 5.

	Class	Variables	Root dry biomass ^a (g m ⁻²)
Cereal crops	Farming systems	Organic	189 ± 13
		Conventional	131 ± 9
	Species	Wheat	184 ± 8
		Barley	135 ± 12
	Year	2008	199 ± 10
		2010	170 ± 10
		2013	118 ± 18
		2014	152 ± 18
Catch crops and weeds	Farming systems	Organic	88 ± 11
		Conventional	49 ± 15
	Species	Catch crops	105 ± 10
		Weeds	32 ± 17

^a Mean ± S.D.

The most reliable estimates of root biomass in catch crops and weeds were obtained by using fixed root biomass for catch crops and weeds separately for different farming systems (Table 6). Adding factors such as catch crop characteristics (e.g. legume based) did not improve predictions. Similar to the cereal crops, using allometric relationships reduced the prediction accuracy for root biomass in catch crops and weeds.

3.3. Fixed root biomass estimation

According to the results above, we suggest using fixed root biomass classified by farming systems and species for cereals, and by farming systems for catch crops and weeds (Table 5). Table 7 shows the estimated root biomass by least square means taking into account the most influential factors for cereals (farming systems, species and year), and for catch crops and weeds (farming systems, catch crops or weeds). The root biomass of wheat and barley varied between years from 118 to 199 g m⁻²; however, there was consistently higher root biomass in wheat compared with barley (Tables 5 and 7). The difference in cereal root biomass between organic and conventional farming was 79 g m⁻² (Table 5) and 58 g m⁻² (Table 7). Considering the small difference between the arithmetic means (Table 5) and the least square means (Table 7) for catch crops and weeds, the unbalanced data collected did not appear to have caused much difference to the estimated root biomass.

4. Discussion

4.1. Factors affecting root biomass

Root biomass of cereal crops, catch crops and weeds was affected by both environmental and management factors (Tables 4 and 6). The results showed significant effects of year, species and farming systems on root biomass in cereal crops. For catch crops and weeds, significant differences in root biomass were observed between catch crops and weeds and also between organic and conventional farming systems. We acknowledge the existence of confounding data, which with

imbalanced data could lead to biased estimates of influential factors on root biomass. However, the analyses clearly pointed to differences in root biomass between farming systems, where data from the same site and year was included for both farming systems.

The reason for the observed factors influencing root biomass may be found in how photosynthesized products are allocated between shoots and roots. During the growing period, shoots and roots interact closely to allocate the photosynthesized material from shoots and the absorbed nutrients from roots (Thornley, 1972). The relative allocation between shoots and roots changes over time in response to the relative need of photosynthesized material and nutrients (Thornley, 1972; Poorter and Nagel, 2000). Less supply of below-ground resources (e.g. nutrients and water) would induce allocation of more photosynthates to roots, while less aboveground resources (e.g. less light) could cause more allocation to shoots (Thornley, 1972; Poorter and Nagel, 2000). Thus for any given species, it is the environment and the soil conditions that determines how much can be photosynthesized and how much is allocated to shoots or roots. The ratio between shoot and root biomass is therefore the result of changing allocation patterns during the growing period. The dynamic association between shoots and roots means that allometric ratios are not well suited for calculating root biomass, since the final allometric ratios can be quite variable, especially under stressed environmental and soil nutritional conditions.

Environmental conditions (e.g., radiation, precipitation and temperature) varied between the experimental years (Table 3). Therefore, the total carbon assimilation, the fraction allocated to roots and root distributions within the soil profile could also differ between years. In our data, the lowest root biomass for cereals in 0–25 cm was observed in 2013, whereas a higher level of root biomass was found for the other years. The spring of 2013 was characterized by drier conditions than for the other years, which may have caused plants to develop deeper roots and less dense roots in the upper soil layer in 2013. This was also indicated by the observed root biomass (data not shown) that showed less difference in root biomass between 2013 and 2014 for the depth 0–60 cm than for 0–20 cm. Genotypic variation between species could cause different specific allocation strategies (Fakhri et al., 1987; Clark et al., 2003), and thus cause root biomass differences among species. From the aspects of species, catch crops had higher biomass than weeds, because catch crop species were chosen to fit the growing conditions after main crops (Snapp et al., 2005).

As to farming systems, nutrients, especially nitrogen, in organic farming are less readily available, even though the total input is not always less than in the conventional systems (Stockdale et al., 2002). This lower availability of nutrients is one of the major causes of relatively higher allocation of photosynthates to roots (Poorter and Nagel, 2000; Lonhienne et al., 2014).

4.2. Differences between root biomass estimation methods

The main objective of this work was to compare root biomass estimation methods, particularly the use of fixed allometric relations versus fixed root biomass. The results showed that using fixed root biomass based on the most influential factors provided the most robust estimation with MBE_p close to 0, and generally the lowest $RMSE_p$. Using allometric relations for estimating root biomass resulted in higher MBE_p and $RMSE_p$ than using fixed root biomass, in terms of both most influential factors and commonly used factors (factors in brackets in Tables 4 and 6). Generally, shoot/root ratios provided negative MBE_p and lower $RMSE_p$ than other ratios. Shoot/all or root/all ratios generally provided positive MBE_p and higher $RMSE_p$. Root/shoot ratios generally had a higher positive MBE_p and the highest $RMSE_p$.

As discussed above, root biomass of a certain species depends on environmental and management factors. A robust and unbiased estimate of root biomass requires that the MBE_p is close to zero and the $RMSE_p$ from cross validation is as small as possible. In root/shoot, shoot/root, root/(shoot + root) or shoot/(root + shoot) ratios, either

one part (shoot or root) or the total biomass appears as the denominator. The allometric ratios for individual measures may vary greatly due to the variation in either above- or belowground biomass, which may cause biases in the estimation of the mean allometric ratio. Furthermore, with allometric ratios root biomass will be estimated only from observed shoot biomass, and any uncertainty in observed shoot biomass will be translated to uncertainty in root biomass amplified by the uncertainty in the allometric relationship.

Generally, we observed the following relations between organic farming and conventional farming: 1) more shoot biomass associated with less root biomass was found in conventional farming, and the opposite in organic farming; 2) more total (shoot + root) biomass associated with less root biomass in conventional farming, and a relatively more equal distribution between shoots and roots in organic farming; 3) the difference in root biomass between the two farming systems (highest root biomass in organic farming) is generally smaller than that in shoot biomass (highest shoot biomass in conventional farming). If we estimated root biomass with the existence of all these three relations, root biomass would be highly overestimated when using root/shoot ratios, less underestimated when using shoot/root ratios, and less overestimated using root/(root + shoot) ratios. Thus, the highly dynamic relations between shoot and root biomass is affected by the type of farming systems as well as by the actual management. Therefore, root biomass can for the climatic conditions of northern Europe more reliably be estimated using fixed values depending on farming system and plant species rather than assuming a dependency on shoot biomass.

4.3. Perspectives

Our results from Denmark show that the most practical and accurate estimates of root biomass are obtained by using fixed root amounts that depend on farming system and species (Table 5). It would be valuable to have similar analyses for other climatic and soil conditions, and for other types of farming systems. From our results, considering only farming systems for cereals would give almost similar performance. For catch crops and weeds separate fixed values should be used to provide the best estimates. The observed differences in root biomass between years, especially in the upper soil layer, indicate that robust root biomass estimates should be based on measurements over several years.

Most studies on root biomass in cereals have been conducted in conventional farming systems, and our estimates of root biomass generally agree with findings from other studies in northern Europe. As corrected by Eq. (1) to a depth of 0–25 cm: Van Noordwijk et al. (1994) in the Netherlands measured root of winter wheat as 133–154 $g\ m^{-2}$; Kätterer et al. (1993) reported winter wheat root biomass in Sweden of 79–90 $g\ m^{-2}$; Braim et al. (1992) reported barley root biomass in Britain of around 107–116 $g\ m^{-2}$; Pietola and Alakukku (2005) reported root biomass for barley and oats at anthesis in Finland of 98 and 215 $g\ m^{-2}$, respectively; Głab et al. (2014) reported triticale root biomass of 94–160 $g\ m^{-2}$. These values are comparable with our results of $142 \pm 30\ g\ m^{-2}$ for wheat and $129 \pm 19\ g\ m^{-2}$ for barley.

In other parts of the world, we would also recommend use of fixed root amounts for estimation for root biomass, because estimated root biomass with allometric ratios from our results are not only inaccurate, but also biased (Tables 4 and 6). However, there are also limitations for fixed root estimation, because roots are inadequately sampled across the world. Therefore, in cases where no root biomass observations are available and where climate and soil conditions differ substantially from reference sites, the use of allometric ratios may become inevitable. In such situations, we would recommend use of shoot to root ratio for root biomass estimation (Tables 4 and 6), even though shoot to root ratio may induce underestimation of root biomass. In any case, our results clearly point to the need for improving the globally available data on root biomass, and ideally these data should be made available in an open repository for use by both experimentalists and modellers.

Soil carbon sequestration plays a potential role in mitigation of climate change and root biomass contributes with a significant carbon input (Gattinger et al., 2012). Our results indicate that roots in organic farming systems may contribute more to soil carbon sequestration than in conventional systems. Taghizadeh-Toosi et al. (2016) similarly reported that the root carbon input can be considered constant across different nitrogen fertiliser rates. The estimates of fixed root amount (Table 5) can be used to improve calculations of belowground carbon input in modelling. Assuming the percentage of carbon in roots as 45% (Chirinda et al., 2012), organic farming would then bring in roughly 0.6 Mg ha⁻¹ more C input than conventional farming from both cereals and catch crops.

5. Conclusions

A statistical analysis of root biomass data from field experiments in Denmark showed that the use of fixed root biomass provided lower error of prediction for estimation of root biomass than the use of fixed allometric ratios. The most robust estimation of root biomass was found with fixed root biomass depending on farming system and plant type. However, there was some variation between years in root biomass of cereals. There was consistently greater root biomass of cereal crops in organic compared to conventional systems, and there was greater root biomass in wheat compared to barley. The results also showed greater root biomass in catch crops compared with weeds.

Acknowledgements

The work was part of the RowCrop project supported by GUDP under the Danish Ministry of Environment and Food, and partly supported by China Scholarship Council (CSC). The technical assistance of staff at Foulum, in particular Erling E. Nielsen is gratefully acknowledged.

References

Anderson, E.L., 1988. Tillage and N fertilization effects on maize root growth and root:shoot ratio. *Plant Soil* 108, 245–251.

Berti, A., Morari, F., Dal Ferro, N., Simonetti, G., Polese, R., 2016. Organic input quality is more important than its quantity: C turnover coefficients in different cropping systems. *Eur. J. Agron.* 77, 138–145.

Bolinder, M.A., Angers, D.A., Dubuc, J.P., 1997. Estimating shoot to root ratios and annual carbon inputs in soils for cereal crops. *Agric. Ecosyst. Environ.* 63, 61–66.

Bolinder, M.A., Janzen, H.H., Gregorich, E.G., Angers, D.A., VandenBygaart, A.J., 2007. An approach for estimating net primary productivity and annual carbon inputs to soil for common agricultural crops in Canada. *Agric. Ecosyst. Environ.* 118, 29–42.

Braim, M.A., Chaney, K., Hodgson, D.R., 1992. Effects of simplified cultivation on the growth and yield of spring barley on a sandy loam soil. 2. Soil physical properties and root growth; root: shoot relationships, inflow rates of nitrogen; water use. *Soil Tillage Res.* 22, 173–187.

Campbell, C.A., Zentner, R.P., Liang, B.C., Roloff, G., Gregorich, E.G., Blomert, B., 2000. Organic C accumulation in soil over 30 years in semiarid southwestern Saskatchewan-effect of crop rotations and fertilizers. *Can. J. Soil Sci.* 80, 179–192.

Chirinda, N., Olesen, J.E., Porter, J.R., 2012. Root carbon input in organic and inorganic fertilizer-based systems. *Plant Soil.* 359, 321–333.

Clark, L.J., Whalley, W.R., Barraclough, P.B., 2003. How do roots penetrate strong soil? *Plant Soil* 255, 93–104.

Fakhri, A.B., Nona, R.C., Phyllis, D.C., Louis, F.P., 1987. Allocating resources to reproduction and defense. *Bioscience* 37 (1), 58–67 How Plants Cope Plant Physiological Ecology.

Głab, T., Ścigalska, B., Łanuz, B., 2014. Effect of crop rotation on the root system morphology and productivity of triticale (\times Triticosecale Wittm). *J. Agric. Sci.* 152, 642–654.

Gattinger, A., Muller, A., Haeni, M., Skinner, C., Fließbach, A., Buchmann, N., Mäder, P., Stolze, M., Smith, P., Scialabba, N.E.-H., Niggli, U., 2012. Enhanced top soil carbon stocks under organic farming. *Proc. Natl. Acad. Sci. U. S. A.* 109, 18226–18231.

Gyldenkerne, S., Petersen, B.M., Olesen, J.E., 2007. Konsekvenser og muligheder ved Danmarks deltagelse i Kyoto-protokollens artikel 3.4 på landbrugsområdet (Consequences and possibilities in participation of Denmark in the Kyoto Protocol article 3.4 within agriculture). Working Report from Environmental Protection Agency 5/2007. Ministry of Environment, Copenhagen.

Hansen, E.M., Munkholm, L.J., Olesen, J.E., 2011. N-utilization in non-inversion tillage systems. *Soil Tillage Res.* 113, 55–60.

Hansen, S., 1984. Estimation of potential and actual evapotranspiration. *Hydrol. Res.* 15, 205–212.

Hirte, J., Leifeld, J., Abiven, S., Oberholzer, H.R., Hammelehle, A., Mayer, J., 2017. Overestimation of crop root biomass in field experiments due to extraneous organic matter. *Front. Plant Sci.* 8, 284. <http://dx.doi.org/10.3389/fpls.2017.00284>.

Hodge, A., Stewart, J., Robinson, D., Griffiths, B.S., Fitter, A.H., 2000. Competition between roots and soil micro-organisms for nutrients from nitrogen-rich patches of varying complexity. *J. Ecol.* 88, 150–164.

Huggins, D.R., Fuchs, D.J., 1997. Long-term N management effects on corn yield and soil C of an Aquic Haplustoll in Minnesota. In: Paul, E.A., Paustian, K., Elliott, E.T., Cole, C.V. (Eds.), *Soil Organic Matter in Temperate Ecosystems: Long-Term Experiments in North America*. CRC Press, New York, pp. 121–128.

Jenkinson, D.S., 1981. The fate of plant and animal residues in soil. In: Greenland, D.J., Hayes, M.H.B. (Eds.), *The Chemistry of Soil Processes*. Wiley, New York, NY, pp. 505–561.

Johnson, J.M.F., Allmaras, R.R., Reicosky, D.C., 2006. Estimating source carbon from crop residues roots and rhizodeposits using the national grain-yield database. *Agron. J.* 98, 622–636.

Kätterer, T., Hansson, A.C., Andrén, O., 1993. Wheat root biomass and nitrogen dynamics-effects of daily irrigation and fertilization. *Plant Soil* 151, 21–30.

Kätterer, T., Bolinder, M.A., Andrén, O., Kirchmann, H., Menichetti, L., 2011. Roots contribute more to refractory soil organic matter than above-ground crop residues, as revealed by a long-term field experiment. *Agric. Ecosyst. Environ.* 141, 184–192.

Keel, S.G., Leifeld, J., Mayer, J., Taghizadeh-Toosi, A., Olesen, J.E., 2017. Large uncertainty in soil carbon modelling related to carbon input calculation method. *Eur. J. Soil Sci.* <http://dx.doi.org/10.1111/ejss.12454>. (in press).

Lal, R., 2004a. Soil carbon sequestration to mitigate climate change. *Geoderma* 123, 1–22.

Lal, R., 2004b. Soil carbon sequestration impacts on global climate change and food security. *Science* 304, 1623–1627.

Li, X., Petersen, S.O., Sørensen, P., Olesen, J.E., 2015. Effects of contrasting catch crops on nitrogen availability and nitrous oxide emissions in an organic cropping system. *Agric. Ecosyst. Environ.* 199, 382–393.

Lonhienne, T.G., Trusov, Y., Young, A., Rentsch, D., Näsholm, T., Schmidt, S., Paungfoo-Lonhienne, C., 2014. Effects of externally supplied protein on root morphology and biomass allocation in Arabidopsis. *Sci. Rep.* 4, 5055.

Muñoz-Romero, V., Benítez-Vega, J., López-Bellido, R.J., Fontán, J.M., López-Bellido, L., 2009. Effect of tillage system on the root growth of spring wheat. *Plant Soil* 326, 97–107.

Mueller, T., Thorup-Kristensen, K., 2001. N-fixation of selected green manure plants in an organic crop rotation. *Biol. Agric. Hortic.* 18, 345–363.

Munkholm, L.J., Hansen, E.M., Olesen, J.E., 2008. The effect of tillage intensity on soil structure and winter wheat root/shoot growth. *Soil Use Manage.* 24, 392–400.

Mutegi, J.K., Peterson, B.M., Munkholm, L.J., Hansen, E.M., 2011. Belowground carbon input and translocation potential of fodder radish cover-crop. *Plant Soil* 344, 159–175.

Olesen, J.E., Askegaard, M., Rasmussen, I.A., 2000. Design of an organic farming crop-rotation experiment. *Acta Agric. Scand. B: Soil Plant Sci.* 50, 13–21.

Pearsall, W.H., 1927. Growth studies. VI. On the relative size of growing plant organs. *Ann. Bot.* 41, 549–556.

Pietola, L., Alakukku, L., 2005. Root growth dynamics and biomass input by Nordic annual field crops. *Agric. Ecosyst. Environ.* 108, 135–144.

Poorter, H., Nagel, O., 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review. *Aust. J. Plant Physiol.* 27, 595–607.

Powlson, D.S., Whitmore, A.P., Goulding, K.W.T., 2011. Soil carbon sequestration to mitigate climate change: a critical re-examination of the true and false. *Eur. J. Soil Sci.* 62, 42–53.

Rasmussen, J., Eriksen, J., Jensen, E.S., Høgh-Jensen, H., 2010. Root size fractions of ryegrass and clover contribute differently to C and N inclusion in SOM. *Biol. Fertil. Soils* 46, 293–297.

SAS, 1996. SAS Institute SAS/STAT STAT™ Software: Changes and Enhancements Through Release 6 11. SAS Institute, Cary, NC.

Smucker, A.J.M., 1984. Carbon utilization and losses by plant root systems. *ASA Spec. Publ.* 49, 27–46.

Snapp, S.S., Swinton, S.M., Labarta, R., Mutch, D., Black, J.R., Leep, R., Nyiraneza, J., O'Neil, K., 2005. Evaluating cover crops for benefits, costs and performance within cropping system niches. *Agron. J.* 97, 322–332.

Stockdale, E.A., Shepherd, M.A., Fortune, S., Cuttle, S.P., 2002. Soil fertility in organic farming systems-fundamentally different? *Soil Use Manage.* 18, 301–308.

Taghizadeh-Toosi, A., Christensen, B.T., Glendinning, M., Olesen, J.E., 2016. Consolidating soil carbon turnover models by improved estimates of belowground carbon input. *Sci. Rep.* 6, 32568. <http://dx.doi.org/10.1038/srep32568>.

Taylor, H.M., 1986. Methods of studying root systems in the field. *HortScience* 21, 952–956.

Thornley, J.H.M., 1972. A balanced quantitative model for root: shoot ratios in vegetative plants. *Ann. Bot.* 36, 431–441.

Thorup-Kristensen, K., 2001. Are differences in root growth of nitrogen catch crops important for their ability to reduce soil nitrate-N content, and how can this be measured? *Plant Soil* 203, 185–195.

Van Noordwijk, M., Brouwer, G., Koning, H., Meijboom, F.W., Grzebisz, W., 1994. Production and decay of structural root material of winter wheat and sugar beet in conventional and integrated cropping systems. *Agric. Ecosyst. Environ.* 51, 99–113.

Wahlström, E.M., Hansen, E.M., Mandel, A., Garbout, A., Kristensen, H.L., Munkholm, L.J., 2015. Root development of fodder radish and winter wheat before winter in relation to uptake of nitrogen. *Eur. J. Agron.* 71, 1–9.

Warembourg, F.R., Paul, E.A., 1977. Seasonal transfers of assimilated ¹⁴C in grassland: plant production and turnover, soil and plant respiration. *Soil Biol. Biochem.* 9, 295–301.