



Root decomposition at high and low N supply throughout a crop rotation



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ABSTRACT

Soil nitrogen (N) dynamics can be modified by cover crops in rotations with cereals. Although, roots are a major source of N, little is known about the dynamics of root decomposition of cash and cover crops. The objective of this study was to assess the effects that cover crop species have on i) the decomposition of spring wheat roots during the growth of cover crops, and ii) the decomposition of cover crop roots during the growing season of spring wheat. The experiment aimed also at comparing three non-winter hardy cover crops of varying shoot C/N ratios under low and high N input levels of 6 and 12 g N m⁻² y⁻¹, respectively. The experiment included spring wheat (*Triticum aestivum* L.) as the main crop and non-winter hardy cover crops (yellow mustard (*Sinapis alba* L.), phacelia (*Phacelia tanacetifolia* Benth), and sunflower (*Helianthus annuus* L.) as well as bare soil fallow treatment. Minirrhizotrons were used to non-destructively assess the spatial and temporal patterns of root growth and decomposition from 0.10 to 1.00 m. Simultaneously, we grew all crops in soil columns to measure destructively C and N content in the roots. We concluded that wheat root decomposition was not affected by cover crop species. In contrast, during the growing season of wheat root decomposition of yellow mustard was on average twice as high for phacelia and sunflower as a consequence of a higher production of roots with a significantly higher C/N ratio compared to the other cover crops.

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1. Introduction

Understanding the processes that affect nitrogen (N) uptake and utilization is of major importance with respect to the quality of crop products and the costs of production (Gastal and Lemaire, 2002). Cover crops alter the total supply of N and the timing of N availability within a crop rotation (Thorup-Kristensen, 1993b; Thorup-Kristensen, 1993a; Thorup-Kristensen, 1994). The N taken up by cover crops may be saved from loss through N leaching (Thorup-Kristensen et al., 2003), a process that negatively impact groundwater quality (Sprague et al., 2011; Galloway et al., 2014; Galloway et al., 2015). Although, cover crops allowed for an effective

reduction of N leaching compared to fallow (Tonitto et al., 2006), the efficacy shown by cover crops in reducing N leaching during growth is often relatively lower when the entire crop rotation is considered (Herrera and Liedgens, 2009; Herrera and Delgado, 2010; Plaza-Bonilla et al., 2015). As a result, the N saved by growing cover crops does not always increase N utilization by the main crop (Thomsen and Christensen, 1999; Macdonald et al., 2005; Sapkota et al., 2012). The N taken up by the cover crop will be available if the N demand of the following crop and the mineralization of the cover crop residues are well synchronized (Fraser et al., 2013; Ketterings et al., 2015). Mineralization of the shoot residues of the cover crops depends on the residue C/N ratio (Justes et al., 2009) among a set of several factors that Thorup-Kristensen et al. (2003) reviewed in detail. In contrast, less information was published on the mineralization of root residues. This lack of studies is especially acute for non-destructive screening that allows for understanding the dynamics of the decomposition of root residues.

Abbreviations: N, nitrogen; HN, high N input (12 g N m⁻² yr⁻¹); LN, low N input (6 g N m⁻² yr⁻¹).

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Root characteristics play an important role in determining the effects of cover crops on soil N and C dynamics. For example, a rapid establishment of the root system, was shown to be essential for a cover crop to reduce the amount of $\text{NO}_3\text{-N}$ leaching after the harvest of spring wheat (Herrera et al., 2010) while higher root growth in the subsoil was suggested to increase crop N uptake (Dinnes et al., 2002; Thapa et al., 2015). Roots are also critical for the transfer of nutrients saved by the cover crops to the succeeding main crop, as the N accumulated in their tissues is later released during their decomposition and made available for the subsequent crops. Storage of N in the root system is likely to be different among cover crop species and the way their roots decompose may affect the N release during the main crop season. In addition, with no tillage and removal of crop residues, roots are fundamental to maintain soil C and N levels. However, life cycle data about the dynamics of root decomposition in cereal crop rotations are scarce. The influence of very few factors has been investigated on root decomposition. For example, there are indications of a higher root decomposition of wheat on sandy soils compared to a silty clay loam soils (Swinnen et al., 1994) and the contribution to soil organic matter from maize roots was 1.5 times higher than that of maize shoots (Allmaras et al., 2004). Genotype may also influence patterns of root mortality, as indicated by the wide variation in root death rates observed in cultivars of tomato subjected to salt stress (Snapp and Shennan, 1994).

Root growth and decomposition was followed for three complete years in an experiment where spring wheat cover crop rotation was rotated with cover crops. Simultaneously, all the crops were grown each year in columns to assess C/N characteristics of their shoots and roots. The objective of this study was to assess the effects that cover crop species have on i) the decomposition of spring wheat roots during the growth of cover crops, and ii) the decomposition of cover crop roots during the growing season of spring wheat. The experiment aimed also to compare three non-winter hardy cover crops of varying shoot C/N ratios: yellow mustard, sunflower and phacelia, under low and high N input, i.e., 6 (LN) or 12 $\text{g N m}^{-2} \text{y}^{-1}$ (HN).

2. Materials and methods

Two types of experiments were conducted in the Swiss midlands near Zurich (47° 26' N, 8° 40' E) from March 2008 to November 2010; a rhizotron experiment which is regarded as the main experiment of this study and a complementary experiment using soil columns.

2.1. Rhizotron experiment

The rhizotron experiment was conducted outdoors in a field facility with 24 rhizotrons, each one was a watertight, double-walled fiberglass container insulated from outside. The inner surface area of the container was 1.00 m^2 (1.0 × 1.0 m) and the depth of the soil column in the rhizotrons was 1.10 m. At both ends of the two rows of rhizotrons, there were additional rhizotron-like containers to reduce border effects. Shading screens along the edges of the rhizotrons simulated border rows of plants.

The rhizotrons were filled with soil of the uppermost layer (0.00–0.30 m) from a nearby sandy loam area in February 2000. According to the methods given in parentheses, the soil contained 20 g kg^{-1} organic matter (Walkley-Black), 540 g kg^{-1} sand, 290 g kg^{-1} loam and 170 g kg^{-1} clay. The soil pH (CaCl_2), assimilable K (NH_4 acetate), P (Olsen), and total N (Kjeldahl) were 8.0, 26.7 g kg^{-1} , 0.4 g kg^{-1} , and 2.1 g kg^{-1} , respectively. The soil column in the rhizotrons overlaid three layers of quartz sand of increasing

texture and two layers of glass foam. A more complete description and evaluation of the facility can be found in Liedgens et al. (2000).

Each rhizotron contained 10 minirhizotrons (at soil depths of 0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.45, 0.60, 0.80, and 1.00 m) enabling non-destructive and frequent observations of root growth and senescence throughout the growing season (Smit et al., 2000). The minirhizotrons were 1.20 m long with an external diameter of 60 mm; these were placed horizontally in the rhizotrons to minimize root tracking.

The experiment simulated an annual crop rotation in which spring wheat (*Triticum aestivum* L. cv. Carasso) was followed by cover crops or soil without cover. The control treatment consisted of leaving the soil without cover (fallow) during autumn and winter. The non-winter hardy cover crops sunflower (*Helianthus annuus* L.), phacelia (*Phacelia tanacetifolia* Benth.), and yellow mustard (*Sinapis alba* L.). In addition to those four soil cover treatments, we included an additional treatment in which spring wheat received either a low N (LN; 6 $\text{g N m}^{-2} \text{y}^{-1}$) and a high N (HN; 12 $\text{g N m}^{-2} \text{y}^{-1}$) input. Treatments were arranged in complete randomized blocks and replicated three times. Each rhizotron was one experimental unit (plot) and was submitted to the same combination of soil cover and N input during the entire experiment.

Spring wheat was sown on 18 March 2008, 26 March 2009, and 8 March 2010 in all rhizotrons. The seeding rate was 420 seeds m^{-2} , and the rows were 0.14 m apart. Before each spring wheat sowing, fertilizer was applied at rates of 6 g m^{-2} of Foskal[®] (0.7, 2, 0.1, 0.4, and 0.2 g m^{-2} P, K, Mg, Ca, and S, respectively). Nitrogen was supplied in all rhizotrons only to spring wheat at a rate of 6 g m^{-2} of ammonium nitrate (NH_4NO_3) before sowing (i.e. LN and HN treatments). During the growing season of spring wheat, an additional 6 g N m^{-2} of ammonium nitrate was applied at the beginning of tillering to half the rhizotrons in each crop succession. Rhizotrons that received 12 g N m^{-2} constituted the HN treatment.

Following the same row arrangement of spring wheat, cover crops were sown without tilling the soil in the inter-rows on 5 August 2008, 17 August 2009, and 2 August 2010 at rates of 375 seeds m^{-2} (yellow mustard; hereafter mustard), 522 seeds m^{-2} (phacelia), and 100 seeds m^{-2} (sunflower). The sowing depth of all crops was 20–30 mm. No N was applied to the cover crops. Thus, the two different N input levels (i.e., LN and HN) resulted only from fertilization of the spring wheat crop.

2.2. Soil columns experiment

Due to the presence of minirhizotrons and the objective of having environments representative of conservation agriculture conditions, rhizotrons have been managed since 2000 as to minimize soil disturbance. Therefore, root samples could not be obtained from the rhizotrons. To obtain root C and N data, we simultaneously conducted an experiment in soil columns. Each column was a watertight, temperature-isolated container made of PVC. The inner diameter of the columns was 0.30 m and the depth of the soil in the columns was 0.85 m. Columns were filled with sandy loam soil. Before filling the columns, soil was sieved through a 2 mm sieve and roots were removed in order to have a substrate free of roots. All the crops, i.e. spring wheat ($n = 5$ per year) and cover crops ($n = 15$ per year) were sown and harvested each year in the columns simultaneously with the rhizotrons.

The columns with spring wheat received an application of 6 g N m^{-2} just before sowing and an application of 6 g N m^{-2} at the beginning of tillering. Therefore, the N input corresponded to the HN treatment of the rhizotrons. There was no N input corresponding to the LN treatment of the rhizotrons. The columns with cover crops received an application of 2 g N m^{-2} just before sowing, as it was estimated that this amount corresponded to the residual N left after spring wheat with HN in the rhizotrons. The layout was a

randomized, complete block design with five replications per year and one factor (cover crop treatment) in which each column was one experimental unit (plot).

2.3. Shoot sampling

Spring wheat was harvested on 5 August 2008, 17 August 2009, and 2 August 2010, at physiological maturity. After the first severe frost, the shoots of the cover crops were harvested on 20 November 2008, 24 November 2009, and 16 November 2010 in both rhizotron and columns experiments. Cover crops and spring wheat shoots were cut at ground level. The entire fresh weight of the shoots within a plot, as well as that of an aliquot (~15%), was determined for each crop. In the rhizotron experiment, the rest of the cover crop shoots were chopped and returned to the corresponding rhizotron, and distributed uniformly over the soil surface, simulating the management of cover crop residues without incorporation into the soil. In contrast, spring wheat grains and straw above 10 cm from soil surface were removed following common practice in environments with high biomass production. The spring wheat aliquot was threshed for the separation of grain and straw. In the columns experiment, all biomass was removed and not returned to the columns.

All aliquots were dried at 65 °C for 48 h for the determination of dry weights. These were used to estimate the corresponding dry weights per m². The dried samples were further ground (Fuchs-Mühlen MM 125 H, Maximilian Fuchs and CO., Vienna, Austria) and N concentration in grain and straw was determined with a CHN-1000 AutoAnalyzer (LECO Corporation, St. Joseph, MI, USA).

2.4. Root sampling

In the rhizotron experiment, root images were recorded at the minirhizotron–soil interface using a special camera system (Bartz Technology Co., Santa Barbara, CA, USA) from strips 18 mm wide and 243 mm long, corresponding to 18 single images, respectively. The camera system was connected to a computer to convert single images (13.5 × 18 mm) to a digital format using a frame grabber (I-Cube INC, Maryland, US). Images were taken every four days during the growing seasons of spring wheat and the cover crops. The images, recorded throughout the season at the same position in the minirhizotron, were organized into image time series. This allowed for the sequential screening of new and disappearing roots at each soil position. Therefore, on each sampling date an independent record of each of the two processes was generated instead of just net values. The screening of the image time series was carried out blockwise by trained operators. It was necessary to train the operators to avoid misinterpretation of objects in the images as roots (e.g. worms or soil pores). We differentiated roots of spring wheat and cover crops from each other based on the time of the year that were visible for the first time in the images.

In the columns experiment, the PVC columns were opened by previously prepared divisions on the side. The soil inside was divided at 0.05 m depth intervals from 0 to 0.30 m and at 0.10 m intervals from 0.30 to 0.85 m. The roots were washed manually in a 470- μ m sieve, organic debris and other materials were removed by decanting the samples, and root samples were then stored at -5 °C. After the fresh weight of roots was determined, they were dried for 48 h at 65 °C, weighed and submitted for C and N analysis following the same protocol than the shoots.

2.5. Data analysis

Data from minirhizotrons may be screened as number of roots or root length. Whether an object in the images was considered a root or not was decided according to [Upchurch and Ritchie \(1983\)](#).

Because we lack objective visual criteria to determine whether a root is functional ([Smit et al., 2000](#)), a root was considered to be dead when it was no longer visible in the successive minirhizotron images. Thus, the obtained response variables were the cumulative number of roots and cumulative root length, i.e., the increases in roots and in root length between the sowing date and the target observation date. These variables were converted into a surface unit (cm²) and here, as in numerous other studies ([Coleman et al., 1996](#); [Pregitzer et al., 2002](#); [Crocker et al., 2003](#)) were correlated. We present only results on root length cm² and hereafter we refer to them as root length density.

Root decomposition has been more extensively analyzed in perennial species than in annual crops. In perennial species, different types of survival analysis have been considered to study root decomposition. Contrary to expressing root decomposition in terms of the probability of single roots not dying as done with root survivorship in perennial species elsewhere (e.g. [Anderson et al., 2003](#)), we followed [Block and Van Rees \(2006\)](#) and we considered root decomposition in terms of decrease of root length density. We based this decision on the recommendations for studying root decomposition in annual crops ([Smit et al., 2000](#)) and because we consider this metric more useful to potentially extend the use of the reported results for modeling purposes. The rate of root decomposition was calculated as the difference on root length density between two sampling dates divided by the time interval between them.

Analysis of variance for the shoot and root data were performed using the function “lme” in R ([R Development Core Team, 2007](#)). The cover crop and N supply treatments were set as fixed effects, while the blocks were set as random effects. The analyses were performed separately for each type of experiment (rhizotron and columns). The relationship between shoot and root C:N ratios was also studied with the function “lme” and with cover crop treatment and blocks as fixed and random effects, respectively.

3. Results

3.1. Growing conditions

Annual precipitation was 1213 mm, 1098 mm, and 1001 mm in 2008, 2009, and 2010, respectively. For the three years of the study, precipitation was within the range observed during 25 years but above the 25 year average (1132 mm) in 2008 and below this average in 2009 and 2010. Mean air temperature was comparable in 2008 (9.62 °C) and 2009 (9.87 °C) and both were above the 25 year average (9.60 °C). In contrast, the mean air temperature was lower in 2010 (8.81 °C) and below the 25 year average. The distribution of both also did not show a different pattern to that observed for the 25 years period.

3.2. Growing season of cover crops

Sunflower was the cover crop that tended to have the highest shoot biomass, while mustard tended to have the least ([Table 1](#)). The ranking among the cover crops according to shoot biomass N concentration was reversed; mustard had the highest N concentration and sunflower the lowest. Mustard generally took up the most N (data not shown), as much as 12 g N m⁻² (HN in 2009). It was the cover crop with the highest N uptake in 2009 and in 2010 under both N input levels. Phacelia had the highest coefficient of variation in N uptake; 33% under LN and 27% under HN while the corresponding values for mustard were 10% and 16%, respectively. A higher N availability during the growth of the cover crops that resulted from the supply of N to the previous spring wheat, increased the biomass yield and shoot N concentration of the cover crops, by 36% and 21% on average, respectively.

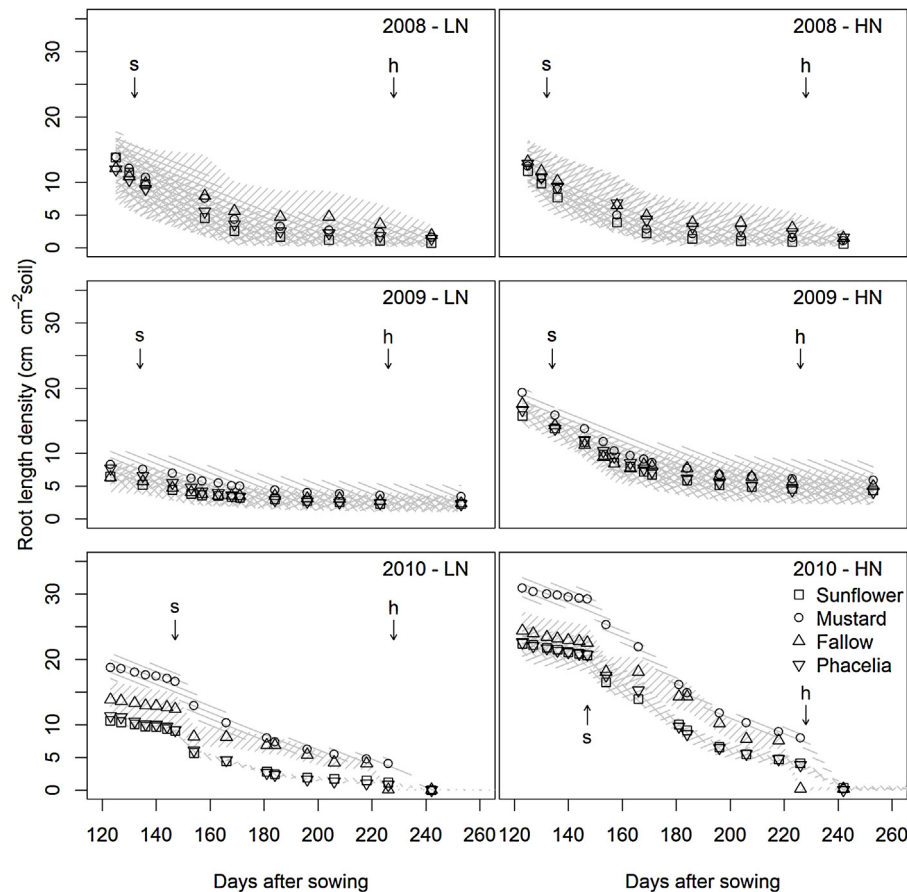


Fig. 1. Length density of decomposing roots of spring wheat during the growing season of cover crops as influenced by year, soil cover treatment, and N supply in the rhizotron experiment. LN: $6 \text{ g N m}^{-2} \text{ y}^{-1}$ and HN: $12 \text{ g N m}^{-2} \text{ y}^{-1}$. “s” and “h” show sowing and harvest date, respectively, of cover crops. Days after sowing are days after sowing spring wheat and shaded areas are the standard errors of the means of each treatment.

Table 1

Mean values of biomass and shoot N concentration of cover crops as affected by year and N supply in the rhizotron experiment.

Cover crop	2008		2009		2010	
	LN	HN	LN	HN	LN	HN
Biomass yield (g m^{-2})						
Mustard	533 b ^a	783 b	475 b	740	462 b	700 b
Phacelia	619 a	767 b	499 b	691	506 ab	756 ab
Sunflower	644 a	823 a	742 a	783	629 a	801 a
Biomass N concentration (%)						
Mustard	1.06 ab	1.12 ab	1.44 a	1.62 a	1.29 a	1.61 a
Phacelia	1.25 a	1.64 a	1.15 a	1.65 a	0.78 b	0.95 b
Sunflower	0.77 b	0.82 b	0.86 b	0.98 b	0.73 b	0.92 b
Root length density (cm cm^{-2} soil) before first severe frost						
Mustard	19.87a	20.23a	17.08a	26.94a	18.10a	20.87a
Phacelia	12.51b	12.93b	10.82b	16.98b	11.05b	16.05b
Sunflower	17.40ab	16.89ab	10.58b	18.74b	10.62b	17.81ab

Within columns, values for the same N supply level followed by different letters are significantly different according to LSD tests ($p < 0.05$).

The decomposing roots of the previous spring wheat were only affected by N supply but not by the soil cover treatment, despite a trend of these roots to decompose at a slower rate with the fallow than with cover crops (Fig. 1). Few spring wheat roots decomposed before anthesis (5%, 8% and 7% in 2008, 2009 and 2010 averaged across the two experimental factors, respectively). The root length density of spring wheat at the beginning of the cover crop growth was highly variable across years, it ranged from 7 (LN – 2009) to 25 (HN – 2010) $\text{cm}^{-1} \text{ cm}^{-2}$ soil (Fig. 1).

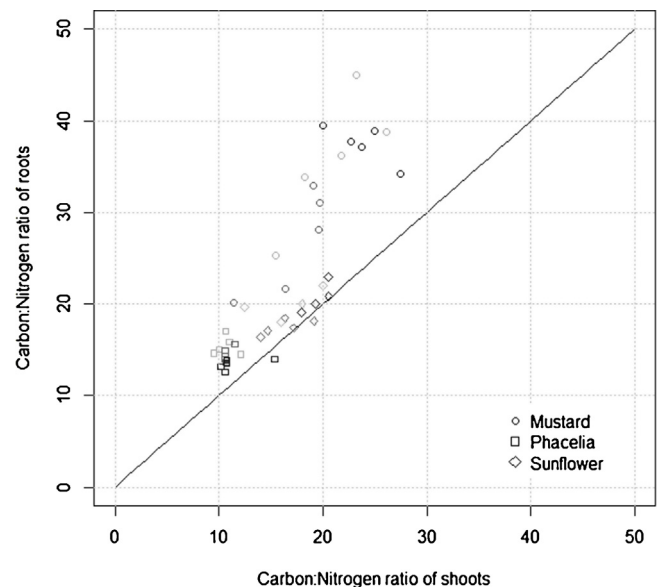


Fig. 2. Relationship between the Carbon:Nitrogen ratios in the shoots and in the roots of cover crops grown in the soil column experiment. The solid line indicates the 1:1 ratio. Light, medium, and dark gray color of symbols represent results obtained in 2008, 2009, and 2010, respectively.

Root C/N ratios obtained from soil columns were on average 14, 19, and 33 for phacelia, sunflower, and mustard, respectively. Fig. 2 shows C/N ratios of shoot and roots of the cover crops. Phacelia had

Table 2
Mean values of selected shoot parameters of spring wheat as affected by year and N supply in the rhizotron experiment.

Previous soil cover	2008		2009		2010	
	LN	HN	LN	HN	LN	HN
	Grain yield (g m ⁻²)					
Fallow	303	496	381 a [†]	618 b	363	592
Mustard	–	–	358 ab	668 a	343	607
Phacelia	–	–	388 a	691 a	342	610
Sunflower	–	–	334 b	667 a	324	607
	Straw yield (g m ⁻²)					
Fallow	680	961	760 b	1271 b	759 b	1228 b
Mustard	–	–	801 a	1273 b	809 a	1274 b
Phacelia	–	–	822 a	1398 a	830 a	1383 a
Sunflower	–	–	699 c	1275 b	785 b	1226 b
	Grain N concentration (%)					
Fallow	1.90	2.41	2.76 a	2.70	2.11	2.24
Mustard	–	–	2.68 a	2.82	2.07	2.23
Phacelia	–	–	2.56 b	2.85	2.16	2.17
Sunflower	–	–	2.57 b	2.78	2.13	2.29
	Straw N concentration (%)					
Fallow	0.79	0.93	0.52	0.47 b	0.47 b	0.35 b
Mustard	–	–	0.57	0.49 b	0.59 a	0.48 a
Phacelia	–	–	0.50	0.46 b	0.44 b	0.31 b
Sunflower	–	–	0.55	0.55 a	0.49 b	0.53 b
	Root length density (cm cm ⁻² soil) at harvest					
Fallow	13.94	13.57	6.37	17.57	13.85 b	24.41 b
Mustard	–	–	8.29	19.33	18.76 a	30.88 a
Phacelia	–	–	7.75	16.67	11.34 b	22.62 b
Sunflower	–	–	6.48	15.74	10.59 b	22.39 b

Within columns, values for the same N supply level followed by different letters are significantly different according to LSD tests ($p < 0.05$).

both the lowest shoot C/N ratio and root C/N ratio among the cover crops. The relationship between root and shoot C/N ratio was found to be apart from a 1:1 relationship for phacelia and mustard while it was closer for sunflower. In all cases, C/N ratios in roots were higher than in shoots, showing less N in the roots than in the shoot. Mustard tended to have higher C/N ratios than the other cover crops in both shoots and roots (Fig. 2). The N content of mustard was similar than the other cover crops in the shoot but significantly lower in the roots.

3.3. Growing season of spring wheat

There were little consistent effects of the cover crops on the grain yield, biomass production and N concentration of the succeeding spring wheat (Table 2). In 2009, grain N was significantly higher after mustard than after phacelia or sunflower. However, this effect could not be confirmed in 2010. Without exception, a higher N supply increased grain and straw yields of spring wheat. Except for the fallow treatment, the higher N supply increased or maintained the grain N concentration of the spring wheat compared to LN. In contrast, the straw N concentration of spring wheat was lower with HN than with LN for all the cover crop treatments, except sunflower.

At the sowing date of spring wheat the root length density of the previous cover crops ranged between 9.2 and 23.1 cm cm⁻² soil; it then decreased linearly during the early stages of the growing season of spring wheat (Fig. 3). This was followed by a phase in which the root length density of the cover crops was low (around 5 cm cm⁻² soil) and it remained constant for several weeks. That phase coincided with the reproductive stages of spring wheat. One year after sowing the cover crops, we still observed root length densities of 5.23, 2.27, and 1.90 cm cm⁻² soil under HN for mustard, sunflower, and phacelia, respectively. The corresponding values under LN were 4.83, 2.27, and 1.71 cm cm⁻² soil.

Consistent effects of species and N supply were found on the root length density of the decomposing cover crops. A higher N input in

the rotation had variable effects on the root length density of the cover crops before the first frost; it resulted from no increase (most of 2009) to a 63% increase in 2010. Averaged across all sampling dates, the increase due to higher N was 1% in 2009 and 55% in 2010. As a result, in 2009 the rate of root decomposition was similar under both N levels and in 2010, it was 7% higher under HN than under LN.

In 2009 and 2010 and at the two N supply levels, the root length density of mustard was significantly higher than that of sunflower and phacelia (Fig. 3). Although, in 2010 the roots of all cover crops had similar rates of decomposition, the roots of mustard decomposed initially at a lower rate than sunflower. This was also observed in 2009 even though the differences were smaller. The rate of decomposition of mustard's roots throughout the entire growing season of wheat was 0.11 cm⁻¹ cm⁻² soil d⁻¹ in 2009, 0.10 cm⁻¹ cm⁻² soil d⁻¹ in 2010 at HN, and 0.05 cm⁻¹ cm⁻² soil d⁻¹ in 2010 at LN. The rate of root decomposition of phacelia compared to mustard was 40% lower at HN averaged across both years and 20% lower at LN in 2010. Additional factors to note are that a significantly higher density of mustard roots was found at the beginning of the growing season of spring wheat and the roots of this cover crop had a different dynamics of decomposition; while around 75% of the roots of sunflower and phacelia were decomposed during the early stages of spring wheat, this was only 60% for mustard. Therefore, the roots of mustard showed a different dynamics of decomposition as compared to phacelia and sunflower. The rate of root decomposition was similar under both N levels in 2009, while in 2010 it was 7% higher under HN than under LN. Therefore, more roots decomposed under HN in 2010 because there were more roots with this treatment at the beginning of the growing season. However, we did not find clear evidence of N priming effects accelerating the decomposition of cover crop roots.

4. Discussion

In previous studies, we observed that mustard clearly modified the dynamics of NO₃-N and NH₄-N leaching during the growing season of spring wheat and we found both a lower N leaching of mustard and a higher N leaching of spring wheat after mustard as compared to fallow, phacelia, or sunflower (Herrera and Liedgens, 2009). Therefore, in the present study we investigated with more details which factors could explain those results, we focused particularly on the dynamics of root decomposition throughout the entire crop rotation and we found evidence for a different dynamics in the decomposition of roots of mustard as compared to the other studied cover crops. Cover crops may influence main crops through the decomposition of crop residues (Rasse and Smucker, 1998; Radicetti et al., 2016). Swift decomposition has been proposed as a mechanism by which barley benefits from a preceding crops (Nauugaard-Nielsen et al., 1998). During the cover crop season, mustard produced significantly more roots than the other cover crops and as a result there were more roots of this cover crop than of phacelia or sunflower during the growing season of wheat (Fig. 3). However, the roots of mustard had a higher C/N ratio than those of phacelia and sunflower (Fig. 2). Despite similar rates of decomposition, roots of mustard may have released less N than those of phacelia and sunflower. Our findings about the role of root chemical composition on the decomposition rates of roots are in agreement with reports of experiments conducted in grasslands (e.g. Kong and Six, 2010; Birouste et al., 2012). Therefore, the choice of cover crop species influences the input of root carbon and N during the growing season of the main crop by two characteristics: by the total input which depends on the capacity of the cover crop to produce root biomass (Table 1) and by the dynamics of root decomposition (Fig. 3) which depends on the total quantity of roots

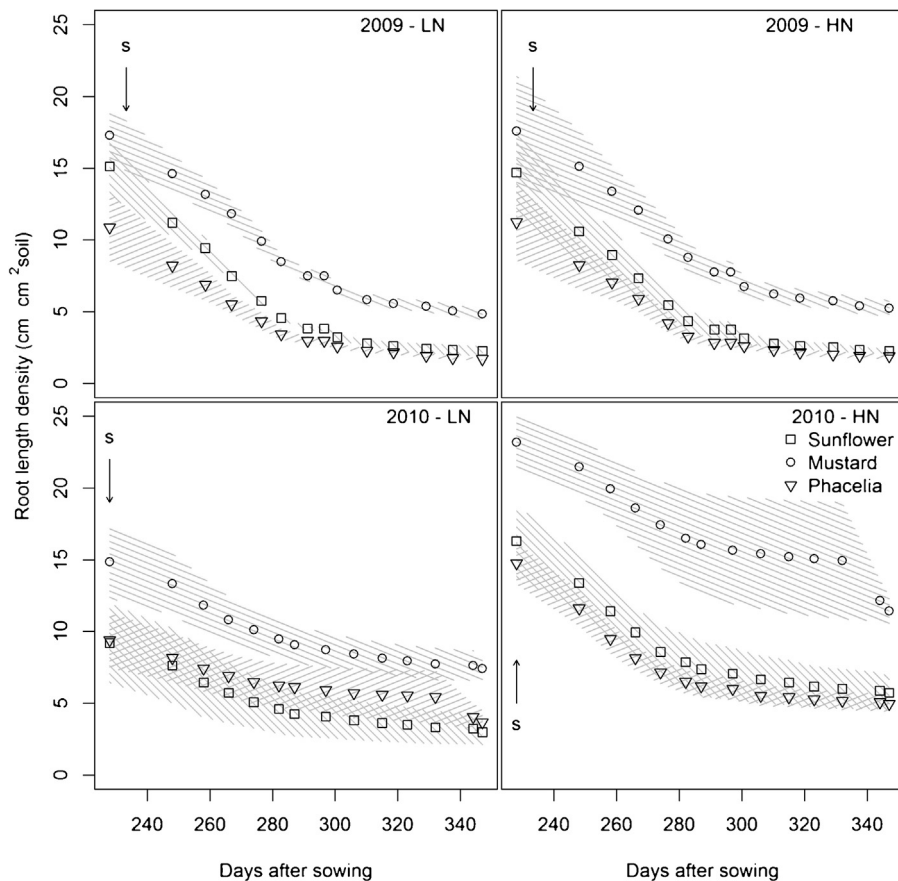


Fig. 3. Length density of decomposing roots of cover crops during the growing season of spring wheat as influenced by year, cover crop species, and N supply in the rhizotron experiment. LN: $6 \text{ g N m}^{-2} \text{ y}^{-1}$ and HN: $12 \text{ g N m}^{-2} \text{ y}^{-1}$. "s" show sowing date of spring wheat. Days after sowing are days after sowing the cover crops and shaded areas are the standard errors of the means of each treatment.

during the growing season of the main crop and the tissue characteristics of the root residues (Fig. 2). An additional important result of the analysis of C/N ratios is that root C and N concentrations of the cover crops cannot be predicted from shoot values (Fig. 2). Therefore, conclusions about C and N release from roots cannot be derived from shoot measurements only.

Growth of new roots but also death of existing roots, both determine the localization of nutrient and water uptake and allow for the adjustment of root activity with regard to the availability of resources. The precise screening of root dynamics depends on accurate methods to quantify roots. According to Eissenstat and Yanai (1997) results on the effect of root decomposition on soil fertility have been inconsistent due to differences in methodology and thus, more direct measurements of root decomposition are needed to better understand this effect. The inaccessibility of the root system and the difficulty of measuring simultaneous root production and mortality have historically limited our ability to study fine root decomposition (Jackson et al., 1997). Estimates of net root decomposition during the growing season are only possible if separate information on root growth and root decomposition is obtained. The possibility of separating growth and decomposition of root systems gives the opportunity to investigate how different factors influence each of the processes independently (Van Noordwijk et al., 1994). Minirhizotrons allow for multiple root observations of the same soil position throughout the entire growing season of the crops (Smucker, 1993). Accounting for root decomposition independently of root growth provides a more precise understanding of rhizosphere processes than relying only on standing root density (Goss and Watson, 2003). For example, Gibbs and Reid (1992) found that measuring only net root length underestimated root gross pro-

duction of winter wheat by as much as 36%. Experiments, in which the root dry matter was determined by washing soil samples provided variable results and changes in root dry matter during grain filling, mixing up the effects of increasing root dry matter, brought about by the growth of new roots, and the decrease in dry matter caused by the decomposition of roots. Studying root decomposition for the entire crop rotation was important to understand the effects of the cover crop species on N dynamics that occurred beyond a particular growing season and to weight the relative importance of this process during the growing seasons of both main and cover crops. These findings extended the limited information that exists regarding root decomposition in cropping systems and crop rotations.

Besides cover crop species, another factor that affected root decomposition was the N input; higher N availability increased significantly the amount of wheat roots that decomposed and tended to increase the amount of cover crop roots. Our results are in line with those of Cai et al. (2015) for maize roots. These results show that the level of N in a crop rotation influences significantly the input of root C and N. Other studies showed that a higher supply of N increases soil organic matter (Grandy et al., 2013) and rhizodeposition (Allmaras et al., 2004). In contrast, we did not find evidence of N accelerating decomposition of roots and therefore, having a priming effect (Cheng et al., 2003; Zhu et al., 2014). The lack of priming effect has been reported in other studies with wheat (Liljeroth et al., 1994; Zang et al., 2016) and it can be explained by the use of mineral N instead of organic N as the main N source and by the fact that N may not have been limited for the microbial decomposers in our study (Liljeroth et al., 1994; Chen et al., 2014; Zang et al., 2016).

A consistent benefit of cover crops for spring wheat grain yields was not evident from the present study (Table 2). Increases in grain yield after a preceding crop were reported for wheat after sunflower and oilseed rape (Debaeke et al., 1996; Dachler and Kochl, 2003) and for barley after fodder radish (Robinson et al., 1994). We did not observe negative effects following substitution of the fallow for cover crops; for some combinations of years and N inputs cover crops tended to decrease grain N concentration of spring wheat, but these effects were generally not significant. Thus, we did not find in our conditions evidence of pre-emptive competition for N (Thorup-Kristensen, 1993a; Sorensen et al., 1994; Thorup-Kristensen et al., 2003). Pre-emptive competition has been observed (c.f. Thorup-Kristensen, 1993a) for vegetable crops that depend on early N uptake. This is not the case for wheat, which continues to absorb high amounts of N late in the growing season (Page et al., 1978; Barraclough, 1986; Fowler, 2003). As regards to cover crops, phacelia proved to be less reliable than the other species in terms of N uptake. Phacelia as in previous studies had the highest coefficient of variation in N uptake among the cover crops that we included.

There were no differences in the decomposition of wheat roots during the growth of the cover crops (Fig. 1). As a consequence, the direct screening of root decomposition that we used did not show any detectable effect of biofumigation; an effect attributed to some crucifers and reported to influence soil microorganisms (Hossain et al., 2015). Similarly, reported cover crop-specific differences in microbial or enzymatic activity affecting root decomposition (Mendes et al., 1999; van der Krift et al., 2001) may not exist among the set of selected cover crops.

We concluded that wheat root decomposition was not affected by cover crop species. In contrast, during the growing season of wheat root decomposition of yellow mustard was on average twice as high for phacelia and sunflower as a consequence of a higher production of roots with a significantly higher C/N ratio compared to the other cover crops.

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