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ORIGINAL PAPER

Assessing nitrogen fluxes from roots to soil associated to rhizodeposition by apple (*Malus domestica*) trees

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Abstract The mass transfer from root to soil by means of rhizodeposition has been studied in grasses and forest trees, but its role in fruit trees is still unknown. In this study, N fluxes from roots to soil were estimated by applying a ^{15}N mass balance technique to the soil–tree system. Apple (*Malus domestica*) trees were pre-labelled with ^{15}N and then grown outdoors in 40 L pots for one vegetative season in (1) a coarse-textured, low organic matter soil, (2) a coarse-textured, high organic matter soil, and (3) a fine-textured, high organic matter soil. At tree harvest the ^{15}N abundance of the soils was higher than at transplanting, but the total amount of ^{15}N present in the tree–soil system was similar at transplanting and tree harvest. The soils had a strong effect on N fluxes from and to the soil. In the fine-textured soil, 11% of the total plant-derived nitrogen was transferred to the soil, compared with 2–5% in the two coarse-textured soils. Rhizodeposition was higher in the fine soil (18% of the primary production) than in the coarse-textured soils, whereas higher soil organic matter depressed rhizodeposition. Nitrogen uptake was almost double in the coarse-textured, high organic matter soil versus the other soils. Our results indicate that below-ground primary productivity is significantly underestimated if based on root production data only. Rhizodeposition represents a major process, whose role should not be underestimated in carbon and nitrogen cycles in orchard ecosystems.

Keywords Apple · Nitrogen flux · Soil organic matter · Rhizodeposition

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Introduction

Plant mass transfer into the soil occurs by aboveground litter, by root death and by exudation of organic compounds. While decomposition of aboveground litter and consequent humus formation have received extensive attention (Berg and McClaugherty 2003; Tagliavini et al. 2007), the other two processes, often referred to as rhizodeposition received attention only recently, especially for their role in sustainable agriculture. Understanding carbon (C) and nitrogen (N) cycles would be more accurate if estimates of root C and N rhizodeposition were available. Several studies have been published on rhizodeposition in grass and forest ecosystems (Hogh-Jensen and Schjoerring 2001; Dixon and Turner 1991; Mayer et al. 2003), but data on this phenomenon in fruit trees is lacking.

Rhizodeposition of N varies from 6 to 30% of total plant N among species of legumes and grasses (Jensen 1996; Mayer et al. 2003; Sawatsky and Soper 1991; Lynch and

Whips 1990; Janzen 1990; Janzen and Bruinsma 1993), due to different experimental conditions, plant species, soil texture, soil water content (Pabin et al. 1998; Taylor and Gardner 1963; Beukes 1984) and nitrogen availability (West et al. 2004).

Carbon or nitrogen fluxes from roots to soil are measured in several ways. Traditional methods based on variation in root biomass are hampered by the inability to take into account simultaneous root production and mortality. Root observations using minirhizotrons (Bohm 1979) are helpful for qualitative assessments of root turnover.

The use of stable isotopes allows a more quantitative approach. Both natural abundance and enrichment studies have been performed. Ineson et al. (1996), for example, grew birch seedlings in pots containing C_4 soil derived from beneath a maize crop, and studied the rhizodeposition-induced variation of soil ^{13}C abundance. The most frequently used approach, however, is the enrichment of the system with the less abundant isotope (^{13}C or ^{15}N) (Robinson 2001; Dawson et al. 2002).

Enrichment is the addition to a system of material with an isotopic ratio significantly different from the natural background level, allowing the study of fluxes and transformations. For example, Hendricks et al. (1997) studied the depletion of soil ^{15}N caused by unlabelled N derived from roots of red pine growing in soil previously enriched with ^{15}N. Some assumptions have to be met in order to avoid possible misjudgements leading to errors in calculating N fluxes by stable isotopes: (1) the distribution of the applied ^{15}N has to be uniform throughout the system (Davidson et al. 1991), and (2) it has to be assumed that there is no isotopic discrimination during biological processes (Peterson and Fry 1987; Brearley et al. 2005; Kolb and Evans 2003).

In this paper we approached the study of rhizodeposition by growing pre-labelled apple trees in soils of natural ^{15}N abundance. By quantifying the changes in soil ^{15}N enrichment at the end of experimental period, the flux of N from roots into the soil was assessed by mass balance (Dawson et al. 2002). Soils used in this experiment differed in texture and fertility in order to test the effect of those factors on rhizodeposition.

Materials and methods

Labelling plant material and growing conditions

Fifteen one-year-old apple (*Malus domestica*, Borkh.) trees belonging to the cultivar Gala (Galaxy) grafted on M9 rootstock were planted in the winter of 2000/2001 in 40 L pots filled with coarse sand and grown outdoors at the Experimental Station of the University of Bologna in Cadriano (Bologna, Italy; 44° 35′ N, 11° 27′ E, 33 m a.s.l.). During the 2001 and 2002 vegetative seasons, trees received a complete modified Hoagland solution (5 mM KNO_3, 2.0 mM $MgSO_4 \cdot 7H_2O$, 2.0 mM KH_2PO_4, 5 mM $Ca(NO_3)_2$, 9.2 μM $MnCl_2 \cdot 4H_2O$, 46.4 μM H_3BO_3, 0.12 μM Na_2MoO_4, 0.8 μM $ZnSO_4 \cdot 7H_2O$, 0.37 μM $CuSO_4$, 50 μM Fe-EDTA) with N as labelled $^{15}NH_4^{15}NO_3$ (10 at % ^{15}N). Each tree received a total of 10 g of labelled N in ten equal applications of 1 g each spread over the year.

At the beginning of February 2003, the total number of buds was counted. Trees were then pruned to standardize total shoot length to an average of 340 ± 5 cm tree^{-1} (SE). Three randomly chosen plants were harvested and divided into roots and stems. Dry weight, total N and ^{15}N content of each sampled organ was determined. The remaining plants were removed from pots, roots were cleaned from the sand in water, and tree fresh weight was measured. Their dry weight and biomass partitioning above- and belowground was estimated based on the fresh to dry weight ratio and the partitioning in the three harvested trees. Trees were then moved to the Experimental Station of Laimburg (Bolzano-Bozen, Italy; 46° 21′ N, 11° 18′ E, 250 m a.s.l.) and on 10 March 2003 transplanted into 60 L pots filled with one of three soil types, selected for their chemical and physical composition (Table 1). Soils were collected just before transplanting, cleaned of debris (coarse roots, old wood, stones, etc.) but not sieved. One of the soils, coming from the Experimental Station of University of Bologna in Cadriano, was collected from the alleys of a pear orchard and had a fine texture and high organic matter and total nitrogen content (referred to as FT-HOM). The two other soils (referred to as CT-LOM and CT-HOM) were collected from the alleys of an apple orchard at the Research Centre for Agriculture and Forestry at Laimburg. Both had a coarse texture but differed in total organic matter and nitrogen content, cation exchange capacity (CEC), and available phosphorus concentration (all lower in the CT-LOM than in the CT-HOM soil, Table 1). Total N content was similar in the CT-HOM and in the FT-HOM soils.

Trees were allowed to grow for one vegetative season under a transparent shelter. Soil water potential was maintained between –0.01 MPa (field capacity) and –0.04 MPa by addition of demineralised water twice a week. No N addition occurred during the growing season.

Soil sampling and tree harvesting

Fruits were picked when ripe in August. All absscised leaves were collected twice a week during senescence by wrapping the tree canopies with a wide-mesh net to intercept fallen leaves until complete abscission. Trees were harvested on 9 December 2003 (291 days after transplanting).

Table 1 Main chemical and physical characteristics of soils (average ± SE)

Soil type	Texture (g kg^{-1})			Soil organic matter (g kg^{-1})	pH	C_{org} (g kg^{-1})	N_{tot} (g kg^{-1})	Available P (mg kg^{-1})	Cation exchange capacity (cmol$_+$ kg^{-1})	Exchangeable K (mg kg^{-1})	Exchangeable Mg (mg kg^{-1})
	Sand	Silt	Clay								
CT-HOM	387	586	27	20.3 ± 0.6	7.3 ± 0.1	12.11 ± 0.07	1.29 ± 0.03	147.5 ± 9.1	11.0	182.5 ± 7.5	107.5 ± 23.4
CT-LOM	360	621	19	8.5 ± 1.7	7.4 ± 0.1	5.35 ± 0.05	0.78 ± 0.01	60.0 ± 7.1	8.5	135.0 ± 10.4	70.0 ± 19.7
FT-HOM	104	542	354	23.0 ± 0.4	7.3 ± 0.1	11.95 ± 0.07	1.34 ± 0.05	95.0 ± 2.9	19.4	170.0 ± 7.1	152.5 ± 7.5

At harvest, trees were excavated from pots and the root system gently shaken to remove the soil. The following organs were collected for each harvested plant: axes (current year growth of stems), stems (lignified organs of the plant excluding the current year growth), fine roots (less than 2 mm diameter) and coarse roots (more than 2 mm diameter). Roots were separated manually and washed under tap water on a fine-mesh sieve to eliminate soil particles. Each plant organ was oven dried at 60°C with forced ventilation for 48 h, weighed, milled and sieved to pass a 0.2 mm mesh.

The net dry weight gains of each organ were determined by subtracting the estimated initial from the measured final dry weights of each individual tree. The fresh weight of the soil present in each pot was determined and a sub-sample of about 5 kg was collected and dried at 105°C for 72 h to derive the total soil dry weight. The dry soil was then ground for analysis. The remaining soil was resuspended in water and filtered through a sieve of 5 mm mesh net to recover any remaining roots.

^{15}N analysis and N flux from tree to soil associated to rhizodeposition

The concentration of total nitrogen (N_{tot}) and ^{15}N abundance in plant organs and soil samples were determined by an elemental analyser coupled with a mass spectrometer for stable isotope determination (Delta Plus, Finnigan-Mat, Germany). Each plant organ was analysed at least twice and each soil sample was analysed at least thee times. The mass of ^{15}N in excess of natural levels in tree organs and soils was calculated as follows:

$$^{15}\mathrm{N(mg)} = \frac{\mathrm{N_{tot}\ (mg)} \cdot {}^{15}\mathrm{N\ excess\ (atom\%)}}{100}$$

The ^{15}N excess (atom %) was calculated by subtracting the natural abundance of ^{15}N (0.3663%) from the abundance of ^{15}N in samples. The amount of ^{15}N in tree organs and in the soil was used to calculate total tree and soil ^{15}N contents.

To determine the net N flux from roots to soil associated with rhizodeposition, we applied a ^{15}N mass balance to the tree–soil system, assuming that all ^{15}N originally present in trees remained in the tree–soil system during the experiment. Because ^{15}N was present in the soil at transplanting only at natural abundance, it was assumed that all the ^{15}N exceeding natural abundance levels in the soil at the end of the period was derived from roots.

The net flux of N from roots to soil by rhizodeposition was calculated by multiplying the total N mass in soil by the ratio between ^{15}N excesses in soil and in roots:

$$\mathrm{N\ flux_{root\rightarrow soil}\ (mg)} = \mathrm{total\ N_{soil}(mg)} \cdot \frac{{}^{15}\mathrm{N\ excess_{soil}(\%)}}{{}^{15}\mathrm{N\ excess_{root}(\%)}}$$

where the ^{15}N excess in the root has been considered as an average of ^{15}N excesses measured at transplanting and at the harvest of trees in December.

Data on N flux from roots to soil were used to estimate rhizodeposition:

$$\mathrm{rhizodeposition\ (mg)} = \frac{\mathrm{N\ flux_{root\rightarrow soil}\ (mg)}}{\mathrm{N_{root}(\%)}} \cdot 100$$

This estimate is based on the assumption that roots did not absorb any labelled N during the experiment.

Belowground production was estimated as the sum of the estimated rhizodeposition and the gain in root biomass, assuming that organic matter transferred to the soil by rhizodeposition has the same C:N ratio as the living root tissues.

The amount of N absorbed by trees during the season was calculated as the difference between total N content at the December harvest and at transplanting. We also calculated the average N concentration of trees considering N concentration and mass of single organs. Nitrogen use efficiency (NUE) was calculated as the ratio between the increase of total tree biomass and nitrogen uptake during the season.

Statistical analysis

The experiment had a completely randomized design. The data were subjected to analysis of variance (ANOVA). The statistical significance of differences among means was determined using a least significant difference (LSD)

test ($P < 0.05$). All data are reported as average ± standard error (SE). Data on tree productivity and rhizodeposition, and NUE and biomass allocation to rhizodeposition were subjected to linear correlation analysis by StatGraphics (StatPoint, Inc.).

Results

^{15}N distribution and N uptake

At transplanting, trees had an average ^{15}N enrichment of 5.41 ± 0.38 (SE) at.% and the mass of ^{15}N was, on average, distributed 28% belowground and 72% aboveground. The ^{15}N present in the tree–soil system did not significantly change from transplanting to tree excavation, indicating that the system was suitable for applying a mass-balance approach. Specifically, we recovered 191.6 ± 30.3 (SE) mg ^{15}N tree^{-1} in the trees at transplanting and 195.8 ± 16.6 mg ^{15}N tree^{-1} in the soil–tree system at the final harvest. Roots and stems markedly reduced their initial ^{15}N content which was in part allocated to new growth and in part transferred to the soil (Fig. 1).

Tree nitrogen uptake in the three soils was different. Those in CT-HOM soil absorbed approximately twice the amount of N as those in the other soils (Table 2). Average N concentration of trees was also highest in CT-HOM soil (Table 2).

There were no significant differences in the total N concentration in the three soils from the beginning to the end of the season, but the ^{15}N abundance of the three soils collected at tree harvest was higher than those at transplanting (data not reported in table). At the end of the season, higher ^{15}N abundances were recorded in FT-HOM soil (0.4516 ± 0.0081 at.% ^{15}N) than in the two CT soils (0.3941 ± 0.0156 at.% ^{15}N). As a consequence, the estimated flux of nitrogen from roots to soil was highest in the FT-HOM soil and lowest in the two CT soils (Table 2).

Rhizodeposition, and above- and belowground production

Rhizodeposition differed among the three soils, being highest in FT-HOM, intermediate in CT-LOM and lowest in CT-HOM soil (Table 3).

Above- and belowground net primary production (ANPP and BNPP, respectively) were both highest for trees grown in FT-HOM soil, which also showed the highest values of increase in tree biomass (Table 3).

Tree NPP was positively correlated with the amount of C ($r^2 = 0.53$, data not reported) and N (Fig. 2) in rhizodeposition. Nitrogen use efficiency (NUE) was lower ($P = 0.0071$, not reported in tables) in the CT-HOM soil trees (112 ± 9) than in the other two soils (248 ± 18 in FT-HOM and 222 ± 33 in CT-LOM). Analysing the whole dataset, we found a significant and positive linear correlation between the biomass allocation to rhizodeposition and NUE (Fig. 3).

Discussion

Our understanding of carbon and nitrogen cycles in ecosystems is often limited by the availability of reliable estimates of root C and N deposition by plants into the soil. We have quantified N flux from roots to soil and have provided an estimate of the magnitude of rhizodeposition, demonstrating an effect of soil type on rhizodeposition and biomass allocation. During one vegetative season, trees in the fine-textured soil (FT-HOM) transferred to the soil 11% of the total plant-derived nitrogen (nitrogen found in the plant at harvest plus plant-derived nitrogen transferred to the soil), compared with 5% in CT-LOM trees and only 2% in CT-HOM. These values are consistent with those of Mayer et al. (2003), who found that N flux from roots to soil accounted for 13% of total plant N for faba bean and pea and 16% for white lupin at

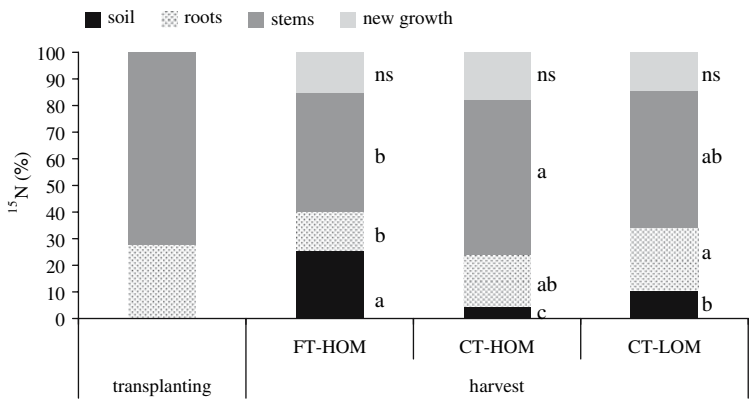

Fig. 1 Relative distribution of ^{15}N mass at transplanting (% of total tree content) and at tree harvest (% of total soil–tree content)

Table 2 Tree nitrogen uptake and N fluxes from root to soil and average values of N in trees at their excavation (average ± SE)

Soil type	Tree nitrogen content at transplanting (mg tree^{-1})	Nitrogen uptake (mg tree^{-1})	Nitrogen flux from roots to soil (mg tree^{-1})	Average tree N concentration (% d.w.)
CT-HOM	3,683.7 ± 157.7	2,628.4 ± 467.6 a	122.1 ± 11.9 b	0.75 ± 0.03 a
CT-LOM	3,729.7 ± 268.9	1,305.7 ± 137.1 b	197.6 ± 35.7 b	0.52 ± 0.04 b
FT-HOM	3,553.3 ± 204.3	1,806.7 ± 137.1 b	595.2 ± 70.6 a	0.61 ± 0.06 b

Different letters within columns indicate statistically significant differences (LSD test at 0.05 level)

Table 3 Distribution of net primary productivity of trees (g tree^{-1}) (average ± SE)

Compartment	Soil type		
	CT-HOM	CT-LOM	FT-HOM
Fruits	101.3 ± 18.7	78.2 ± 17.6	136.9 ± 4.3
Leaves	40.3 ± 4.0	33.0 ± 2.0	46.1 ± 6.6
Shoots	8.9 ± 1.8 b	7.5 ± 1.2 b	15.6 ± 4.0 a
Stem	63.8 ± 28.4	31.0 ± 25.3	82.4 ± 19.5
ANPP	*214.3 ± 40.7 ab*	*149.7 ± 29.5 b*	*281.0 ± 27.9 a*
Roots	68.6 ± 21.4	96.6 ± 12.6	80.1 ± 14.3
Rhizodeposition	15.7 ± 1.4 c	31.0 ± 5.2 b	80.6 ± 5.5 a
BNPP	*84.4 ± 21.7 b*	*127.6 ± 14.8 ab*	*160.7 ± 15.1 a*
Total NPP	*298.7 ± 41.4 b*	*277.4 ± 16.1 b*	*441.7 ± 18.2 a*
Total tree biomass gain	*282.9 ± 40.4 ab*	*246.4 ± 17.0 b*	*361.1 ± 23.6 a*

Different letters within rows indicate statistically significant differences (LSD test at 0.05 level)

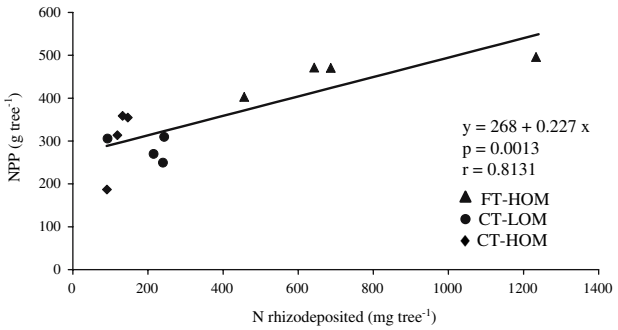

Fig. 2 Correlation between rhizodeposited N and net primary productivity of apple trees

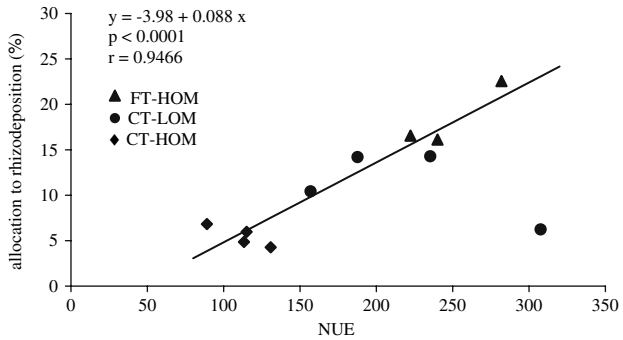

Fig. 3 Correlation between NUE (calculated as the ratio between the increase of total tree biomass and the nitrogen uptake during the season) and allocation of NPP to rhizodeposition (the data with NUE> 300 has been identified as an outlier and excluded from the correlation analysis)

maturity. Relatively higher values were reported by Sawatsky and Soper (1991) for grasses (71%). Our quantitative approach did not allow assessment of the relative contribution of potential sources of N flux from roots to soil. Rhizodeposition may occur as sloughing-off of root border cells, secretion of mucilage by roots, senescence of root epidermis, mycorrhizal turnover, root exudation and root death, with the latter two processes being considered quantitatively more important (Nguyen 2003). The study of the concentration of N in the mass transferred from roots to soil through the different rhizodeposition processes has received relatively little attention. Grayston et al. (1996) reported that C:N ratio in root exudates ranges from 2.5 to 13.0, in line with data by Smith (1976) who found C:N ratio of about 5 for three deciduous forest trees, but attributed most exudated N to NH_4. Organic N concentration in root exudates (Smith 1976) was around 1%, similar to the N concentration used here for calculating rhizodeposition from N fluxes. In apple, minirhizotron data suggest that around 50% of new roots die within 4–6 weeks of appearance in summer (Wells and Eissenstat 2001). The need for high root turnover is likely related to the fact that in young apple roots the respiration associated with their maintenance represents a substantial cost, not compensated by nutrient uptake.

Belowground primary productivity was calculated as the increase in root biomass plus rhizodeposition. Our data clearly indicate that considering only the former process leads to a dramatic underestimate of BNPP and to the erroneous conclusion that trees performed similarly in the three soils (Table 3). It is well accepted that trees growing in low-fertility soils tend to allocate proportionally more NPP to root growth than to canopy growth (Tingey et al. 2005), as part of a strategy for expanding their ability to take up limiting nutrients. This theory is supported if we compare the trees in the two coarse-textured soils, which differed in N availability. Trees grown in CT-LOM soil allocated about 35% of the NPP to the growth of fine roots, against 24% for trees grown in CT-HOM soil, and allocated to the root system slightly less than 46% of total NPP.

Even if an increased N availability often increases the aboveground partitioning of newly fixed carbon, it has been reported that it might also increase the amount of rhizodeposition (Warembourg and Estelrich 2001). Indeed, while it has been reported that root life spans differ between species typical of nutrient-rich and those typical of nutrient-poor environments (Van der Krift and Berendse 2002). Our data do not support this hypothesis and suggest that in a relatively short period, enhanced soil fertility is not able to increase rhizodeposition (Table 3).

In our experiment, soil texture (compare CT-HOM and FT-HOM) significantly affected rhizodeposition and consequently the allocation of newly formed biomass to the root system. High values of rhizodeposition in the fine-textured soil are in agreement with literature data (Boeuf-Trembley et al. 1995; Dexter 2004) that explain higher rhizodeposition in fine soils as the consequence of higher mechanical impedance of soil and recurrent anaerobic condition, which should promote the sloughing-off of root cap cells (Nguyen 2003). An alternative explanation considers the uneven distribution of nutrients due to the slow diffusion typical of fine-textured soil (nutrient patches), which might stimulate intensive root colonization in particular spots followed by root decay (Stark 1994; Hodge 2006).

It is interesting to note that, soil N being similar, root growth was relatively unaffected by soil texture (80 vs. 69 g tree^{-1} in FT-HOM and CT-HOM, respectively, Table 3), despite a near doubling of photosynthate flux from the shoots in the fine-textured soil. Clearly, this data do not consider the carbon costs for new growth associated with root respiration and root rhizodeposition. The positive correlation between NPP and rhizodeposited N (Fig. 2) might suggest that increased availability of photosynthate generates higher flux of C and N from roots to soil.

Our quantification of total rhizodeposition is likely an underestimation as it does not consider either root exudation or root turnover occurring during the winter period. It has in fact been shown that apple roots with diameter of less than 0.5 mm have an over winter survival (October to May) of less than 50% on average (Eissenstat et al. 2001). Underestimates of rhizodeposition could also arise from having estimated this process through the net ^{15}N releases in the soil, and not considering the fact that part of the rhizodeposited N could have been reabsorbed by the roots.

There was a positive and significant correlation between NUE and biomass allocation to rhizodeposition (Fig. 3). One potential explanation as to why trees grown in CT-LOM soil exhibited a higher NUE than those in CT-HOM is that that low leaf N negatively affects photosynthesis by limiting ribulose-1,5–bisphosphate carboxylase/oxygenase (Rubisco) activity (Cheng and Fuchigami 2000a). However, the relationship between leaf N concentration and CO_2 assimilation in apple leaves is curvilinear (Cheng and Fuchigami 2000b), therefore a reduced N leaf concentration does not automatically result in proportional reduction of carbon fixation.

In conclusion, our evidences indicate that a significant part of tree net primary production and tree N is partitioned to roots and from roots to soil. Not considering the latter process, as often reported in attempts to describe partitioning of products of photosynthesis in fruit trees (Palmer et al. 2002), leads only to a partial comprehension of C allocation. Even if it varied among soils, the flux of N and newly-fixed C from root to soil was comparable with that derived from leaf abscission. To be available for plant uptake again, nutrients contained in the root litter need to be mineralised during its decomposition, a process likely dependent on root biochemical composition and the soil environment (Van der Kift et al. 2001). Under our experimental conditions, the rate of rhizodeposition was more dependent on soil texture than on soil N availability. Considering that decomposition of plant residues within the soil is more likely to produce stable soil organic matter than decomposition on the soil surface, the role of rhizodeposition on soil carbon sequestration should not be underestimated.

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