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CSIRO PUBLISHING
www.publish.csiro.au/journals/cp *Crop & Pasture Science*, 2009, **60**, 289–294

Role of root exudates and root turnover in the below-ground N transfer from *Canavalia ensiformis* (jackbean) to the associated *Musa acuminata* (banana)

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Abstract. Jackbean is an annual legume frequently used as green manure in tropical intercropping systems with bananas. Although the beneficial effect of nitrogen (N) release from above-ground residues on banana nutrition is well known, little information is available on the N transfer from jackbean roots before and after the above-ground harvest. The aim of this study was to assess the relative contribution of exudates and root turnover in the N transfer from jackbean to banana in a greenhouse experiment. Nitrogen transfer was studied in a 6-month trial using the ^{15}N leaf feeding method, and estimated with a box model of ^{15}N dilution based on the observed data of ^{15}N content in exudates and decomposing roots. For the sowing–harvest period, the amount of N transferred from jackbean exudates represented 16% of banana N uptake and 0.7% of jackbean N uptake. Therefore, the N transfer flux via exudates was 23 times higher in terms of N input for the recipient plant than in terms of N output for the donor plant. This value, which is an index of the effectiveness of N transfer, was lower than those reported previously for other soil–plant systems in greenhouse conditions. This would be due to differences in root traits of the recipient plants. The amount of transferred N from root turnover after jackbean harvest represented 52% of banana N uptake in that period. The box model described N transfer from both legume N sources adequately ($r^2 = 0.92$). For the whole experiment, 38% of banana N uptake was derived from jackbean (6% from exudates and 32% from root turnover), and 62% from soil N. The results indicated that N transfer from root exudates of jackbean would be a useful but minor process compared with N release from root turnover in soil. The experimental and theoretical approach proposed in this study may be useful in screening studies to assess the capability of herbaceous legumes to transfer N.

Introduction

Bananas (*Musa* sp.) are grown in Central America and in the Caribbean region with large amounts of nitrogen (N) fertiliser and pesticides, which induce serious problems of water contamination (Cattan *et al*. 2007). The intercropping of bananas and herbaceous legumes has been proposed as an alternative practice to reduce the use of agrochemicals and to ensure environmental sustainability (Wortmann and Sengooba 1993; Arim *et al*. 2006). Jackbean [*Canavalia ensiformis* L. (DC)] is one of the most popular legumes intercropped with bananas due to its effectiveness as green manure and capability to control soil-borne pests (Fischler and Wortmann 1999; Arim *et al*. 2006). Regarding the effect of jackbean as green manure, several authors have already shown the positive effect of the above-ground residues on crop yields (McIntyre *et al*. 2001; Monneveux *et al*. 2006). However, the nutritional effect of N coming from the turnover of below-ground residues and N transfer via root exudates remains unclear.

Below-ground N transfer from root exudates of legumes has received particular attention in the last two decades because of increasing environmental and economic pressures. Because most of the studies have been in agroforestry and pasture systems, including only perennial legumes (Høgh-Jensen and Schjoerring 2000; Sierra *et al*. 2007), little is known about the ability of annual legumes to transfer fixed N. Motisi *et al*. (2007) applied the natural ^{15}N abundance method to estimate N transfer from jackbean to banana in a greenhouse experiment. Although they obtained strong evidence of N transfer via exudates, they concluded that the estimate of the transferred N was unrealistic because ^{15}N fractionation inside banana plants induced an erratic change in its isotopic signature. Moreover, ^{15}N fractionation also occurred during root turnover after cutting down the jackbean, which prevented the estimate of the N released from that process. The same was also observed in the post-pruning period for the leguminous tree *Gliricidia sepium* (Jacq.) Kunth ex Walp. associated with the tropical grass *Dichanthium aristatum* (Poir) C.E. Hubbard (Sierra *et al*. 2007). Undoubtedly, in soil–plant systems presenting strong ^{15}N fractionation, the ^{15}N leaf feeding method would be more suitable to obtain reliable estimates of N transfer because it allows ^{15}N fractionation to be ignored (Høgh-Jensen and Schjoerring 2000).

The objectives of this study were: (*i*) to assess the capability of jackbean to transfer N to banana and the relative contribution of root exudates and root turnover to the transferred N, and (*ii*) to propose an experimental and theoretical approach to use in screening studies to evaluate the ability for N transfer of legume species. The contribution of exudates and root turnover to the transferred N was assessed by using the ^{15}N leaf feeding

10.1071/CP08215 1836-0947/09/030289

procedure. Nitrogen transfer was estimated with a box model of ^{15}N dilution, which was based on the measurements of the isotopic signature of exudates and decomposing roots.

Materials and methods

Design of the greenhouse experiments

The study consisted of two experiments with distinctive objectives. The objectives of Expt 1 were to assess the N transfer from jackbean to banana (*Musa acuminata* Colla, cv. Petite-Naine) and to determine the ^{15}N content of decomposing roots of jackbean after its harvest. The objective of Expt 2 was to determine the ^{15}N content of root exudates of jackbean. The isotopic signatures of exudates and decomposing roots are required as inputs to the box model used to estimate N transfer. The soil used in both experiments was an acid, dark red Ferralsol (FAO taxonomy) located at the Duclos Experimental Station of the Institut National de la Recherche Agronomique in Guadeloupe (French Antilles) (16°15′N, 61°40′W). Soil was taken by removing the 0–0.2 m layer from a 10-m^2 quadrat in a plot that was bare for 6 months before soil sampling. Some characteristics of the soil were: clay content 0.72 g/g, pH (H_2O) 5.4, organic C 21.6 g/kg, organic N 1.6 g/kg, cation exchangeable capacity 15.1 mol_c/kg, exchangeable Al 0.4 mol_c/kg. The soil was manually ground to reduce soil aggregates to less than 10 mm, and was put into twenty-eight 35-L pots (top diam. 0.4 m) in a greenhouse. Eighteen pots were used for Expt 1 and 10 pots were used for Expt 2. Recommended rates of P and K, equivalent to 100 kg P/ha and 100 kg K/ha, were applied to each pot and mixed with the first 100 mm of the potting soil. Both experiments were carried out simultaneously and laid out in separate greenhouse beds. Every 3 days the arrangement of the pots in the bed was randomly changed to avoid microclimatic effects within the greenhouse. Soil moisture in the pots was kept at 0.35–0.40 kg/kg (70–80% of water-holding capacity; Motisi *et al*. 2007).

Experiment 1

Healthy 6-week-old banana plants grown by tissue culture were planted in the centre of each of the 18 pots. Five banana plants were used to determine the initial ^{15}N content of the recipient plant. The first banana sampling was done 52 days after planting (DAP) by using 2 pots. On the same day, 4 seeds of jackbean were sown in each of the remaining 16 pots. Seeds were placed in 4 cardinal points of the pot at 20 mm from its inner wall. At 76 DAP, a transparent plastic cylinder 600 mm high by 340 mm diameter was placed around the banana plants and fitted to the soil surface. On the same day, jackbean was leaf-labelled with a ^{15}N-enriched KNO_3 solution (49.5 at % excess) containing 1‰ (v/v) of a no-N surfactant. The solution was spread on the leaves of the 4 plants in each pot using a flat paintbrush (bristles 5 mm wide by 8 mm long). This was done 3 times a week at a rate of 5 mL per pot at each date, i.e. a total of 11 mg ^{15}N per pot. During labelling, the soil in the pots was covered with a plastic film to avoid ^{15}N contamination. The film was removed 6 h after labelling and a new film was put in place before the next ^{15}N application. The plastic cylinder was kept on the pots throughout the experiment to avoid ^{15}N contamination by direct contact between jackbean and banana leaves.

Bananas and jackbeans were sampled at 76 (before ^{15}N labelling), 94, 108, 122, and 136 DAP. At each sampling date, above-ground parts and roots of each species were sampled separately. The 4 jackbean plants of each pot were sampled together. At 136 DAP, the above-ground parts of the jackbean plants were cut, removed from the pots, and roots were left to decompose in the soil. After this, banana plants and jackbean roots remaining in the soil were sampled at 150, 172 and 193 DAP. Plant sampling was made by introducing the pots into 50-L containers containing tap water. The water level was ~10 mm above the soil surface. The pots were left in water for 2 h to allow a gentle detachment of roots from the soil. Then, the plants were removed and the roots were washed carefully. Soil mineral N was measured at the time of each plant sampling. All samplings were made using 2 replicates for each sampling date, i.e. 9 sampling dates × 2 replicates = 18 pots.

Plant samples were dried for 96 h at 70°C to determine dry matter, and ground to <0.2 mm for isotopic analysis. Total N and ^{15}N content of plant samples were determined by an element analyser (Carlo Erba EA 1110; Carlo Erba Strumentazione, Milan, Italy) connected to a mass spectrometer (Thermo-Finnigan Delta Plus; Termo-Quest, Bremen, Germany) through a ConFlo II interface (Thermo-Finnigan), in the Service Central d'Analyses of the CNRS (Vernaison, France).

Experiment 2

In this experiment, jackbean was grown alone without banana plants. Jackbean were sown and labelled on the same date and using the same procedure described for Expt 1. Root exudates of jackbean were measured at 76 (before ^{15}N labelling), 94, 108, 122, and 136 DAP by using the procedure described by Sierra *et al*. (2007). Exudate measurements were made using 2 replicates for each sampling date, i.e. 5 sampling dates × 2 replicates = 10 pots. Plants were sampled as described for Expt 1. After this, the plants were immersed in a pot containing 10 L of distilled water and kept in the greenhouse for 96 h for exudation. The 4 plants of each pot were treated together. The pot was covered with a plastic film to avoid contamination and an air pump was used to ensure water aeration. At the end of the exudation period, the solution was filtered using Whatman No. 1 filter paper and concentrated by oven drying at 50°C for 10 days. The pH of the solution was kept near 4 to avoid NH_3 volatilisation. The final solid residue was weighed and ground to <0.2 mm for isotopic analysis. At the end of the exudation period, above-ground parts and roots of the plants were also collected separately and treated as described above for isotopic analysis.

Box-model of N transfer

Nitrogen transfer was estimated using the box model described by Sierra *et al*. (2007). Briefly, the model considers 5 N compartments: N in soil organic matter, soil mineral N (N source for the associated crop), N in roots of the recipient plant, N in the above-ground parts of the recipient plant, and N released by the donor plant (N source for the associated crop). The last corresponds to N in exudates (before the cut of the donor plant) and N in decomposing roots (after cut). The model calculates the isotopic signature of the recipient plant and N transfer based on the observed data of ^{15}N in the N sources and biomass N in the recipient plant. Although the model also

accounts for ^{15}N fractionation affecting ^{15}N flux inside the recipient plant, this option was not used in this study because the effect of such fractionation is negligible at the relatively high level of ^{15}N content observed in Expts 1 and 2. Similarly, ^{15}N fractionation during N mineralisation was not considered because Sierra and Nygren (2006) reported that its effect on the estimate of N transfer is very small for experiments lasting less than 1 year.

Calculations with the model were made at daily time intervals. The dates of plant sampling, ^{15}N labelling, and jackbean cutting were those applied in Expt 1. Data of N and ^{15}N content in banana and in jackbean decomposing roots were those measured in Expt 1. Data of exudate ^{15}N content were those obtained in Expt 2. Soil mineral ^{15}N content ($\delta^{15}N_{min}$) was estimated from the experimental data of N and ^{15}N content of the banana plants before jackbean sowing (i.e. at 0 and 52 DAP):

$$\delta^{15}N_{min} = [\delta^{15}N_{ban\text{-}52} - (pN_{ban\text{-}0} \times \delta^{15}N_{ban\text{-}0})]/(1 - pN_{ban\text{-}0}) \quad (1)$$

and

$$pN_{ban\text{-}0} = N_{ban\text{-}0}/N_{ban\text{-}52} \quad (2)$$

where $\delta^{15}N$ is the per thousand ^{15}N enrichment relative to atmospheric nitrogen (0.3663%); $\delta^{15}N_{ban\text{-}0}$ and $\delta^{15}N_{ban\text{-}52}$ are the banana $\delta^{15}N$ values obtained at 0 (initial value) and 52 DAP, respectively; $N_{ban\text{-}0}$ and $N_{ban\text{-}52}$ are the total N content in banana plants at 0 and 52 DAP, respectively. Equation 1 implies that the fraction of the N content at 52 DAP corresponding to N uptake from the soil source (i.e. $1 - pN_{ban\text{-}0}$) had an isotopic signature of $\delta^{15}N_{min}$. The fraction of the N in banana derived from jackbean was then estimated by fitting the experimental data of $\delta^{15}N$ in banana plants (above-ground parts and roots). The model was run using the ModelMaker 3.0 program (Model Kinetix 2000), and the fit of the experimental data was performed using the Marquardt method included in that program.

Statistical analysis

Differences between plant stages for N uptake were analysed using slope *t*-test assuming a linear increase of plant N content with time for each period. Differences in N content were analysed date by date using *t*-test. Differences of N transfer estimated with the model were analysed using *F*-test. These analyses were conducted with SAS *v.* 8.02 software (SAS Institute 1999).

Results

Experiment 1

The rate of N uptake by banana plants varied with time and decreased in the order: planting–jackbean sowing (2.5 mg N/day) > after jackbean cut (2.0 mg N/day) > sowing–cut of jackbean (0.8 mg N/day) ($P < 0.05$) (Fig. 1). Total N uptake of banana at the end of Expt 1 was 310 mg N/plant. For the sowing–cutting period, the rate of N uptake of jackbean was higher than that of banana (e.g. 4.5 mg/day.plant) ($P < 0.05$). At the time of the jackbean cut, total N uptake was 379 mg N/jackbean plant (i.e. 1516 mg N/pot).

The rate of disappearance of the N biomass of jackbean roots remaining in the soil after the cut varied over time and was higher just after the cut ($P < 0.05$) (Fig. 1); e.g. 13.9 mg N/day for the 136–150 DAP period, >4.1 mg N/day for the 150–172 DAP period, >0.1 mg N/day for the 172–193 DAP period. Two months after the jackbean was cut, only 12% of the root N biomass was still present in the pots. Soil mineral N concentration decreased during the period of the highest plant N uptake (Fig. 2). The decrease was higher for the 0–94 DAP period (0.22 mg N/kg.day) than for the 94–136 DAP period (0.05 mg N/kg.day) ($P < 0.05$). After this, soil mineral N increased just after the jackbean cut and then decreased towards the end of the experiment. Calculations made from the experimental data indicated that 62% of the N released by root

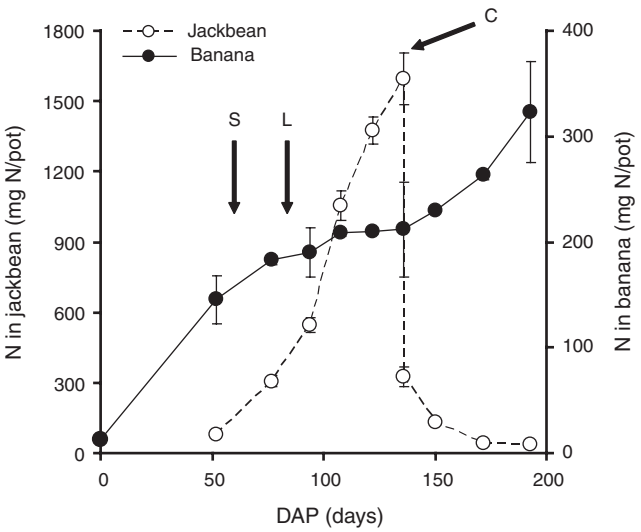

Fig. 1. Cumulative N content in jackbean and banana in Expt 1. DAP refers to days after banana planting; S, L, and C refer to the time of sowing, ^{15}N labelling, and cut of jackbean, respectively. For jackbean, data after cutting are for N in roots remaining in soil. Vertical bars indicate standard deviation ($n = 2$).

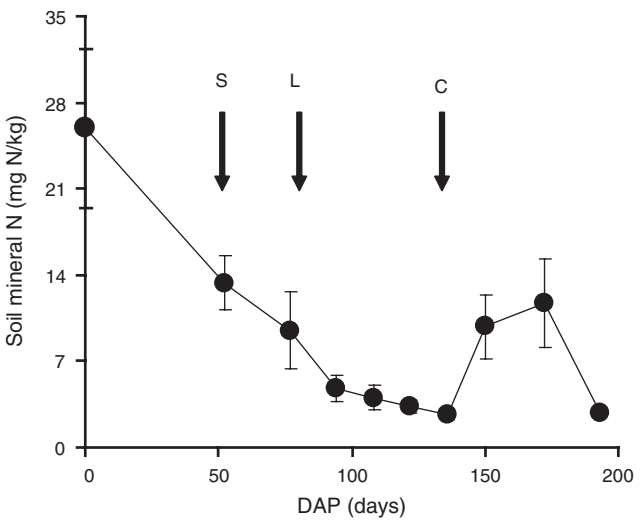

Fig. 2. Soil mineral N content in Expt 1. DAP refers to days after banana planting; S, L, and C refer to the time of sowing, ^{15}N labelling, and cut of jackbean, respectively. Vertical bars indicate standard deviation ($n = 2$).

turnover was not recovered either in banana plants or as soil mineral N.

The initial $\delta^{15}N$ of banana was higher for the above-ground parts (0.23 ± 0.12) than for roots (-0.54 ± 0.22) ($P < 0.05$). The $\delta^{15}N$ increased up to the time of jackbean sowing and then decreased slightly up to ^{15}N labelling ($P < 0.05$) (Fig. 3*a*). After this, the $\delta^{15}N$ increased rapidly, mainly after the jackbean cut (Fig. 3*a*, *b*). The $\delta^{15}N$ was higher for the above-ground parts than for roots in the sowing–labelling period; the opposite was observed from labelling to the end of the experiment ($P < 0.05$) (Fig. 3*c*). Recovery of ^{15}N in banana plants was 0.1% at the time of the jackbean cut and 1.8% at the end of Expt 1.

Recovery of ^{15}N in jackbean averaged $95 \pm 3\%$, of which 86% was present in the above-ground parts and 9% in roots. Changes in $\delta^{15}N$ in jackbean were similar for the above-ground and root biomass: an initial increase due to ^{15}N labelling, followed by a fast decrease and then a slow decrease up to the time of the jackbean cut (Table 1). The $\delta^{15}N$ of roots remaining in soil after the cut was similar to that observed just before the cut ($P < 0.05$). For the soil, the δ^{15} was 13.4 ± 0.2 for the organic N and 7.3 ± 0.4 for the mineral N (Eqn 1). These values indicate that ^{15}N fractionation during N mineralisation was ~6 ‰.

Experiment 2

There were no significant differences between Expts 1 and 2 for the N and ^{15}N content of the above-ground and root biomass of jackbean ($P < 0.05$) (data not shown for Expt 2). The amount of exudate N released from jackbean roots during the exudation period (i.e. 4 days) averaged $0.5 \pm 0.2\%$ of the N content of the jackbean plants. No significant differences were observed between dates ($P < 0.05$). The $\delta^{15}N$ of exudates was always lower than the $\delta^{15}N$ of the above-ground and root biomass ($P < 0.05$) (Table 1). No significant differences were found for exudate ^{15}N after the labelling ($P < 0.05$) (Table 1).

Estimate of N transfer

Nitrogen transfer was estimated from the ^{15}N content of exudates (Expt 2) and decomposing roots of jackbean (Expt 1). The model described adequately the changes in $\delta^{15}N$ of banana plants (Fig. 3); e.g. $r^2 = 0.99$ and RMSE = 1 for the planting–jackbean cut period, and $r^2 = 0.92$ and RMSE = 18 for the whole Expt 1. Table 2 shows the estimated fraction of N in banana derived from jackbean. The contribution of N from the turnover of jackbean roots was higher than that derived from root exudates ($P < 0.05$). The rate of N transfer was 0.13 mg N/day from root exudates in the sowing–cutting period and 1.0 mg N/day from root turnover in the period after cutting. For the sowing–cutting period, although the amount of N transferred from jackbean exudates represented 16% of the N uptake of banana (Table 2), it corresponded to only 0.7% of the N uptake of jackbean. This implies that the N transfer flux via exudates was 23 times higher in terms of N input for the recipient plant than in terms of N output for the donor plant.

Data presented in Table 2 were estimated assuming a constant rate of N transfer with time. To analyse how this simplification affected the estimates of N transfer, additional calculations were made by fitting each observed $\delta^{15}N$ value of banana. For the sowing–cutting period, N transfer was $15.9 \pm 0.2\%$ and no significant differences were observed between dates ($P < 0.05$).

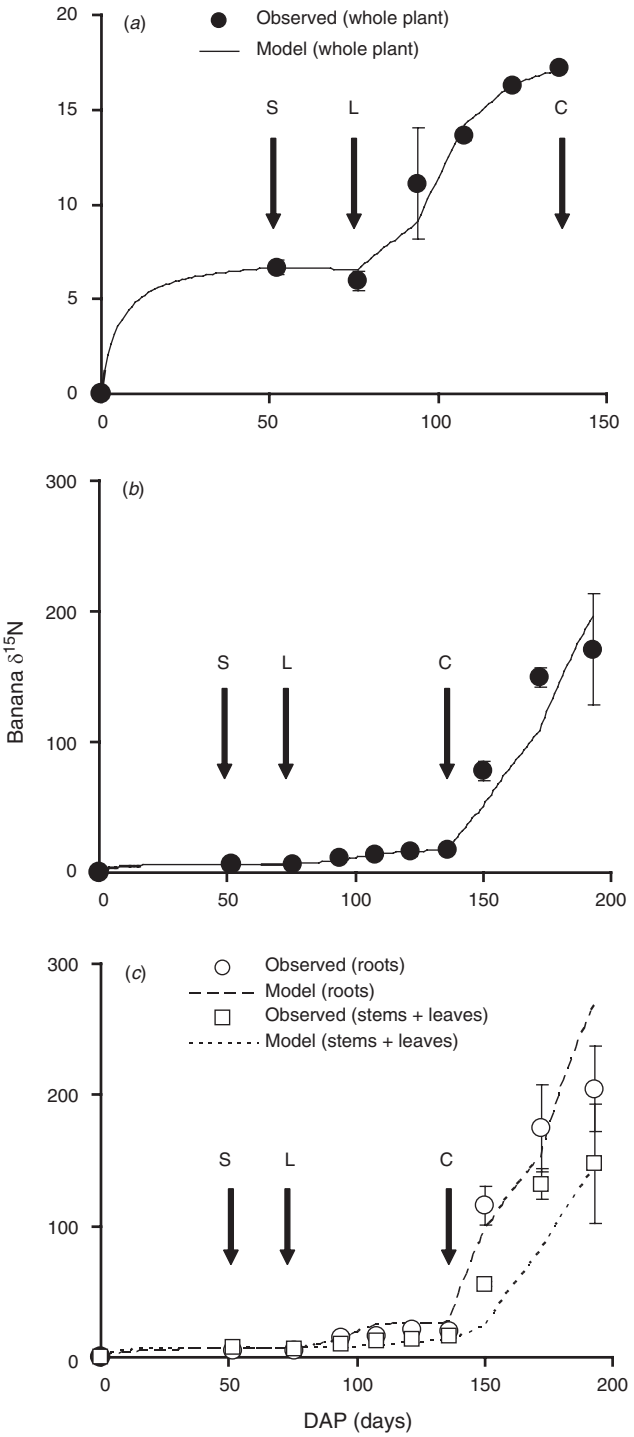

Fig. 3. Observed and simulated $\delta^{15}N$ values of banana in Expt 1: (*a*) data of the whole banana plants for the banana planting–jackbean cut period, (*b*) *idem* (*a*) for the whole experiment, (*c*) data for the above-ground parts and for roots. DAP refers to days after banana planting; S, L, and C refer to the time of sowing, ^{15}N labelling, and cut of jackbean, respectively. Vertical bars indicate standard deviation ($n = 2$).

This indicates that the assumption of a constant rate was reasonable for that period. After the cut, although the estimated N transfer varied with time, the total amount of

Table 1. Change in $\delta^{15}N$ over time in jackbean

Within columns, values followed by the same letter are not significantly different at $P < 0.05$. Data correspond to Expt 1 for the above-ground and root biomass, and to Expt 2 for exudate. DAP refers to days after banana planting. Jackbean was sown at 52 DAP. L and C refer to the time of ^{15}N labelling and cutting of jackbean, respectively. Root $\delta^{15}N$ after jackbean cut corresponds to that of decomposing roots remaining in soil. The values correspond to the mean ± standard deviation ($n = 2$)

DAP	Above-ground $\delta^{15}N$	Root $\delta^{15}N$	Exudate $\delta^{15}N$
76 (L)	6.3 ± 2.1a	7.9 ± 0.5a	0.2 ± 0.1a
94	7179 ± 1045d	1660 ± 55c	421 ± 13b
108	4806 ± 420c	1173 ± 102b	384 ± 16b
122	2347 ± 995b	1172 ± 112b	454 ± 35b
136 (C)	2239 ± 115b	955 ± 28b	386 ± 15b
150		995 ± 20b	
172		980 ± 25b	
193		1149 ± 39b	

Table 2. Nitrogen transfer from jackbean to banana estimated with the box model

The values correspond to the fraction (%) of banana N uptake coming from each N source. Sowing and cutting refer to jackbean

Period	N source		
	Soil	Exudate	Root turnover
Sowing–cutting	84	16	0
Cutting–end of experiment	48	0	52
Sowing–end of experiment	62	6	32

transferred N was similar to that obtained with the assumption of a constant rate. For example, the estimated N transfer was 72% for the 136–150 DAP period, 58% for the 150–172 DAP period, and 44% for the 172–193 DAP period. With these values, the total N transferred via root turnover was 52 mg/pot. Assuming a constant rate of N transfer (i.e. 52%, Table 2), the transferred N was 57 mg/pot.

Discussion

Effect of N transfer on the N nutrition of banana

In a greenhouse experiment carried out with the same soil used in this study, Motisi *et al*. (2007) reported that N from N_2 fixation represented nearly 80% of the total N content of jackbean. Similar values were observed for jackbean by Ojiem *et al*. (2007) in several field experiments. With this value and taking into account the total N uptake of jackbean in the sowing–cutting period of Expt 1, it can be calculated that jackbean absorbed 303 mg N/pot from the soil. For banana in the same period, N uptake from soil was only 56 mg N/pot. This suggests that interspecies competition for soil N could take place in the sowing–cutting period. The relatively low concentration of soil mineral N observed just before the jackbean cut supports this hypothesis (Fig. 2). Even if competition occurred in that period, it seems that this did not affect N transfer from jackbean to banana because the estimated rate was not significantly different between dates and was always close to 16%.

This pattern changed completely after the jackbean cut. A higher soil N availability for banana (Fig. 2) because of the lack of interspecies competition as well as the N released from the turnover of jackbean roots induced a great increase in the N content of banana (Fig. 1). For example, the rate of N uptake of banana from the soil mineral N was 0.6 mg N/day before jackbean harvest and 0.8 mg N/day afterwards. Moreover, the estimates made with the model indicated that more that half the N uptake of banana after the jackbean cut came from root turnover.

Comparison between leguminous N sources

The procedure of ^{15}N labelling used in this study was likely to show a big difference in $\delta^{15}N$ between the soil and the leguminous N sources, which was a key factor to obtain reliable estimates of N transfer (Høgh-Jensen and Schjoerring 2000). Although ^{15}N in jackbean was diluted after labelling due to N uptake from the soil and N_2 fixation (Table 1), root and exudate $\delta^{15}N$ were relatively high, which allowed ^{15}N fractionation in soil and inside banana plants to be ignored (Sierra *et al*. 2007). Concerning ^{15}N fractionation in soil, if part of the released N was recycled by soil microorganisms before its uptake by the recipient plant, then the δ^{15} of the N coming from the leguminous sources could change due to the fractionation caused by microorganisms. The lower the $\delta^{15}N$ of the original source, the higher is the effect of the fractionation process. In our study this effect may be assumed to be very small. For example, if all the exudate N was recycled by soil microbes having a fractionation equal to that estimated for N mineralisation (i.e. 6‰), N entering banana plants had a $\delta^{15}N$ 2% less than that measured for exudates, and N transfer would be only 0.5% higher than the original estimates presented in Table 2.

The box model described satisfactorily the experimental data and allowed the relative importance of root exudates and root turnover in the N transfer process to be assessed. The simulated change in banana $\delta^{15}N$ over time reflected the contribution of each N source (Fig. 3). The initial increase was due to N uptake from the soil, which had a $\delta^{15}N$ higher than that of the initial plants. After this, the slight but significant decrease up to jackbean labelling was due to N transfer via exudates with a very low $\delta^{15}N$ (Table 1). Finally, the faster $\delta^{15}N$ increase after the jackbean cut compared with that observed for the labelling–cutting period was due to the greater $\delta^{15}N$ of decomposing roots in relation to exudates, as well as a greater N transfer in that period. Because the root N content of banana was lower than that of the above-ground parts, exudate ^{15}N was less diluted in the root compartment. For this reason, root $\delta^{15}N$ after labelling was higher than above-ground $\delta^{15}N$ (Fig. 3*c*). Some discrepancies between the model and the experimental data observed after the jackbean cut could be associated with the assumption of a constant rate of N transfer. However, our calculations showed that the estimate of the total amount of transferred N only varied slightly by considering a fluctuating rate of N transfer.

In terms of daily rate, N transfer via root turnover after the jackbean cut was 8 times higher than that observed from root exudates. Moreover, in the present study we analysed only the effect of decomposing roots but not the total green manure effect, which includes the turnover of the above-ground parts. Taking into account that the above-ground N/root N ratio of jackbean averaged 3.5, the total green manure effect had to be higher than that estimated in our experiment (Crespo and Fraga 1997). In an incubation experiment using a soil–jackbean roots mixture,

Motisi (2005) found that 3 months after the beginning of the incubation nearly 60% of the N released by roots was in the soil organic matter and the microbial biomass. This was due to the relatively low C/N ratio of jackbean roots (i.e. ≈16), and explains why more than half of the N released from decomposing roots in our study was not recovered, either in banana plants or as soil mineral N.

Jalonen *et al*. (2007) reported that most of the exudate N released by the leguminous tree *Gliricidia sepium* was immobilised by soil microorganisms, and that N transfer via exudates requires intimate contact between the roots of the donor and recipient plants. The comparison of our results with those reported for other soil–plant systems supports this hypothesis. In a greenhouse experiment carried out on the *G. sepium–Dichanthium aristatum* association, Sierra *et al*. (2007) found that the amount of N transferred via exudates was 57 times greater in terms of N input for *D. aristatum* than in terms of N output for *G. sepium*. This value was 2.5 times higher than that found for the jackbean–banana association. The characteristics of the root system of the recipient plant could play a major role in the effectiveness of N transfer via exudates. For example, roots of the grass *D. aristatum* are thinner and their branching density is higher than those of banana (Cruz 1997; Lecompte and Pagès 2007). These root traits could favour root contact between the donor and the recipient plants and thus enhance the entry of exudate N in the recipient plant. Regardless the underlying mechanisms affecting N transfer, the ratio of the N input for the recipient plant to the N output for the donor plant might be a useful index in screening studies to compare the ability of different legume species to transfer N to the associated crop.

The relative plant density (i.e. number of jackbean plants/number of banana plants = 4) used in this study was the same as that used in farm conditions (Damour 2004). Although the results of our greenhouse experiment cannot be extrapolated directly to field conditions, it may be hypothesised that N transfer via exudates would be less in the field. In fact, banana and jackbean are cropped in rows 1-m apart (Damour 2004), so root contact between species would be less than in our potting soil. The picture may be different for N released from root turnover because the mineralised N may be taken up by mass flow. The results obtained in this study suggest that N transfer from jackbean exudates would be a suitable but minor process compared with the green manure effect.

Acknowledgments

This work was funded by the Départment Environnement et Agronomie of INRA (France). We thank S. A. Sophie, F. Solvar, and M. J. Serin for their excellent technical assistance during the experiments, and A. Scaife for reviewing the English manuscript.

References

Arim OJ, Waceke JW, Waudo SW, Kimenju JW (2006) Effects of *Canavalia ensiformis* and *Mucuna pruriens* intercrops on *Pratylenchus zeae* damage and yield of maize in subsistence agriculture. *Plant and Soil* **284**, 243–251. doi: 10.1007/s11104-006-0053-9

Cattan P, Bussiere F, Nouvellon A (2007) Evidence of large rainfall partitioning patterns by banana and impact on surface runoff generation. *Hydrological Processes* **21**, 2196–2205. doi: 10.1002/hyp.6588

Crespo G, Fraga S (1997) Comparison of green fertilizers for forage maize production (*Zea mays*) in a ferrasol soil. *Cuban Journal of Agricultural Science* **31**, 145–150.

Cruz P (1997) Effect of shade on the carbon and nitrogen allocation in a perennial tropical grass, *Dichanthium aristatum*. *Journal of Experimental Botany* **48**, 15–24. doi: 10.1093/jxb/48.1.15

Damour G (2004) Analyse et modélisation des interactions pour l'eau et bilan de services dans une association banane-canavalia. MS Thesis, Institut National Agronomique Paris-Grignon, Paris, France.

Fischler M, Wortmann CS (1999) Green manure for maize–bean systems in eastern Uganda: agronomic performance and farmers' perceptions. *Agroforestry Systems* **47**, 123–138. doi: 10.1023/A:1006234523163

Høgh-Jensen H, Schjoerring JK (2000) Below-ground nitrogen transfer between different grasslands species: direct quantification by ^{15}N leaf feeding compared with indirect dilution of soil ^{15}N. *Plant and Soil* **227**, 171–183. doi: 10.1023/A:1026535401773

Jalonen R, Nygren P, Sierra J (2007) Root exudates as pathway for nitrogen transfer from a tropical leguminous tree. In 'Proceedings of the International Symposium Nitrogen – 2007'. (Lancaster University: Lancaster, UK)

Lecompte F, Pagès L (2007) Apical diameter and branching density affect lateral root elongation rates in banana. *Environmental and Experimental Botany* **59**, 243–251. doi: 10.1016/j.envexpbot.2006.01.002

McIntyre BD, Gold CS, Kashaija IN, Ssali H, Night G, Bwamiki DP (2001) Effects of legume intercrops on soil-borne-pests, biomass, nutrients and soil water in banana. *Biology and Fertility of Soils* **34**, 342–348. doi: 10.1007/s003740100417

Model Kinetix (2000) 'Maker 3: user manual.' (ModelKinetix: Reading, UK)

Monneveux P, Quillérou E, Sanchez C, Lopez-Cesati J (2006) Effect of zero tillage and residues conservation on continuous maize cropping in a subtropical environment (Mexico). *Plant and Soil* **279**, 95–105. doi: 10.1007/s11104-005-0436-3

Motisi N (2005) Rôle de la litière souterraine dans le transfert d'azote dans une culture associée légumineuse herbacée–banane. MS Thesis, Institut National Agronomique Paris-Grignon, Paris, France.

Motisi N, Tournebize R, Sierra J (2007) Test of the natural ^{15}N abundance method to estimate the effect of the legume *Canavalia ensiformis* (canavalia) nitrogen transfer on the associated *Musa acuminata* (banana) nitrogen nutrition. *Cultivos Tropicales* **28**, 77–83.

Ojiem JO, Vanlauwe B, de Ridder N, Giller KE (2007) Niche-based assessment of contributions of legumes to the nitrogen economy of Western Kenya smallholder farms. *Plant and Soil* **292**, 119–135. doi: 10.1007/s11104-007-9207-7

SAS Institute (1999) 'SAS user's guide.' (SAS Institute: Cary, NC)

Sierra J, Nygren P (2006) Transfer of N fixed by a legume tree to the associated grass in a tropical silvopastoral system. *Soil Biology & Biochemistry* **38**, 1893–1903. doi: 10.1016/j.soilbio.2005.12.012

Sierra J, Daudin D, Domenach AM, Nygren P, Desfontaines L (2007) Nitrogen transfer from a legume tree to the associated grass estimated by the isotopic signature of tree root exudates: a comparison of the ^{15}N leaf feeding and natural ^{15}N abundance methods. *European Journal of Agronomy* **27**, 178–186. doi: 10.1016./j.eja.2007.03.003

Wortmann CS, Sengooba T (1993) The banana–bean intercropping system—bean genotype × cropping system interactions. *Field Crops Research* **31**, 19–25. doi: 10.1016/0378-4290(93)90047-Q

Manuscript received 1 July 2008, accepted 24 November 2008