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Nitrogen use efficiency of monoculture and hedgerow intercropping in the humid tropics

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Abstract

The design of productive and efficient intercropping systems depends on achieving complementarity between component species' resource capture niches. Spatiotemporal patterns of capture and use of pruning and urea nitrogen (N) by trees and intercrops were elucidated by isotopic tracing, and consequences for nitrogen use efficiency were examined. During the first cropping season after applying urea-^{15}N, maize accounted for most of the plant ^{15}N recovery in *Peltophorum dasyrrachis* (33.5%) and *Gliricidia sepium* (22.3%) hedgerow intercropping systems. Maize yield was greatest in monoculture, and maize in monoculture also recovered a greater proportion of urea ^{15}N (42%) than intercropped maize. Nitrogen recovery during active crop growth will not be increased by hedgerow intercropping if hedgerows adversely affect crop growth through competition for other resources. However, hedgerows recovered substantial amounts of ^{15}N during both cropping cycles (e.g. a total of 13–22%), showing evidence of spatio-temporal complementarity with crops in the spatial distribution of roots and the temporal distribution of N uptake. The degree of complementarity was species-specific, showing the importance of selecting appropriate trees for simultaneous agroforestry. After the first cropping season 17–34% of ^{15}N applied was unaccounted for in the plant-soil system. Urea and prunings N were recovered by hedgerows in similar amounts. By the end of the second (groundnut) cropping cycle, total plant ^{15}N recovery was similar in all cropping systems. Less N was taken up by the maize crop from applications of labelled prunings (5–7%) than from labelled urea (22–34%), but the second crop recovered similar amounts from these two sources, implying that prunings N is more persistent than urea N. More ^{15}N was recovered by the downslope hedgerow than the upslope hedgerow, demonstrating the interception of laterally flowing N by hedgerows.

Introduction

Nitrogen management is particularly difficult on soils where plant rooting depth is constrained by aluminium toxicity, a common problem in the Ultisols which cover 11% of the tropics (Sanchez, 1976). Hedgerow intercropping has been recommended for improving agronomic nitrogen use efficiency (NUE) on strongly leached soils. The labour requirements for frequent pruning to manage competition between trees and crop plants are often a constraint to farm-level application, but hedgerow intercropping can still be used as a model system for testing our understanding of the processes governing efficiency in any perennial intercropping system. The agronomic efficiency of use of a material may be simply defined as the ratio of outputs or yields to inputs (Huxley, 1999). The definition of NUE that is used here is the mass of N within the crop plant per mass of N applied. Nitrogen taken up by trees in agroforestry systems may be returned to the soil and used by subsequent crops, or may be considered part of the output if these trees have direct value as timber, fodder or fruit trees.

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The use efficiency of N in an alley cropping agroforestry system, relative to that in a crop monoculture, depends on a variety of interactions. Trees affect N extraction rates both through their own uptake and through influencing crop growth and N uptake. Trees may also affect rates of N loss, for example by increasing transpiration and thus reducing water throughput, or by increasing infiltration rates or the proportion of preferential flow (Suprayogo et al., 2002). The quality of tree residues affects N supply dynamics to the soil (Handayanto et al., 1994). In systems where trees are primarily included for their soil fertility benefit, benefits will occur only when the trees acquire resources that the crop would not otherwise acquire (Cannell et al., 1996). Thus the success of the system depends on limiting competition for resources and increasing the temporal and spatial complementarity of resource capture. This may be achieved in tree-crop associations if tree roots are active deeper in the soil than crop roots (Young, 1986). Deep nutrient uptake by trees is important where reserves of nutrients occur at depth because of weathering or prior leaching, or if trees intercept N that would otherwise be leached (the 'safety-net' hypothesis; van Noordwijk et al., 1996).

Isotopic labeling of materials allows the fate of nutrients applied to agroforestry systems to be monitored. Recent studies have demonstrated differences in vertical distribution of root activity between trees (Lehmann et al., 2001), and between trees and associated crops (Rowe et al., 2001). Surface applications of ^{15}N have also been used to demonstrate strong competition for N by *Erythrina indica* trees used as support for *Piper nigrum* vines (Wahid et al., 2004). Recoveries of ^{15}N from surface applications made across the width of the alley in hedgerow intercropping systems reflect overall NUE (Rao and Shinde, 1990). Van-Lauwe et al. (1998) reported ^{15}N budgets following application of high quality *Leucaena* and low quality (i.e. with higher C:N ratio and greater lignin content) *Dactyladenia* prunings to alley cropping systems. Little of the applied N ($< 10\%$) was taken up by the maize crop in either case. Recovery by the hedgerows was greater (35% of that applied, over 858 days) for the higher quality *Leucaena* prunings than for the low quality *Dactyladenia* (7.1%). Xu et al. (1993) also found that the amount of ^{15}N recovered by maize after application of *Leucaena* prunings was small (5% after 52 days) in comparison with recovery of ^{15}N labelled ammonium fertilizer (50%). Giller and Cadisch (1995) found similar low residue recoveries and concluded that this was in many cases due to inefficient utilization in space and time of the N released from plant residues.

In the current study, ^{15}N labelled materials were applied to a monocrop system, and to intercropping systems with hedgerows of *Peltophorum dasyrrhachis* (Miq.) Kurz and/or *Gliricidia sepium* L.. The location of ^{15}N derived from these materials was monitored by following the size of plant and soil ^{15}N pools over two cropping seasons. The objectives were to explore the dynamics of N availability, leaching and plant uptake within the systems, and to assess overall NUE. We hypothesised (H1) that hedgerow intercropping systems use N more efficiently than monocrop systems, and (H2) that *P. dasyrrachis* hedgerow intercropping systems are more efficient in their use of N than *G. sepium* hedgerow intercropping systems, since *P. dasyrrachis* root systems are spatially distinct from crop root systems (Rowe et al., 2001) and thus have more opportunity to intercept N before it is leached. The rapid mineralisation of high quality (low C:N and low polyphenol content) *G. sepium* prunings compared with low quality (high C:N and polyphenol) *P. dasyrrachis* prunings (Handayanto et al., 1994) was hypothesised (H3) to lead to greater losses of prunings N from *G. sepium* systems, and mixing *P. dasyrrachis* prunings with *G. sepium* prunings was expected to slow the release of N from the *G. sepium* prunings and increase overall NUE (H4).

Materials and methods

Experimental site

The experiment was carried out at the Biological Management of Soil Fertility (BMSF) project site of Universitas Brawijaya/ICRAF/Wye College/PT Bunga Mayang, near Karta, North Lampung, Sumatera, Indonesia (4°31′ S, 104°55′ E), on a field with a gentle slope (4%). The soil was a Plinthitic Kandiudult with a sandy clay topsoil and clay accumulation at depth, particularly below around 1 m (Suprayogo et al., 2002). Aluminium saturation in the subsoil approached 60% (van der Heide et al., 1992). Six cropping systems were established in 1985–1986 to explore the effects of hedgerows on the growth of food crops, of which four were included in the current study: one with no hedgerows ('monocrop'), plus hedgerow intercropping systems using Peltophorum dasyrrhachis ('P-P'), *G. sepium* ('G-G'), and a system in which hedgerows of the latter two species alternated ('G-P') (van Noordwijk et al., 1995). Hedgerows were 4 m apart and trees

were 50 cm apart within the row. Plastic sheets were installed in the soil to 50 cm depth around monocrop plots at setup, to prevent the incursion of tree roots. Two crops were generally grown per year; in the current experiment these crops were maize followed by groundnut. Mean maize yields (t ha^{-1}) over four cropping seasons in 1991–1992 were 2.30 (monocrop), 2.33 (G-G), 3.32 (P-P) and 2.55 (G-P) (van Noordwijk et al., 1995).

Experimental design of ^{15}N study

During the wet season of 1997–8 the fate of fertilizer versus organic N sources was compared in the four cropping systems studied, using ^{15}N urea and ^{15}N labelled prunings. There were four replicated urea plots per treatment but (because of limited supplies of ^{15}N labelled prunings) only two labelled prunings plots per hedgerow intercropping system treatment (G-G, P-P, G-P). No labelled prunings were applied to monocrop plots. Because of the danger of ^{15}N contamination, plots were positioned at least 4 m apart, as suggested for these species by Rowe and Cadisch (2002).

Eight months before the start of the current experiment, *Mucuna pruriens* was sown on all treatment plots as a green manure, but the above-ground biomass was removed before planting. Glyphosate herbicide (Roundup, Monsanto Co., St Louis, MO, USA) was applied, and thereafter the field was kept clear of weeds by regular hand weeding. On 5th December 1997 all hedgerows were pruned. Prunings were applied evenly over the hedgerow and alley. Urea (30 kg N ha−1), KCl (60 kg K ha−1) and triple super-phosphate (60 kg P ha^{-1}) were applied. On 11th December 1997 a crop of maize was sown at a spacing of 65 × 50 cm, in 5 rows along each alley. On 10th January 1998 an additional topdressing of urea (60 kg N ha^{-1}) was applied. This crop was harvested on 11th March 1998 and hedgerows were pruned on 22nd March 1998. A crop of groundnut was sown on 27th March 1998 and harvested on 1st July 1998. An additional application of 60 kg K and 60 kg P ha−1 was made on 28th March 1998, but no N was applied.

On 10th January 1998, ^{15}N labelled materials were applied to 0.5 m wide strips ('microplots') running across the 4 m wide crop alley and centred on a tree on either side (Figure 1). Urea (5.523 atom% ^{15}N) was applied to the ^{15}N microplots at a rate of 60 kg N ha^{-1}. An amount of water equivalent to 10 mm of rainfall was then added to the plot, to wash in the ^{15}N and reduce potential runoff losses. Unlabelled urea (60 kg N ha^{-1}) was applied at this time to the rest of the field, including the border 0.5 m × 4 m strips on either side of the ^{15}N application strip. Labelled tree material was prepared the previous year, by pruning two isolated trees of each species and applying ^{15}N enriched (10 atom% ^{15}N) ammonium sulphate weekly during the regrowth period. After 77 days the labelled regrowth material was pruned, divided into leaves and stems, dried and subsamples finely ground before analysis. Mean N concentrations for the two trees were 3.37 ± 0.03% and 0.95 ± 0.03 % for *G. sepium* leaf and stem respectively, and 2.02 ± 0.02% and 0.57 ± 0.02% for *P. dasyrrachis* leaf and stem. Mean ^{15}N concentrations were 1.52 ± 0.25 atom% and 1.28 ± 0.21 atom% for *G. sepium* leaf and stem respectively, and 2.53 ± 0.10 atom% and 2.25 ± 0.06 atom% for *P. dasyrrachis* leaf and stem. Material from each tree was more homogeneous (e.g. leaf material from the first *G. sepium* tree was 1.96 ± 0.03 atom% ^{15}N). Labelled tree prunings were applied at rates of 5.9 (*G. sepium*) plus 4.1 (P. dasyrrachis), 5.9 and 4.1 t ha^{-1} to G-P, G-G and P-P systems respectively, equivalent to 125, 66 and 201 kg N ha^{-1}. These rates were 25–34% of the dry weights applied following pruning on 5th December. To test whether *P. dasyrrachis* prunings influenced the mineralisation of *G. sepium* prunings, approximately the same amount of *G. sepium* prunings was applied to the G-P system as in the G-G system, along with *P. dasyrrachis* prunings in the same proportion as above; in this system only the *G. sepium* prunings applied were ^{15}N labelled. Equal dry weights of unlabelled prunings from trees growing outside the field were applied on either side of the application strip. Urea was not applied to ^{15}N prunings application plots or border strips.

Plant and soil sampling

Soil was sampled on two occasions for analysis of mineral N, total N and ^{15}N contents. Two replicate samples were taken using a 6 cm diameter auger from six layers by depth (0–5, 5–20, 20–40, 40–60, 60–80 and 80–100 cm), for each cropping system. Within the hedgerow intercropping systems, two replicate samples were taken for each depth at different positions, 0.7 m from the line of the hedgerow, and in the centre, 2 m from hedgerows. Subsamples of 5 g fresh weight were shaken for 2 h in 20 mL 2 M KCl for mineral N analysis, and stored when necessary at −18 °C. Ammonium and nitrate concentrations in the extracts were determined colorimetrically by flow injection analy-

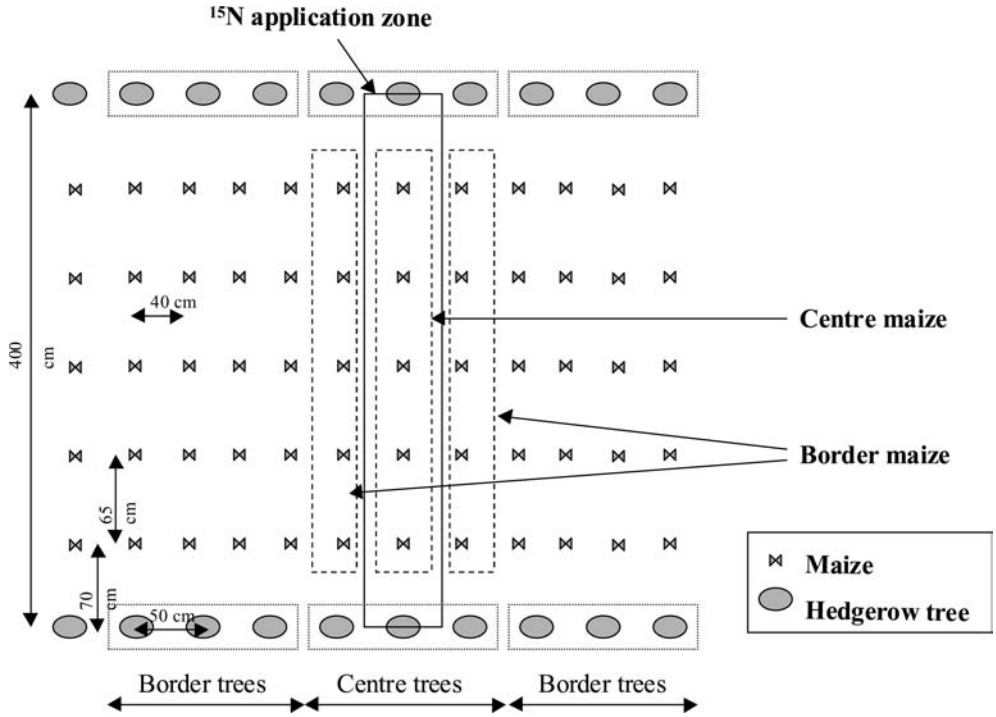

Figure 1. Layout of ^{15}N application plots. ^{15}N was applied in a strip across the crop alley denoted by the solid line. Recovery was calculated for crop plants and trees in centre and border zones, denoted by dashed lines.

ses, using the methods of Alves et al. (1993) and Gine et al. (1980) respectively. An additional subsample was air-dried for total N and ^{15}N analysis. Soil bulk density was measured for samples obtained by driving a 10 cm diameter ×5 cm PVC tube into the side of a pit at the central depth for the layer, following drying at 105 °C for 2 days.

The uptake of ^{15}N by crop plants within the ^{15}N application strip ('Centre' plants: 2 m^2) was monitored, as was uptake by 'Border' crop plants growing in two strips of 0.5 m × 4 m either side of the application strip (4 m^2) (Figure 1). Because of the presumed wider spread of tree root systems, the three trees closest to the application strip were considered 'Centre' trees, (corresponding to an area of 1.5 m × 4 m = 6 m^2 per hedgerow). The three trees either side of these were sampled as 'Border' trees (12 m^2 per hedgerow). Reported ^{15}N recovery is the sum of recoveries calculated separately for 'Centre' and 'Border' areas.

At crop harvests, crop plants were uprooted and subdivided into suitable components. The fresh weight of each component was determined, and subsamples (50–100 g) were weighed, dried and re-weighed to determine dry matter content. Leaves, or pieces of other components, were taken from all plants in the zone sampled. Root samples were obtained from uprooted plants, to avoid contamination by roots from plants from outside the plot. Maize plants were divided at harvest into leaf plus husk, stem, grain, cob cores, and root. Groundnut plants were divided at harvest into grain, husk, stover (leaf plus stem), and roots.

At each pruning, all regrowth was removed from trees and divided into leaf and stem, leaving only the 75–90 cm height main trunk(s). Leaf and stem fresh weight were recorded, and subsamples were dried to determine dry weight ratios. Leaves and stems were carefully subsampled for ^{15}N analysis. The biomass of trunks (the portion of the stem not pruned) was estimated from volume and density measurements. Samples of trunks for ^{15}N analysis were obtained by drilling half way through main stems and collecting the resulting sawdust. The biomass of roots was estimated from augered samples (see below). Dry weights of roots from all depths were summed to give total root weights for each species in the top 100 cm of soil. Samples of tree roots for ^{15}N analysis were obtained from the centre tree in each zone by excavating and cutting a section of root. Litterfall was collected in 0.5 × 0.5 m traps situated beneath the central trees on each plot. Litter was collected and dried every

2 weeks until tree pruning, when all litter collected from each trap was pooled and weighed. Following sub-sampling, the remainder of the plant material was returned to the plot, with the exception of grain, maize cores and groundnut husks which were removed.

Crop yield (of grain or of biomass) from centre and border areas was summed, and converted to yield per unit area using the total plot harvest area of 1.5 m × 4 m = 6 m^2. Tree biomass and N yields were converted to yield per unit field area on the basis of the area (0.5 m × 4 m = 2 m^2) available to each of the trees included in the yield measurement. Total N yield per plot or subplot was calculated as the product of dry matter yield and proportional N content.

Root sampling took place over a three week period, 8–11 weeks after sowing maize. Samples were obtained using an 8 cm diameter coring auger (Anderson and Ingram, 1993). Samples were taken at three distances from the line of the hedgerow (25, 85 and 184 cm) and therefore there were three positions for P-P and for G-G, five positions for G-P, and one position for Monocrop. Sampling positions were halfway along a line from expected maximum L_{rv} (beneath the plant) and expected minimum L_{rv} (furthest from plant), relative to trees for the zone nearest (0–50 cm from) hedgerows, and relative to maize plants for the other samples. Samples were taken from six depth ranges (0–5, 5–20, 20–40, 40–60, 60–80, 80–100 cm depth). From each position and depth 12 replicate samples were taken from different field locations. The collected soil samples were soaked overnight in water and washed over sieves of 2 mm and 0.25 mm mesh size, ensuring that all washing water passed through both sieves. Live roots of different species were separated according to visual characteristics (Rowe et al., 2001) and sorted by diameter class (>2 mm and <2 mm). Root length was measured using the grid intersect method (Tennant, 1975). Presented L_{rv} values do not include roots greater than 2 mm in diameter.

^{15}N recovery calculations

Plant samples were air-dried for 2–3 days in open paper bags, then oven dried at 60 °C for 48 h. Soil and plant samples were ground finely and subsamples were analysed for % N and atom % ^{15}N content using a Europa 20/20 mass spectrometer (PDZ, formerly Europa Scientific, Crewe, UK) coupled to a Roboprep automated C/N analyzer.

After application, the ^{15}N in plant and soil components (i.e., amount (μg) of ^{15}N excess) was expressed as percentage recovery, i.e., the percentage of the amount of ^{15}N applied which was found in the component. The amount of ^{15}N applied was calculated as excess over the ^{15}N natural abundance of total soil N. Natural abundance was found to differ between hedgerow treatments and soil depths, and for each treatment the mean natural abundance at 0–5, 5–20, 20–40, 40–60, 60–80 and 80–100 cm soil depth (which varied from 0.0023 to 0.0040 atom% ^{15}N), weighted by % N content at each depth (data not shown), was used.

Subsamples of all plant components were analysed for ^{15}N content in the centre zone of each plot. For plot borders, the total amount of ^{15}N was estimated from the amount of ^{15}N in components containing most of the N (Rowe and Cadisch, 2002). Average cumulative dry weight of litter fall per 0.5 × 0.5 m littertrap was 4.6 g (*G. sepium*) or 4.9 g (*P. dasyrrachis*). Cumulative litterfall across the whole alley was estimated to contain only 2–5 % of the N content of trees at pruning, and was therefore disregarded in calculations of ^{15}N recovery.

The amount of ^{15}N excess in each soil volume was calculated as the product of volume, bulk density, total N proportion and ^{15}N excess proportion, corrected for background ^{15}N abundance using the mean natural abundance value for the appropriate depth/hedgerow combination. Bulk density was 1.36, 1.39, 1.52, 1.52, 1.55 and 1.50 for soil layers 0–5, 5–10, 20–40, 40–60, 60–80 and 80–100 cm, respectively. Soil volumes were calculated as the product of layer thickness and the application area (Centre zone). Border soil ^{15}N was not measured.

To estimate the amount of ^{15}N which remained in litter at the time of first crop harvest, a further experiment was set up to measure ^{15}N remaining in litter following an equivalent application of ^{15}N labelled prunings to the soil surface. Prunings of *G. sepium* and *P. dasyrrachis* were taken in December 1998 from trees which had been labelled with ^{15}N in the main experiment. Material was taken from two labelled trees per species, and also from unlabelled *P. dasyrrachis* trees. Prunings were separated into leaf and stem, and dried in the sun. Subsamples were taken for determination of N and ^{15}N content. Plastic pipes of 15 cm diameter were cut into 10 cm lengths and then set 5 cm deep into the soil. Prunings were applied on the same day of the year (10th January 1999), and at the same rates (dry leaf t ha^{-1} and dry stem t ha^{-1}), as in the main experiment. The same treatments were used (labelled *G. sepium*, labelled *P. dasyrrachis*, and

labelled *G. sepium* plus unlabelled *P. dasyrrachis*), with 5 replicate pipes per treatment. On March 19th 1999 (after an interval equivalent to that before sampling for the first ^{15}N balance in the main experiment), surface litter remaining was carefully brushed up. ^{15}N recovery was calculated as a percentage of ^{15}N applied.

Statistics

Ranges are indicated in the text and figures as ± one standard error of the mean. Yield and ^{15}N recovery data were analysed using linear regression, with pairwise comparisons made using the RPAIR procedure of Genstat (Payne et al., 1987). Root length density data were log transformed (Log_{10} (L_{rv} cm cm^{-3} + 10^{-4})) before analysis by ANOVA, to reduce heteroscedasticity of variance.

Results

Following 11–12 years of inputs of tree prunings, total topsoil N was greater in G-G and P-P systems than after continuous monocrop (Table 1). However, this effect was not evident below 5 cm depth, and was not found in the mixed G-P system. Large quantities of mineral N (310–449 kg N ha^{-1} in the top metre) were available for plant uptake in all systems at the beginning of the experiment (Table 2) but less than 25% was in the more mobile form of nitrate (data not shown). Analysis at the end of the field season showed an overall decline in total mineral N content in the top metre of soil during the first cropping season. Mineral N contents at 60–100 cm depth, however, were maintained or increased under monocrop and in systems with *G. sepium*, indicating a greater amount of leaching in these than in the P-P system. The amount of mineral N present in the top metre of soil at the beginning of the second crop was greatest in the G-G system (239 kg N ha^{-1}) and least in the systems with *P. dasyrrachis* (139–160 kg N ha^{-1}).

Maize grain yield on ^{15}N application microplots was significantly reduced in the G-G intercropping system compared to monocrop (Figure 2). At the second harvest, microplot groundnut grain and total N yields were significantly greater in monocrop than in hedgerow intercropping systems. Grain and total N yields were not affected by ^{15}N application method.

Tree N yields calculated for the pruning on 22nd March, after 76 and 108 days regrowth for *G. sepium* and *P. dasyrrachis* respectively, showed that the method used for ^{15}N application had no significant effect on N content of regrowth and so data from these treatments were pooled. N yields from the *G. sepium* pruning on 8th January were estimated from main plot dry matter yields multiplied by N content of prunings measured on 22nd March, and included in total N yield. Input of N from prunings during and after the growth of the first crop was greater in the G-G system than in the P-P system (Figure 3). Prunings N input in the G-P system was intermediate. Total organic N inputs (prunings plus maize stover) during this 108 day period were (G-G) 172 kg N ha^{-1}; (P-P) 91 kg N ha^{-1}; (G-P) 138 kg N ha^{-1}; (Monocrop) 51 kg N ha^{-1}.

The proportion of ^{15}N applied as urea which was recovered by maize in the different cropping system treatments corresponded approximately to maize N yield from these treatments (Table 3; Figure 2); less urea ^{15}N was recovered by maize in the G-G system than in monocrop. Total plant (maize + tree) recovery of urea ^{15}N was similar in these four systems. Recovery by *G. sepium* hedgerows of ^{15}N from labelled *G. sepium* prunings was similar to that from ^{15}N urea, but maize recovered a smaller proportion of the ^{15}N from labelled prunings of either species than of urea ^{15}N. Total plant recovery from labelled tree prunings apparently increased in the order P-P → G-P → G-G, corresponding to increasing mean quality of the litter applied, but this trend was not significant.

Recovery by trees and maize of ^{15}N from labelled *G. sepium* prunings was not significantly reduced by the addition of unlabelled *P. dasyrrachis* prunings. Following labelled prunings applications, amounts of ^{15}N remaining in soil plus litter were similar for all hedgerow intercropping systems (Table 3). However, the proportion of this pool which remained in surface litter was much greater (53%) following *P. dasyrrachis* prunings applications than following *G. sepium* prunings applications (10%). More ^{15}N from labelled *G. sepium* prunings remained in litter when these were applied with unlabelled *P. dasyrrachis* prunings. Amounts of ^{15}N remaining in soil (plus litter) were smaller following application as ^{15}N urea than following application as ^{15}N labelled prunings. The smallest deficit in the ^{15}N budget was found following application of ^{15}N urea to the P-P system.

Crop recovery of ^{15}N at the second crop harvest was less than that at first harvest (Table 3). The decline in crop recovery between the two dates was steeper for urea than for labelled prunings applications, suggesting that labelled prunings N is more persistent in

Table 1. Initial total N in soil at different depths in a monocrop system and in *G. sepium* (G-G), *P. dasyrrachis* (P-P) and mixed *G. sepium-P. dasyrrachis* (G-P) hedgerow intercropping systems. Standard errors of the differences between means were 0.003 (Depth; $P < 0.001$), 0.003 (Cropping system; $P < 0.05$) and 0.010 (interaction; $P < 0.001$)

Depth (cm)	Cropping system				
	G-G	P-P	G-P	Monocrop	Mean
	Total N $^{-1}$) in soil (g kg^{-1})				
0–5	0.133	0.144	0.111	0.112	0.125
5–20	0.087	0.080	0.076	0.083	0.080
20–40	0.055	0.050	0.059	0.048	0.055
40–60	0.043	0.039	0.040	0.035	0.040
60–80	0.031	0.032	0.034	0.029	0.032
80–100	0.027	0.028	0.029	0.026	0.028

Table 2. Total mineral N in soil at different depths in a monocrop system and in *G. sepium* (G-G), *P. dasyrrachis* (P-P) and mixed *G. sepium-P. dasyrrachis* (G-P) hedgerow intercropping systems, before sowing a crop of maize and after final harvest (in parentheses). Soil data from two different distances (0.7 m and 2 m) from hedgerows were pooled. Standard errors of the differences between means were 6.8 (Depth; $P < 0.001$), 7.8 (Cropping system; $P < 0.001$) and 19.1 (interaction; $P > 0.05$)

Depth (cm)	Cropping system			
	G-G	P-P	G-P	Monocrop
	Total mineral N in soil (kg ha^{-1})			
0–5	34 (7)	48 (5)	37 (7)	56 (4)
5–20	78 (16)	100 (13)	80 (15)	83 (12)
20–40	54 (46)	96 (25)	63 (23)	66 (19)
40–60	45 (57)	71 (26)	51 (23)	59 (60)
60–80	49 (69)	69 (35)	45 (38)	50 (61)
80–100	50 (44)	65 (35)	36 (54)	46 (53)
Total	310 (239)	449 (139)	312 (160)	360 (209)

the soil system. Recovery by trees of ^{15}N applied as urea or as *G. sepium* prunings (unmixed) was similar to or less than recovery at 70 days after application. Recovery by trees of ^{15}N applied as *P. dasyrrachis* prunings, or as *G. sepium* prunings mixed with unlabelled *P. dasyrrachis* prunings, was greater during the second cropping season than during the first, perhaps indicating that applications of lower quality plant material had a greater residual benefit.

The deficit in the ^{15}N budget (Table 3) represents N losses from the system, due to leaching of N down to depths of greater than 1 m depth or laterally outside the plot boundary, and/or to volatilization and denitrification of N. This deficit was smallest when ^{15}N urea was applied to the P-P system, since retention of ^{15}N in soil was high in this system.

Of the total ^{15}N excess applied, 26–52% remained in soil at the time of the first crop harvest (Table 3). A higher proportion of ^{15}N was retained at shallow depths when ^{15}N was applied as labelled prunings than when ^{15}N urea was applied (Figure 4). However, even in urea treatments the proportion retained in the top 20 cm layer (i.e. 0–5 cm plus 5–20 cm) was considerably greaterthan that found in any deeper layer. In the monoculture/urea treatment, a ^{15}N pulse is visible at 60–100 cm depth, and similar pulses are visible for *G. sepium* labelled prunings treatments, though not when ^{15}N was applied in *P. dasyrrachis* prunings.

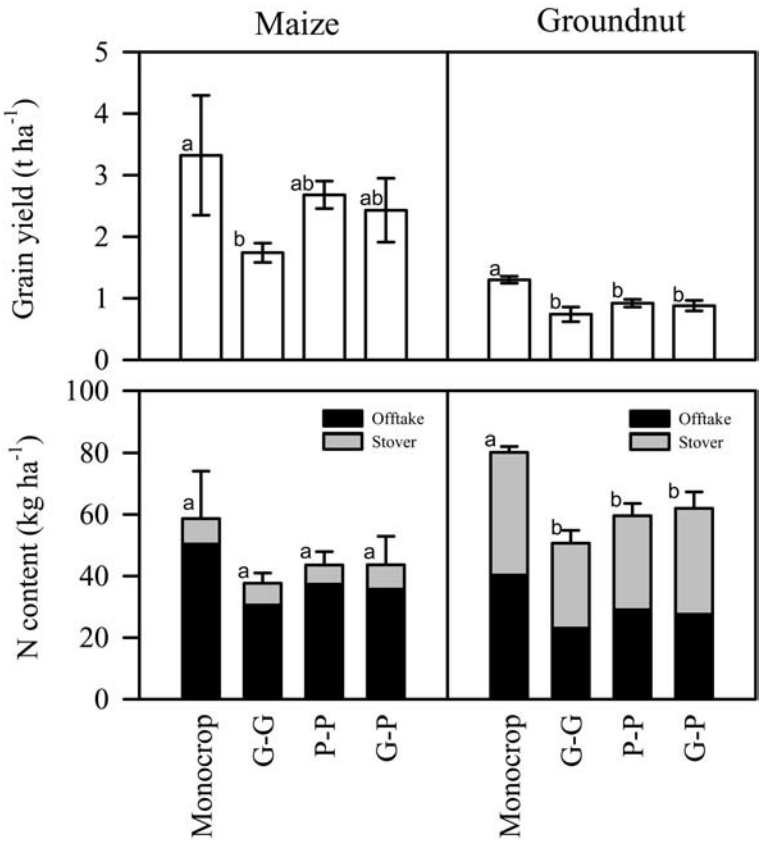

Figure 2. Grain and total crop N yield from ^{15}N application microplots (pooled by ^{15}N application method), in a monocrop system and in *G. sepium* (G-G), *P. dasyrrachis* (P-P) and mixed *G.sepium-P. dasyrrachis* (G-P) hedgerow intercropping systems. Tree prunings yields correspond to 108 days regrowth. Treatments which differed significantly ($P < 0.05$) are indicated with different letters.

In the single tree species hedgerow treatments, recovery of ^{15}N was measured separately for trees either side of the application plot. Recovery of ^{15}N (mean of *G. sepium* and *P. dasyrrachis* systems) by downslope hedgerows was 4.6% and 1.2% from urea and prunings respectively; recovery by upslope hedgerows was less ($P < 0.05$), at 2.1% and 1.4%, respectively (s.e.d. between position means = 0.7), even though the slope on this field was only around 4%. This effect was apparently more pronounced for ^{15}N applied as urea than as labelled prunings.

All species showed a rapid decline in root length density with depth (Figure 5). Species differed however in their root distribution with depth ($P < 0.001$). The decline in log L_{rv} with soil depth was steeper for maize than for the trees and steeper for *G. sepium* than for *P. dasyrrachis*. In the top layers of soil, *G. sepium* L_{rv} was greater than *P. dasyrrachis* L_{rv}, but the two species had similar L_{rv} beneath around 60 cm soil depth. Thus *P. dasyrrachis* had a greater proportion of its root system in the 'safety-net' layer, beneath the main crop rooting layer. The presence of *G. sepium* roots apparently resulted in shallower maize root distributions, with 90% and 87% of maize roots found in the top 5 cm of soil in G–G and G–P systems compared to 76% in P–P and 72% in monoculture (Figure 5).

Discussion

Maize yields from the P-P system were similar to those from monoculture, but those in the G-G system were significantly reduced, presumably because of competition from the tree for light, water and/or other nutrients. It is not clear why the beneficial effect of *P. dasyrrachis* hedgerows reported previously from this site by van Noordwijk et al. (1995) was not seen in this season. The residual effect of the previous *Mucuna* cover crop appears to have provided sufficient

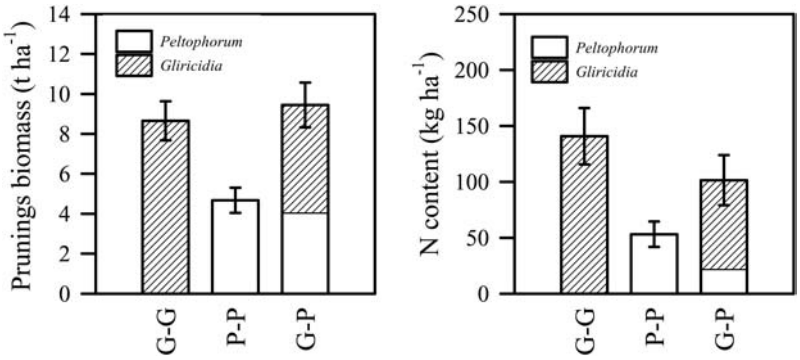

Figure 3. Prunings biomass and total N yields during 108 days regrowth of trees from ^{15}N application microplots (pooled by ^{15}N application method), in *G. sepium* (G-G), *P. dasyrrachis* (P-P) and mixed *G. sepium-P. dasyrrachis* (G-P) hedgerow intercropping systems.

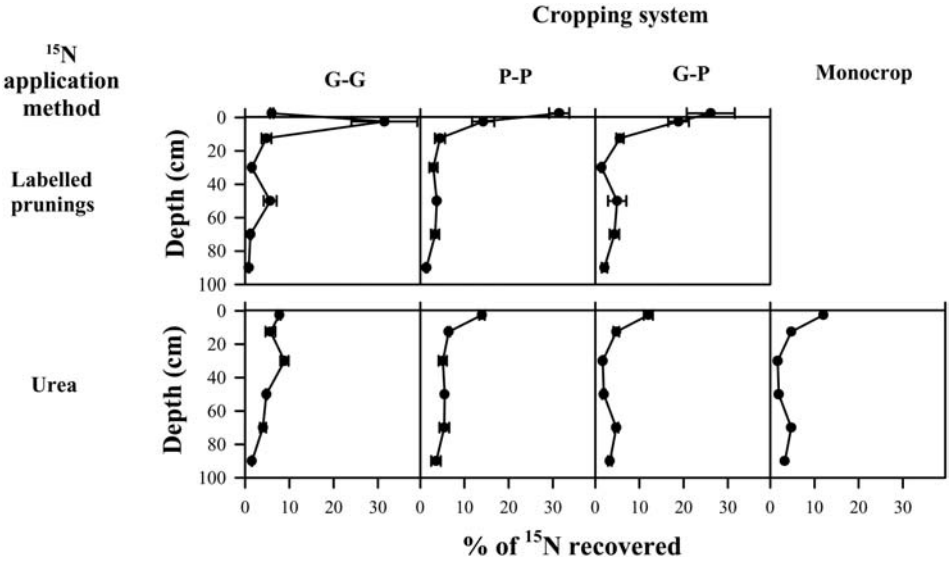

Figure 4. Location of ^{15}N in surface litter and in different soil depths, 70 days after application as ^{15}N labelled urea or prunings, as percentage of ^{15}N excess applied.

N at least for the first crop (Table 2), even though the above-ground biomass was removed, and hence reduced previously observed differences in N availability. The lower than normal rainfall in the year of the experiment resulted in increased crop water stress, and thus increased the competitive effect of tree water uptake.

The first hypothesis did not hold as there was no improvement of the combined plant NUE in the mixed species system compared to the maize monocrop. Use efficiencies of urea-N by maize (22–42%) were within the range reported by other workers. Akinnifesi et al. (1997) reported a NUE (maize N uptake) of 16% following split applications of ^{15}N urea to *Leucaena* hedgerow intercropping systems. NUE is likely to be affected by the time of N application in relation to periods of heavy demand by the crop and by trees. In our experiment ^{15}N was applied at the time of peak maize N demand, and thus a large recovery efficiency might be predicted. However, there was a large background soil mineral-N pool available at the start of the maize growth which may partly account for the low NUE. Maize accounted for the majority of plant N uptake. Leaving aside considerations of crop yield, this implies that NUE will be improved by measures which improve maize growth. Conversely, reduction in maize growth will result in poorer overall NUE, as demonstrated by the smaller total plant recovery in the G-G system. In this system, *G. sepium* does not compensate for reduced maize uptake by taking up more N, in part because N_2 fixation reduces the soil N demand of the tree. This implies that the incorporation of nitrogen

Table 3. Recovery of ^{15}N applied either as urea or labelled prunings to a monocrop system and to *G. sepium* (G-G), *P. dasyrrachis* (P-P) and mixed *G. sepium-P. dasyrrachis* (G-P) hedgerow intercropping systems. The location of ^{15}N is shown in plants and in the top 1 m of soil 70 days after ^{15}N application, and in plants 172 days (groundnut) or 180 days (*G. sepium* and *P. dasyrrachis*) after application. Values within the same row annotated with the same letter were not significantly different ($P < 0.05$)

Plant or soil pool	^{15}N application method						
	Urea				Labelled prunings		
	Cropping system						
	G-G	P-P	G-P	Mon.	G-G	P-P	G-P
a) After 70 days	% of applied ^{15}N recovered						
G. sepium	11.3*b*		4.5^{a}		9.3^{ab}		3.7^{a}
P. dasyrrachis		9.2^{b}	3.5^{a}			3.1^{a}	1.6^{a}
Maize	22.3^{b}	33.5^{bc}	26.5^{bc}	42.0^{c}	5.8^{a}	5.1^{a}	7.4^{ab}
Litter					6.0^{a}	31.4^{b}	26.1^{b}
Soil (0–1 m)	32.6^{a}	40.0^{a}	28.5^{a}	26.0^{a}	52.1^{a}	27.7^{a}	33.1^{a}
Total soil and plant	66.2	82.7	63.0	68.0	73.2	67.3	71.9
Deficit	33.8	17.3	37.0	32.0	26.8	32.7	28.1
b) After 172 or 180 days							
G. sepium	11.5^{a}		6.0^{a}		8.2^{a}		12.5^{a}
P. dasyrrachis		4.0^{a}	3.0^{a}			10.0^{a}	4.0^{a}
Groundnut	5.4^{a}	2.5^{a}	3.7^{a}	5.2^{a}	5.5^{a}	1.8^{a}	2.3^{a}
Total plant	16.9^{c}	6.5^{ab}	12.7^{bc}	5.2^{a}	13.7^{bc}	11.8^{abc}	18.8^{c}

fixing trees into cropping systems may lead to inefficiency in N cycling. This was reflected in a decrease in simulated interception efficiency with increasing N_2 fixation rate (Cadisch et al., 2004). Van Noordwijk and Cadisch (2002) used a series of simulations using the WaNuLCAS agroforesty model to demonstrate that effective N filtering by roots depends on unfulfilled plant N demand, and is thus incompatible with maximising the yield of all components. In a study of N fertiliser use in *Sorghum bicolor* hedgerow intercropping systems, Lehmann et al. (2002) found that N leaching was reduced under hedgerows compared to crop alleys. However the hedgerows recovered six times as much N as the crop, indicating that there was competition, and the crop took up less N than in monoculture.

Total plant N production was considerably greater in the P-P system than the monocrop system, due to the additional N in *P. dasyrrachis* prunings. Greater N inputs in the P-P system than under continuous monocropping resulted, over 11–12 years, in total topsoil N levels around 50% greater than under the latter system. The lack of such an effect in the G-P system may be because the mixture of prunings from the two species was mineralised faster that either alone (Gartner and Cardon, 2004), but this is contradicted by the improved retention of *G. sepium* litter N when mixed with *P. dasyrrachis* litter (Table 3); it is difficult to explain what interactions lead to this result. However, since the systems have an identical history of N fertilizer use and *P. dasyrrachis* is non-fixing, it can be said that *P. dasyrrachis* trees in the P-P system must be meeting their N requirements from complementary sources, spatially or temporally separated from maize uptake. Some of the improved N retention may come from delayed mineralisation of the recalcitrant *P. dasyrrachis* prunings (Handayanto et al., 1994). *P. dasyrrachis* prunings are high in polyphenols which have a strong protein binding capacity and led to immobilization of fertilizer N (Figure 4). Tree safety-net uptake, i.e. N uptake by trees from the soil layer beneath the main crop rooting zone as a proportion of uptake plus N leached out of this layer (Cadisch et al., 2004), must however contribute substantially to the maintenance of relatively high total soil N in the P-P system. This is facilitated by its root system with a high proportion of roots in the subsoil (Figure 5; Rowe et al., 2001) creating an important N sink below the main crop rooting zone.

P. dasyrrachis has a higher proportion of its roots in the subsoil than *G. sepium* (Figure 5; Rowe et al., 2001). This suggests that a greater proportion of its N uptake is derived from subsoil, as concluded by

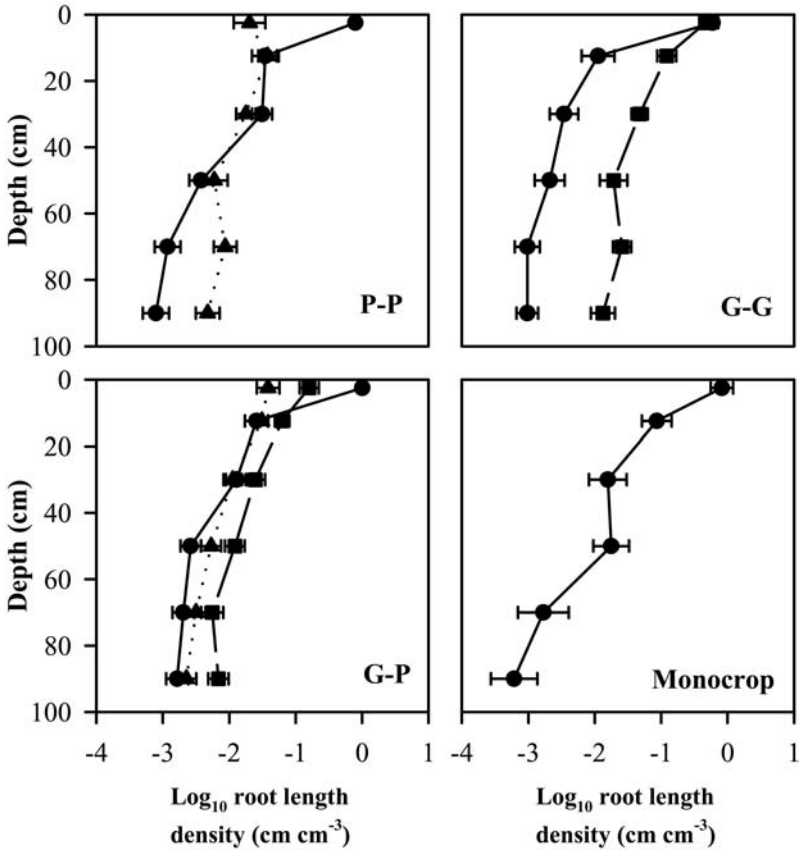

Figure 5. Root length density of maize (●), *G. sepium* (■) and *P. dasyrrachis* (▲) at different soil depths in monocrop and 3 hedgerow intercropping systems; *G. sepium* (G-G), *P. dasyrrachis* (P-P) or alternating *G. sepium* and *P. dasyrrachis* hedgerows (G-P). Pooled means for all horizontal positions.

Rowe et al. (1999) following injections of ^{15}N at different soil depths. In the current study there was substantial downward movement of applied ^{15}N; 2–10% of the ^{15}N applied was found between 60 cm and 100 cm depth after 70 days (Figure 3). The vertical separation between *P. dasyrrachis* and maize N uptake zones, coupled with the rapid leaching of N, seems likely to account for at least some of the demonstrated N uptake complementarity between the *P. dasyrrachis* and the crop. Mineral N contents in deeper soil increased during the cropping season in monoculture and in systems with *G. sepium* (Table 2), implying that these systems were more prone to leaching losses than the P-P system. Thus the results are consistent with the hypothesis (H2) that *P. dasyrrachis* hedgerow intercropping systems are more efficient in their use of N than *G. sepium* hedgerow intercropping systems, since *P. dasyrrachis* root systems are spatially distinct from crop root systems and thus have more opportunity to intercept N before it is leached. Nutrient resources in subsoil are accessible to deep-rooting trees, and the large volume of the subsoil means that these nutrients can represent a substantial resource (Lehmann et al., 2001). However, systems need careful design if this effect is to be usefully exploited, since the depth of tree root activity is dependent on complex interactions between soil type, tree species and management (Lehmann, 2003).

Amounts of N recycled by trees were substantial. Above-ground inputs of organic residue N to soil were 15 to 20 times greater in hedgerow intercropping systems than in monocrop. Amounts of N remaining in soil (plus litter) after 70 days were substantially greater after applying prunings than after applying urea (Table 3). However, inputs of N in pruning materials were substantially less available to the next crop than N applied as urea; crop plants took up proportionally much less N from prunings than from urea applications. Use efficiency of *G. sepium* prunings N over the two seasons (10.9 or 9.4% re-

spectively for G-G and G-P treatments) was less than the use efficiency range (12–29%) reported by Giller and Cadisch (1995). Use efficiency of *P. dasyrrachis* prunings N (7.0%) was even lower; the large amount of *P. dasyrrachis* residue which remained at the surface (Table 3; Figure 3) suggests that this was due to the slow mineralisation of *P. dasyrrachis* leaves relative to *G. sepium* leaves. Thus greater losses of N from *G. sepium* than from *P. dasyrrachis* were not observed, and H3 was not supported. The increased retention in litter of N from *G. sepium* prunings when these were applied with unlabelled *P. dasyrrachis* prunings suggests that the lower quality prunings either moderated the release of N from *G. sepium* leaves, or re-immobilised the released N. This provides some support for H4, though the effect did not result in greater subsequent recovery by groundnut of *G. sepium* N in the G-P system. Trees accounted for a larger proportion of total plant recovery when ^{15}N was applied as prunings than after ^{15}N urea application. This may have been because prunings ^{15}N became available later than urea ^{15}N, at a time when maize N uptake was declining. Overall deficits were similar, suggesting that organic N is also susceptible to leaching and/or gaseous loss.

These efficiencies may somewhat underestimate the actual amount of N taken up by plants as a result of prunings applications, because ^{15}N displaces and makes available N from other soil pools (pool substitution; Jenkinson et al., 1985). The cumulative effects of N release from successive applications of prunings may be greater than is suggested by the release, in subsequent cropping seasons, from a single application. However, the large amount of N remaining in litter in the *P. dasyrrachis* system may be very recalcitrant. In a pot experiment carried out by Cadisch et al. (1998), maize plants recovered only 20% of ^{15}N applied as labelled *P. dasyrrachis* prunings (finely ground and mixed with soil) over three cropping seasons, and the great majority of this was recovered in the first season. The eventual fate of the recalcitrant N fraction is unclear. Oorts et al. (2002) observed that low quality residues showed most significant differences in fine silt fractions resulting in increased CEC values and the largest carbon contents, the latter coinciding with our observations. It may contribute to long term soil fertility, whether through later mineralisation or through favourable effects of the organic matter on soil structure (Hamblin, 1985), but it appears not to become available in substantial quantities to plants within a timespan relevant to farmers'decision-making.

Total plant ^{15}N uptake was greater from *G. sepium* prunings (low C:N and low polyphenol content) than from the lower quality *P. dasyrrachis* prunings (high C:N and polyphenol). This is in accordance with other observations (Cadisch et al., 1998) as it has been well established that the lignin+polyphenol:N ratio determines N release from organic residues (Handayanto et al., 1994; Constantinides and Fownes, 1994). Large differences in losses of labelled pruning N between the systems were not observed, presumably because only small amounts of N were captured and recycled by trees. This is in contrast to results from a less N rich environment where trees recycled up to 35% of high quality pruning N (VanLauwe et al., 1998).

The vertical distribution of ^{15}N in soil 70 days after application (Figure 4) shows that significant amounts were retained at or near the surface, suggesting that some of the applied ^{15}N was protected from leaching and other losses by incorporation into soil organic matter, particularly when applied as prunings. Some of the applied ^{15}N was converted to or remained in soluble form and was leached down the profile. The movement of mineral N down the profile explains the considerably greater proportion of plant recovery accounted for by tree uptake during the second cropping season – the pulse of ^{15}N visible in the monoculture and *G. sepium* labelled prunings treatments is likely to have passed beyond the range of groundnut roots while the crop was establishing. The total proportion of ^{15}N retained in soil 70 days after application did not differ between application methods or hedgerow treatments (Table 3). However, if the N deeper in the profile at this time is indeed more subject to leaching than topsoil N, as expected from the low organic N content of subsoil, greater losses might be expected from urea and labelled *G. sepium* prunings treatments during subsequent seasons.

In pot experiments with ground plant material, Handayanto et al. (1997) observed a strong negative priming effect of *P. dasyrrachis* on the release of *G. sepium* N. In the current study, (unlabelled) *P. dasyrrachis* prunings appeared to moderate the release of ^{15}N from (labelled) *G. sepium* prunings in the G-P system, since amounts of ^{15}N recovered in plants and in soil were similar to those found without addition of *P. dasyrrachis*, but significantly more ^{15}N remained in litter. Thus *P. dasyrrachis* leaves appear to have moderated rather than prevented the release of *G. sepium* N, since uptake of *G. sepium* N by crop plants was not affected.

Priming effects may also occur in single species stands as continuous additions of prunings over time interact with partially decomposed litter from previous applications. Cadisch et al. (1998) observed that continuous application of high quality *G. sepium* prunings had a positive priming effect on the N release from previously applied ^{15}N labelled *G. sepium* prunings. The opposite occurred with polyphenol rich *P. dasyrrachis* prunings, where a negative priming effect was observed. In both occasions the priming effect was less than 2% of the applied N. While such interactions can easily be observed in controlled pot studies it is much more difficult to observed them in spatially variable field experiments.

Considerable lateral leaching of applied N was indicated by the increased ^{15}N uptake by downslope hedgerows relative to upslope hedgerows even on this gentle slope (4%). This also indicates that this lateral flow can be intercepted by trees or crop plants elsewhere in the field, if it remains at soil depths where it is still accessible. Thus even trees planted at relatively wide spacings could have a significant filter function (or lateral 'safety-net'). This is particularly true for soils such as Ultisols where hydraulic conductivity decreases with depth and so a large proportion of the water falling in an intense rainstorm may flow laterally through the top layers of soil. Such a filter will operate most effectively if it is perpendicular to the flow of N, i.e. with hedgerows along contours.

Conclusions

G. sepium hedgerows reduced crop yield, and nitrogen use efficiency (crop N uptake during the first season) was less in the *G. sepium* intercropping system than in monoculture. Thus agroforestry does not always improve resource use efficiency. The hedgerow intercropping systems studied do appear to recycle more N than in monoculture, partly because of separation in space and time of tree root N uptake from that by crop plants. However, this advantage must be set against potential reductions in crop yield due to competition for nitrogen or other resources. Over the years of the previous study the *P. dasyrrachis* system in particular gave improved crop yields over monoculture, but in this experiment crop yields were greatest in monoculture. Competition, and the labour input requred to control it, is a major constraint to adoption of alley cropping systems.

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