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Root distributions partially explain ^{15}N uptake patterns in *Gliricidia* and *Peltophorum* hedgerow intercropping systems

Edwin C. Rowe[1,2], Meine van Noordwijk[3], Didik Suprayogo[4], Kurniatun Hairiah[4], Kenneth E. Giller[1] & Georg Cadisch[1,5]

[1] *Department of Biology, Imperial College at Wye, University of London, Wye, Ashford, TN25 5AH, UK.* [2]*Current address: Institute for Environmental Science, Robinson Building, University of Wales, Bangor, LL57 2UW, UK.* [3] *ICRAF - S.E. ASIA, P.O. Box 161, Bogor 16001, Indonesia.* [4] *Fakultas Pertanian, Jurusan Tanah, Universitas Brawijaya, Jalan Veteran, Malang, Indonesia.* [5]*Corresponding author**

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Abstract

The relative distributions of tree and crop roots in agroforestry associations may affect the degree of complementarity which can be achieved in their capture of below ground resources. Trees which root more deeply than crops may intercept leaching nitrogen and thus improve nitrogen use efficiency. This hypothesis was tested by injection of small doses of $(^{15}NH_4)_2SO_4$ at 21.8 atom% ^{15}N at different soil depths within established hedgerow intercropping systems on an Ultisol in Lampung, Indonesia. In the top 10 cm of soil in intercrops of maize and trees, root length density (L_{rv}) of maize was greater than that of *Gliricidia sepium* trees, which had greater L_{rv} in this topsoil layer than *Peltophorum dasyrrachis* trees. *Peltophorum* trees had a greater proportion of their roots in deeper soil layers than *Gliricidia* or maize. These vertical root distributions were related to the pattern of recovery of ^{15}N placed at different soil depths; more ^{15}N was recovered by maize and *Gliricidia* from placements at 5 cm depth than from placements at 45 or 65 cm depth. *Peltophorum* recovered similar amounts of ^{15}N from placements at each of these depths, and hence had a deeper N uptake distribution than *Gliricidia* or maize. Differences in tree L_{rv} across the cropping alley were comparatively small, and there was no significant difference ($P<0.05$) in the uptake of ^{15}N placed in topsoil at different distances from hedgerows. A greater proportion of the ^{15}N recovered by maize was found in grain following ^{15}N placement at 45 cm or 65 cm depth than following placement at 5 cm depth, reflecting the later arrival of maize roots in these deeper soil layers. Thus trees have an important role in preventing N leaching from subsoil during early crop establishment, although they themselves showed a lag phase in ^{15}N uptake after pruning. Residual ^{15}N enrichment in soil was strongly related to application depth even 406 days after ^{15}N placement, demonstrating the validity of this approach to mapping root activity distributions.

Introduction

Deep rooting trees have been recommended for simultaneous agroforestry systems (Schroth, 1995), on the assumption that root distributions reflect the distribution of nutrient uptake activity. The distribution of root activity will also depend on other factors such as the water content of different soil layers, but the presence of roots at least indicates that uptake can occur. Potential nutrient uptake rates are limited by the quantity of roots per unit soil volume, and are a function of the distribution of root surface area within the soil volume (de Willigen and van Noordwijk, 1987). Root surface area is difficult to measure in practice, and so root diameter is commonly assumed to be constant and only root length is measured. The length of roots per unit soil volume is referred to as root length density (L_{rv}).

* Fax no: +44-0-20-759-42640. E-mail: g.cadisch@ic.ac.uk

The total volume of soil explored by a root system is particularly important when considering uptake of mobile resources such as water and N. Horizontal exploration by crop plants is constrained by competition with their neighbours, and so the volume explored can only be effectively increased by increasing rooting depth. The maximum depth recorded for roots in several major biomes has been reviewed by Jackson (1999) who concluded that plants were generally deeper rooted in arid environments, although plants rooting to >10 m have been recorded for evergreen tropical forest. The benefits of deep rooting derive from acquiring a strongly limiting resource, which is likely to be water in arid environments but may be N in humid environments subject to rapid N leaching.

Root length density data for agricultural crops were reviewed by van Noordwijk and Brouwer (1991). Maize (*Zea mays* L.) root length density varied from 1.5 to 26 cm cm^{-3} in the 0–30 cm depth layer, and from 0.1–3.5 cm cm^{-3} in the 60–90 cm layer. Equivalent L_{rv} values for groundnut (*Arachis hypogaea* L.) were 0.8 – 1.6 cm cm^{-3} at 0–30 cm depth and 0.2 – 0.6 cm cm^{-3} at 60–90 cm depth. Greenwood et al. (1982) found that the L_{rv} of several vegetable crops declined exponentially with depth, and thus that a regression of log L_{rv} against depth removed most of the variation in log L_{rv}. Several recent studies have compared root distributions of agroforestry trees (Akinnifesi et al., 1998; Jama et al., 1998; Mekonnen et al., 1999; Rao et al., 1993; Ruhigwa et al., 1992). Large variations in rooting depth have been found. Akinnifesi et al. (1998) found that the percentage of tree fine roots in the top 0–30 cm of soil varied from 21% for *Lonchocarpus sericeus* to 84% for *Tetrapleura tetraptera*. Jama et al. (1998) found that the slope of plots of log L_{rv} against depth differed significantly between tree species, indicating that some had a deeper root distribution. Such studies usually conclude that deeper rooting trees are better candidates for use when trees and crops are mixed in fields, since they will compete less with crops. However, fewer studies have simultaneously measured crop and tree root distributions, or demonstrated a vertical separation of activity between them. Simulations using the WaNuLCAS agroforestry model (van Noordwijk and Lusiana, 1999) suggest that tree root length densities in the soil layer beneath the main crop rooting zone must be substantial if safety-net N uptake is to occur; recycling efficiencies greater than 50% require an L_{rv} in this 'safety-net zone' of >0.5 cm cm^{-3} (Cadisch et al., 1997).

A previous experiment (Rowe et al., 1999) on the same site demonstrated the potential of ^{15}N for locating root uptake activity at different soil depths. However, in that study root length density distributions were not determined, and ^{15}N was applied only in the centre of crop alleys which may have lead to an underestimation of tree N uptake activity over the whole alley width. The objectives of the current study were (1) to quantify L_{rv} distributions of maize and two tree species (*Gliricidia sepium* and *Peltophorum dasyrrachis*) in three hedgerow intercropping systems; (2) to quantify differences in ^{15}N uptake following application of ^{15}N at different soil depths and at different distances from the hedgerow; and (3) to examine the relationship between differences in L_{rv} distributions and differences in ^{15}N uptake distributions. The overall objective (4) was to infer from these patterns the effect of including these tree species in cropping systems on N leaching. ^{15}N placements were made at different depths, as in the previous experiment. Because rooting depth was thought to be restricted by an aluminium-rich plinthic layer, 65 cm was the deepest we placed ^{15}N. This was deeper than in the previous experiment; we chose this depth to better distinguish between the vertical distributions of N uptake activity of crop plants and trees, and the two tree species. To ensure strong ^{15}N labelling of tree material and a large 'signal to noise' ratio, repeated small applications of highly enriched $(^{15}NH_4)_2SO_4$ were made, over a period of 9 weeks. This approach resulted in little leaching of ^{15}N, and hence ^{15}N uptake was confined mainly to a restricted volume below the ^{15}N application depth.

Materials and methods

Study site

The experiment was carried out on a farmer's field near the village of Negara Jaya in North Lampung, Sumatra (4°31′ S, 104° 55′ E). Soils in the area are Typic Kandiudults with pH (H_2O) around 5.2 in the topsoil and 4.8 in the subsoil. Aluminium in the subsoil solution reaches 106 μmol l^{-1} (van der Heide et al., 1992). Three hedgerow intercropping treatments were established in 1992, consisting of hedgerows of *Gliricidia sepium* (G) and/or *Peltophorum dasyrrachis* (P) spaced 4 m apart. Trees were spaced 0.5 m apart within the row. In the G–G system, crops were grown in alleys between *Gliricidia sepium* hedgerows.

In the P–P system, the hedgerows were of *Peltophorum dasyrrachis*; and in the G–P system *Gliricidia* hedgerows alternated with *Peltophorum* hedgerows. Control plots, without hedgerows, were also established. Two crops were grown per year, December–March (maize) and April–July (groundnut). Rock phosphate was applied at a rate of 500 kg ha^{-1} in April 1995 (i.e. only once), to all hedgerow and control plots. In December of each year from 1995, triple super-phosphate was applied to all hedgerow and control plots at a rate equivalent to 26 kg P ha^{-1} yr^{-1}. KCl was applied at the same time to all treatments, at a rate equivalent to 50 kg K ha^{-1} yr^{-1}. In 1994, following establishment of the hedgerows, a further treatment was imposed on the experiment, in which hedgerows were pruned either at ground level, or at 75 cm above the ground. Hedgerows were maintained thereafter by pruning before sowing each crop. *Gliricidia* was also pruned once during the growth of each crop. All prunings were applied to the alleys as mulch. Crop and prunings yields were monitored. A full description of the initial stages of this trial is given in BMSF (1995). The same hedgerow intercropping trial was used for a previous ^{15}N application experiment (Rowe et al., 1999). However, in the current experiment, we applied ^{15}N at least 8 m from the positions where ^{15}N was applied in the previous experiment. This had been proved to be sufficient distance to avoid the influence of previously applied ^{15}N (Rowe and Cadisch, 2001).

Experimental design

We compared the three hedgerow intercropping systems outlined above with respect to rooting distributions and ^{15}N uptake. ^{15}N was applied at one of three depths; 5, 45 or 65 cm depth. One application per alley was made in the 0 cm pruning-height sub-plot, and one in the 75 cm pruning-height sub-plot. However, pruning and maize yields were similar for both pruning-height treatments, and hence, data were pooled. Applications within the same crop alley were made at the same depth, and were separated by a minimum of 8 m. Applications at different depths were separated by three hedgerows. Applications at 5 cm depth (only) were also made at either of two positions in relation to hedgerows, 'Alley centre' and 'Alley side', 200 cm and 75 cm from the nearest hedgerow, respectively. 'Alley side' placements were only made in G–G and in P–P systems. There were two replicate plots for each hedgerow system, ^{15}N placement depth and alley position combination, except for G–G / 5 cm ^{15}N placement depth / alley centre placements which were replicated four times.

We applied ^{15}N through PVC pipes 25 mm in diameter, installed in pre-augered holes and capped between applications. Individual plot layouts are shown in Figure 1. Four tubes were installed per application plot, spaced 40 cm apart along the line of maize plants. Aliquots of 10 mL $(^{15}NH_4)_2SO_4$ solution were applied per tube, and washed down the tube with 10 mL distilled water. A total of 2 g N with 21.8 atom% ^{15}N was applied per plot, with 20% applied initially and 10% at weekly intervals for the next 9 weeks. The maximum amount of N applied per tube at any one time was therefore 0.1 g. Assuming that applied ^{15}N extended to a radius of 20 cm from each tube (Rowe, 1999), application area was approximately 0.5 m^2, and the application rate was thus equivalent to 40 kg N ha^{-1} within this area.

^{15}N uptake was measured in crop plants within three zones. 'Zone 1' consisted of plants at the five sowing stations 20 cm from application tubes (0.65 × 2 m = 1.3 m^2) (Figure 1). 'Zone 2' consisted of plants at stations beyond these in the same crop row, plus plants in the same length of adjacent rows ('Alley centre' placements: (2.8 m × 1.95 m) – 1.3 m^2 = 4.16 m^2; 'Alley side' placements: (2.8 m × 1.3 m) – 1.3 m^2 = 2.34 m^2). 'Zone 3' consisted of plants at the next station in Zone 2 rows, plus plants in the same length of adjacent rows ('Alley centre' placements: (3.6 m × 3.25 m) – 5.46 m^2 = 6.24 m^2; 'Alley side' placements: (3.6 m × 1.95 m) – 3.64 m^2 = 3.38 m^2). ^{15}N uptake was also measured in the three trees on each side, perpendicular to application tubes. Six trees were thus sampled, which in the G–P system consisted of 3 trees of each species, which were sampled separately. Trees on each side of 'Alley side' placements were also sampled separately, in two zones consisting of three trees each; 'Near' and 'Far'. Tree yields were converted to yield per unit area on the basis of the field area available to each tree, i.e. 0.5 × 4 = 2 m^2.

Experimental sequence

On 3rd December 1996 all hedgerows were pruned. Prunings were applied evenly over the hedgerow and alley. The field was kept clear of weeds by regular hand weeding. Maize was sown on 6th December at a spacing of 65 × 40 cm, in 5 rows along the crop alley. Triple superphosphate and KCl were applied, as previously outlined. The first application of ^{15}N was made on 14th December 1996, and applications were then

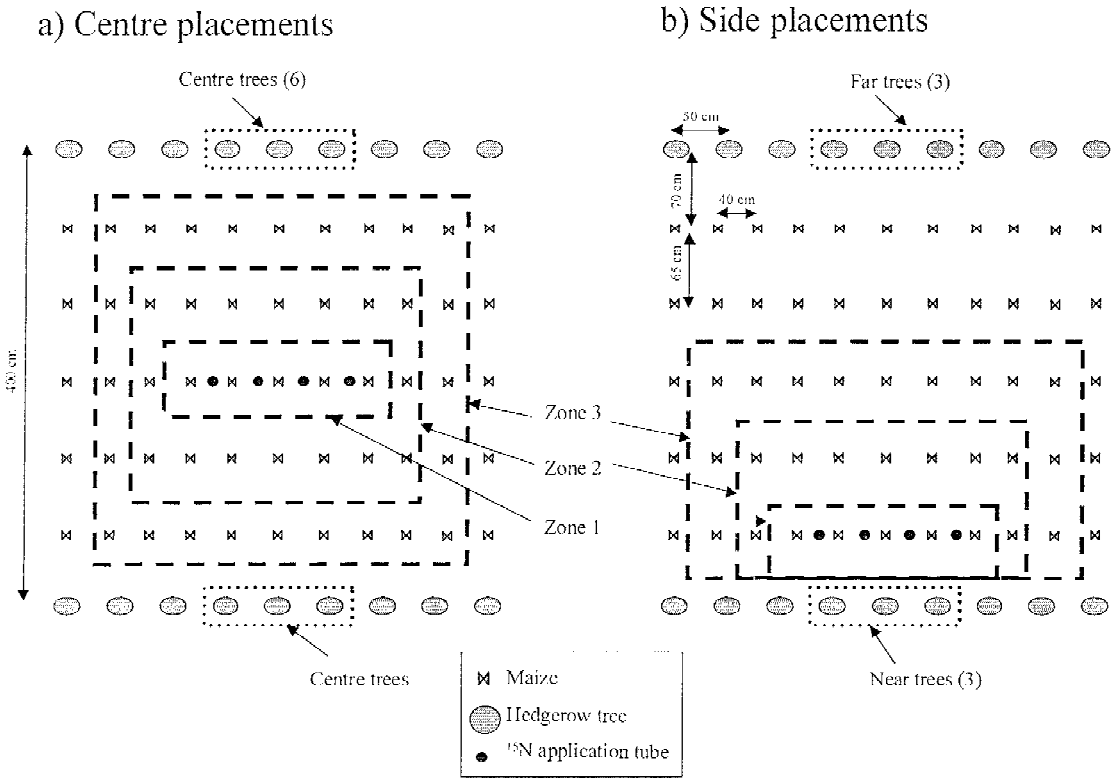

Figure 1. Layout of plots for 'Alley centre' and 'Alley side' placement positions for applications of ^{15}N-labelled fertilizers in the field experiment.

made every 7 days until 8th February 1997. Maize was harvested on 11th March and hedgerows were pruned on 18th March. *Gliricidia* hedgerows in the 75 cm pruning height treatment (only) were pruned again on 13th January 1997, 42 days after the initial pruning, to prevent excessive shading of the crop. Ground-level pruned *Gliricidia* trees, and *Peltophorum* trees, were not pruned on this occasion. Prunings from the trees perpendicular to application sites and the 12 trees adjacent to these trees were removed and replaced with equal weight of unlabelled prunings, to avoid surface inputs of ^{15}N labelled material.

^{15}N sampling procedure

Samples of young leaf material (the first fully opened leaf on a shoot) were taken from maize plants adjacent to application points (Zone 1), and from trees perpendicular to application points. Young leaf samples were taken from maize and trees 8, 28, and 48 days after the first application of ^{15}N. Additional samples of mature leaves (all leaves below the first fully opened leaf; sampled by taking upper, middle and lower leaves from shoots) were taken from trees, 28 days after first application. At maize harvest, samples of grain were taken from all 3 zones, and samples of leaf and stem were taken from zone 1 plants. At the final tree pruning, samples were taken of leaf and regrowing stem material. Samples were dried for 3 days at 60 °C, and ground using a rotary hammer mill with a 1 mm screen. Samples which still retained structure were then finely ground using a piston ball bearing mill. Total N content and ^{15}N enrichment of plant and soil samples was determined using a Europa 20/20 mass spectrometer (Europa Scientific, Crewe, UK) coupled to a Roboprep automated C/N analyzer.

Calculation of yield, N yield and ^{15}N recovery

Maize from each zone of each plot was cut on 11th March 1997, divided into cobs and other shoot biomass, and weighed. Subsamples were weighed, divided into leaf, stem, grain and cob cores, oven-dried and reweighed, to obtain dry weight conversion factors

for each part. Dry weights of each part from each zone were calculated. Maize grain yield was calculated for each application plot as the sum of yields from Zones 1, 2 and 3, and divided by the total area of the plot to give grain yield per unit area. N concentration (%) and ^{15}N enrichment (atom%) were measured in subsamples of grain from each zone, and in subsamples of leaf and stem from zone 1. ^{15}N enrichment was converted to ^{15}N excess over the natural abundance of plant-available soil N, assuming this to be the same as the natural abundance of *Peltophorum* N (0.368511 atom% ^{15}N).

The amount of ^{15}N in each plant component was calculated as follows:

$$^{15}\text{N content } (\mu\text{g}) = \text{biomass (g)} \times \text{N concentration (\%)} \times \text{atom\% excess } ^{15}\text{N} \times 100$$

In a separate ^{15}N recovery experiment (Rowe, 1999), only 8.1% of the total maize shoot ^{15}N recovery was derived from cob cores. In the current experiment, cob core ^{15}N recovery was assumed to be in the same ratio to the total ^{15}N recovery, and was estimated from the sum of grain, leaf and stem recovery. In Zones 2 and 3, ^{15}N recovery from leaf, stem and cob cores was estimated as the grain recovery multiplied by the ratio of leaf, stem and cob core recovery to grain recovery found in Zone 1 of the same plot (Rowe and Cadisch, 2001). The total recovery of ^{15}N by maize was calculated as the sum of recovery from all three zones.

Trees were pruned at the base of new stems, divided into leaf and stem, and weighed. Fresh weights were measured separately for each side of the plot, where the sides were different, i.e. for 'alley side' placements and G–P plots. Subsamples were weighed, dried and reweighed, to obtain dry weight conversion factors for each part. N concentration (%) and ^{15}N enrichment (atom% excess) were measured in subsamples of leaf and stem from each plot, or where sides differed, from each side of the plot.

At the pruning on 13th January 1998 (*Gliricidia* 75 cm pruning height only), N concentration and ^{15}N enrichment were measured in samples of young and mature leaves from the 3 or 6 trees perpendicular to application sites. Recovery was calculated by assuming that 30% of leaf biomass was young and 70% mature, and that ^{15}N enrichment of stems was equal to that of mature leaf samples.

Total ^{15}N recovery, and tree N inputs, were calculated as the sums from both the final pruning and the intermediate (*Gliricidia* 75 cm pruning height only) pruning. Litterfall, root and main stem ^{15}N were not included in this calculation. Trees were actively regrowing during this period (wet season) and so litterfall was not significant.

Recovery of added N was calculated as a percentage:

$$\text{Recovery of added N(\%)} = \frac{^{15}N\ recovered\ (\mu g)}{^{15}N\ applied\ (\mu g)} \times 100$$

where ^{15}N recovered and ^{15}N applied are calculated as excess over the background natural abundance.

The ^{15}N enrichment of soil was examined 407 days after ^{15}N application. A 3 cm diameter auger was used to take samples of soils from beneath 3 randomly chosen application plots per ^{15}N placement depth, from 10 cm depth increments.

Root measurements

Root length and dry weight per unit volume were measured in samples obtained using an 8 cm diameter coring auger (Anderson and Ingram, 1993) 8–11 weeks after maize was sown. Samples were taken adjacent to ^{15}N application plots, immediately outside 'Zone 3', at 3 distances from the line of the hedgerow (0, 75 and 200 cm); therefore, there were 3 positions for P–P and for G–G, and 5 positions for G–P. In the line of the hedgerow soil cores were removed midway between adjacent trees. Sampling positions at 75 and 200 cm from the line of the hedgerow were halfway between (20 cm from) maize planting stations. Samples were taken from 8 depth ranges (0–10, 10–20, 20–30, 30–40, 40–50, 50–60, 60–70, 70–80 cm depth). Samples were washed through 2 mm and 0.25 mm sieves. Soil aggregates were gently broken up by hand. All roots, other than fine root fragments less than approximately 2 mm in length, were picked off both sieves with forceps and stored in water, with a small piece of thymol to retard microbial growth, until they could be measured. Samples were measured within 7 days. Live roots were separated on visual characteristics (Table 1). Roots of each species were separated by diameter class ($>$2 mm and $<$2 mm) and lengths were measured by the grid intersect method of Tennant (1975). Dead roots and roots of weed species were not measured.

Soil water content was measured using a neutron probe, type IH-III (Didcot-Wallingford). PVC tubes were installed in the line of the centre maize row, 2 m from hedgerows. At each point, measurements were

Table 1. Characteristics used to distinguish plant roots

Characteristic	Maize	*Gliricidia*	*Peltophorum*	*Imperata*[1]
Transparency	Translucent	Opaque	Opaque	Opaque
Colour (young roots)	White	Pale yellow brown	Dark red-brown bark, often flaking off very pale red-brown inner bark	White
Colour (mature roots)	White to pale yellow-brown	Pale yellow - brown	Dark red-brown bark, often flaking off very pale red - brown inner bark	White to yellow brown often with fine brown spots
Colour (old roots)	White to pale yellow-brown	Pale yellow - brown	Dark red-brown	White to red - brown or yellow-brown
Colour during aging of sample	Fine dark grey spots, merging to even dark grey colour	Pale yellow - brown	Dark red - brown	White to red brown or yellow-brown
Branching pattern	Coarse (c. 2mm) roots with many fine branches of around 0.5 mm thickness and 0.5 – 5 cm length	Variable Sometimes with many fine (c. 0.5 mm) branches proliferating from one point	Fine (c 0.5 mm) branches generally short and much branched	Coarse 1 – 2 mm roots often with many very fine (c. 0.2 mm) and finely branched roots
Dissociation characteristics	Fine branches break off into 0.5–4 cm sections, with few braches	With aging of sample, outer root sometimes falls away from very tough and woody inner root.		With aging of sample, outer root sometimes falls away from tough inner root
Nodules	No	Sometimes	No	No
Crumching sound when squeezed with forceps	Yes	No	No	Sometimes
Tensile strength	Weak	Strong	Very strong	Strong
Smoothness of 1–2 mm roots	Root hairs very furry appearance when in water	Smooth	Rough	Smooth
Straightness	Usually fairly straight, sometimes coarsely undulating	With short (5–10 mm) undulations	Not undulating. Often curving with a radius of around 3 cm	Usually with slight short undulations

[1] *Imperata cylindrica* (weed).

Table 2. Recovery of applied N by maize following applications of ^{15}N-labelled fertilizer at different depths in the alley centres of *Gliricidia sepium* (G–G), *Peltophorum dasyrrachis* (P–P) and alternating *Gliricidia* / *Peltophorum* (G–P) hedgerow intercropping systems (n = 18 plots)

Hedgerow intercropping system	N recovery by maize (%)			s.e.d.
	G–G	P–P	G–P	
^{15}N placement depth (cm)				
5	50.6	43.6	61.8	$8.0^{n.s.}$
45	35.7	26.1	29.4	$24.8^{n.s.}$
65	51.7	20.5	5.3	$18.6^{n.s.}$
s.e.d.	$26.6^{n.s.}$	7.0†	16.5†	

n.s. = not significant; † = $P<0.10$.

taken every 0.1 m soil depth until 0.8 m. Neutron probe measurements were calibrated by making linear regressions, for each soil depth, of counts against volumetric water content as measured by weighing soil samples of known volume, drying and reweighing.

Changes in leaf ^{15}N enrichment following ^{15}N applications at different depths were analysed by one-way analyses of variance (ANOVA), separately for each species and each point in time, pooling data from all hedgerow intercropping treatments. Maize and tree ^{15}N recoveries were analysed by one-way ANOVA. Log transformed root length densities were analysed using separate three-way (species, depth, distance from hedgerow) ANOVAs for G–G and P–P hedgerow intercropping systems, and by two-way ANOVA (species, depth) for the G–P system, for which the design was unbalanced with respect to distance from hedgerow. Log transformed root length densities were also compared between systems using separate two-way ANOVAs (hedgerow system, depth) for each species.

Results

Soil water content

Soil water content during the rainy season remained close to field capacity in the whole of the top 80 cm of soil in all cropping systems during the growth of the maize crop (Figure 2). Towards the beginning of the dry season differences in water content became evident; on 12th May water content declined in the order G–P>monocrop = P–P>G–G ($P<0.001$). By 17th June, all systems had dried out to a similar extent, at all depths.

Root distribution

Root length density of all species declined with depth in all hedgerow intercropping systems (Figure 3), but this decline was less steep for *Peltophorum* than for *Gliricidia* or maize. The interaction between species and depth was significant ($P<0.001$) in both G–P and P–P systems, but was not significant when comparing *Gliricidia* with maize in the G–G system. The root system of *Gliricidia* was thus largely coincident with that of maize, in contrast to the deeper root system of *Peltophorum*. Maize roots were present, though sparse, in samples from 70 to 80 cm depth; this result was not expected, since Akiefnawati (1995) reported no crop roots below 50 cm depth on a similar soil at the BMSF field station. In order to check the result, a pit was dug to 120 cm depth; maize roots, the identity of which was confirmed by tracing them back to maize plants, could be clearly identified at 80–90 cm depth. Some maize roots were exploiting the channels created by decaying tree roots, an effect also noted by van Noordwijk et al. (1991). However, most of the maize roots found, even deeper in the profile, were in mineral soil. An iron pan was found in many areas of the field, generally at 50–90 cm depth, but this was weakly developed, and was less of an impediment to plant roots than to the root auger.

L_{rv} of trees and maize was similar at all distances from hedgerows in G–G and P–P systems. The hedgerow system had no significant effect on maize L_{rv}, nor on the distribution of maize roots with depth. Neither did the hedgerow system affect the rooting depth of trees. Mean L_{rv} of both tree species was greater in single tree species systems than in the mixed G–P system, reflecting the lower overall number of trees of each species per unit area in the mixed system.

Residual ^{15}N in soil

The distribution with depth of ^{15}N enrichment in soil was strongly related to application depth, even 406 days after the first application (Figure 4). The movement of ^{15}N down the profile through leaching resulted in some enrichment of total soil N below the application point, but below a depth of 20–30 cm beneath the application tube this enrichment was small. While the distribution of ^{15}N enrichment of available soil N during the experiment may not have corresponded exactly to this distribution, the application method was

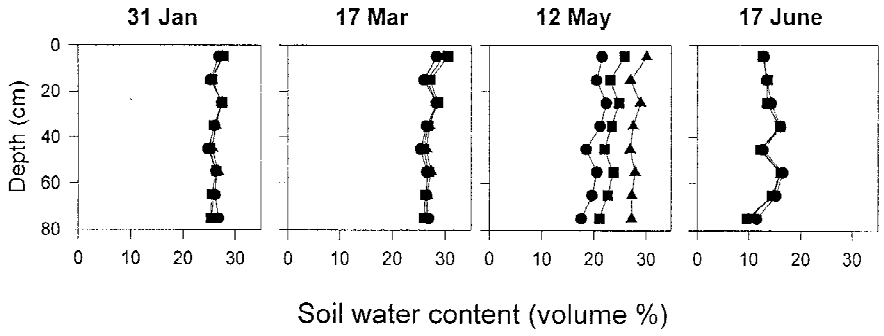

Figure 2. Changes in volumetric soil water content (%) at different depths within *Gliricidia sepium* (●), *Peltophorum dasyrrachis* (■) and alternating *Gliricidia/Peltophorum* (▲) hedgerow intercropping systems.

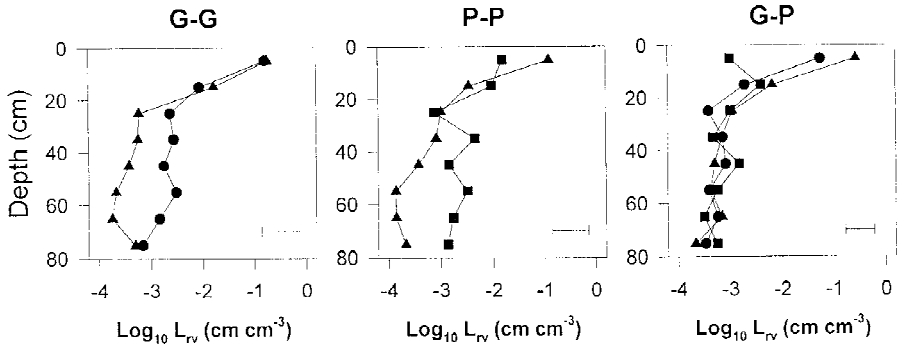

Figure 3. Effect of soil depth on root length density (log L_{rv} cm cm^{-3} +10^{-4}) of maize (▲), *Gliricidia* (●) and *Peltophorum* (■) in intercropping systems with hedgerows of *Gliricidia* (G–G), *Peltophorum* (P–P), and alternating *Gliricidia/Peltophorum* (G–P). Bars represent the standard error of the difference between means for the species × depth interaction.

successful in maintaining a strong ^{15}N signal at, or slightly below, the application depth.

Time course of plant ^{15}N enrichment

The increase in leaf enrichment of all three species was faster following application of ^{15}N at 5 cm depth than for deeper placements (Figure 5). This was particularly true for maize, which showed a different time course of enrichment following placement at different depths, presumably because of the gradual extension of maize roots into the subsoil. There was little initial ^{15}N uptake (at 7 days after the first application) by *Gliricidia* or *Peltophorum* from any of the placement depths, suggesting a lag in demand while the trees recovered from being pruned. At 28 days, all species had taken up ^{15}N from 5 cm depth placements, but relatively little from deeper placements. Between 28 and 48 days, *Peltophorum* took up similar amounts of ^{15}N from deep and shallow placements, and by 88 days had apparently taken up more from 45 cm than from 5 cm placements, though this effect was not statistically significant. By contrast, *Gliricidia* showed an early and large enrichment following ^{15}N placement at 5 cm depth. The concentration of ^{15}N was smaller in *Gliricidia* leaves than in *Peltophorum* leaves (note different scale in Figure 5), since total N production in prunings was around 41% greater for *Gliricidia* than for *Peltophorum* on this field, and around half of this production was derived from atmospheric N_2 fixation (Rowe et al., 1999). Enrichment of *Peltophorum* leaves increased in a similar pattern following placement at all depths, which is consistent with a similar increase in root activity at all depths as the trees regrew.

Recovery of ^{15}N by maize at harvest

A large ^{15}N recovery by maize from shallow ^{15}N placements compared to that from deep placements was seen in P–P and G–P hedgerow treatments, though not in the G–G system (Table 2). On one of the 65 cm

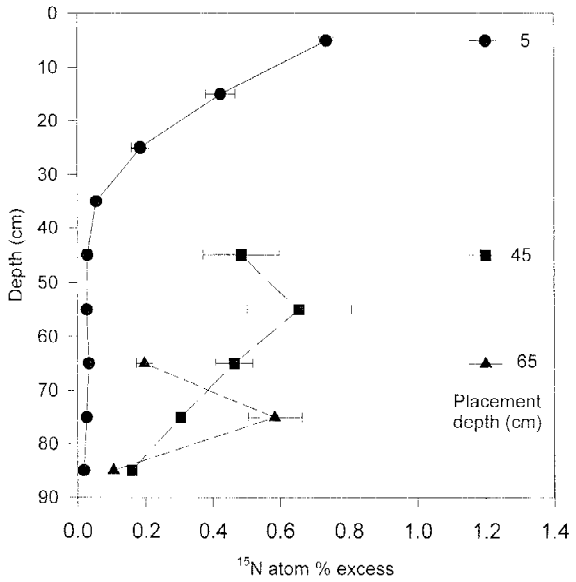

Figure 4. ^{15}N enrichment of total soil N in soil beneath ^{15}N application tubes, 406 days (1934 mm rain) after first application of ^{15}N. Standard errors of the means are shown, except for depth of 85 where only one sample was available.

placement depth plots in the G–G system, recovery was estimated at 73%, leading to a large average ^{15}N recovery from this depth. ^{15}N enrichments of different parts of these maize plants were consistently high, so it is unlikely that this result derived from a sampling error. The large recovery shows that the maize roots observed deeper in the profile were actively taking up nitrogen, at least in some areas of the field. This may be because localized channels allowed the entry of maize roots deeper into the soil. Pooled across the P–P and G–P systems, maize ^{15}N recovery declined with application depth ($P<0.01$).

No significant differences in ^{15}N recovery by maize (total of all 3 zones) were observed following ^{15}N application at different positions within the alley (Table 3). The mean percentage of total ^{15}N recovery derived from Zone 3 maize plants was 0.9%, despite the large area of this zone compared with Zones 1 and 2. This shows that the activity of maize roots declined sharply beyond a horizontal radius of 1 metre, and that horizontal movement of ^{15}N in soil was minimal beyond this distance.

The proportion of the total maize ^{15}N in grain was lower when ^{15}N was placed at 5 cm depth than with deeper placements (Figure 6) ($P<0.01$). This reflects the pattern expected from the developmental sequence of maize parts (leaf → stem → grain) and provides

Table 3. Recovery of applied N by maize following applications of ^{15}N-labelled fertilizer at 5 cm depth at different distances from hedgerows in *Gliricidia sepium* (G–G), *Peltophorum dasyrrachis* (P–P) and alternating *Gliricidia* / *Peltophorum* (G–P) hedgerow intercropping systems (n = 6 plots)

Hedgerow intercropping system	N recovery by maize (%)		s.e.d.
	G–G	P–P	
Placement position			
Centre	50.6	43.6	$3.7^{n.s.}$
Side	51.4	41.7	$13.3^{n.s.}$
s.e.d.	$13.3^{n.s.}$	$3.4^{n.s.}$	

n.s. = not significant.

Table 4. Recovery of N from different depths by hedgerow trees, following application of ^{15}N-labelled fertilizer to the centre of the crop alley; mean of *Gliricidia sepium*, *Peltophorum dasyrrachis* and alternating *Gliricidia*/*Peltophorum* hedgerow intercropping systems. Standard errors of the means are shown in parentheses (n = 18 plots)

Placement depth (cm)	N recovery (% per tree)	
	Gliricidia	*Peltophorum*
5	0.34 (0.05)	0.43 (0.25)
45	0.13 (0.07)	2.76 (1.44)
65	0.12 (0.05)	0.92 (0.59)
s.e.d.	0.08*	$1.28^{n.s.}$

n.s. = not significant; * = $P<0.05$.

Table 5. Recovery of N by hedgerow trees from different positions within the crop alley in *Gliricidia sepium* (G–G) and *Peltophorum dasyrrachis* (P–P) hedgerow intercropping systems, following application of ^{15}N-labelled fertilizer at 5 cm depth. Standard errors of the means are shown in parentheses (n = 6 plots)

Position	N recovery (% per tree)	
	Gliricidia	*Peltophorum*
Near side	1.35 (0.43)	0.16 (0.08)
Centre	0.34 (0.05)	0.43 (0.25)
Far side	0.02 (0.01)	0.01 (0.01)
s.e.d	0.38*	$0.33^{n.s.}$

n.s. = not significant; * = $P<0.05$.

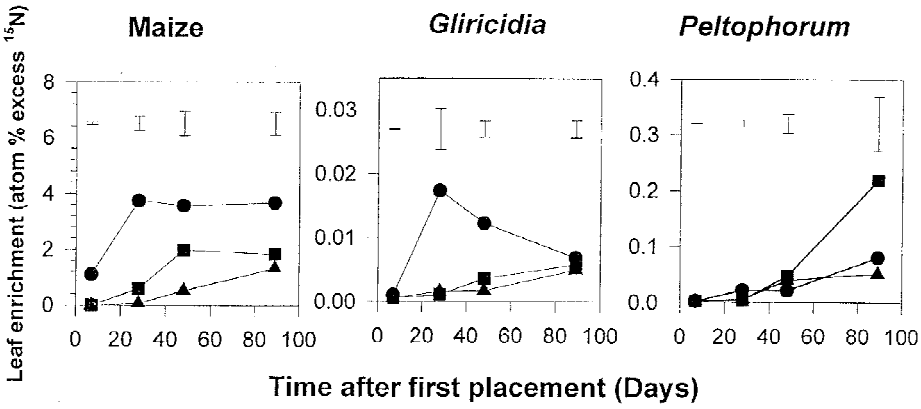

Figure 5. Changes in ^{15}N enrichment in leaves of maize, *Gliricidia* and *Peltophorum* following ^{15}N placement at 5 cm (●), 45 cm (■) or 65 cm (▲) depth, in the first 89 days after placement. Pooled means for *Gliricidia sepium* (G–G), *Peltophorum dasyrrachis* (P–P) and alternating *Gliricidia/Peltophorum* (G–P) hedgerow intercropping systems. Note different scales for each species. Bars represent one standard error of the difference between means.

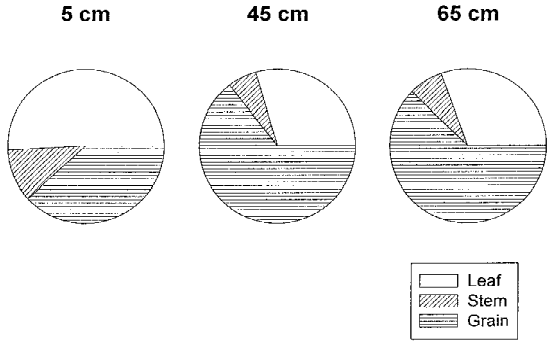

Figure 6. Effect of placement depth of ^{15}N-labelled fertilizer on the proportion of ^{15}N recovered in different maize parts. Pooled means for *Gliricidia sepium* (G–G), *Peltophorum dasyrrachis* (P–P) and alternating *Gliricidia/Peltophorum* (G–P) hedgerow intercropping systems.

further evidence that the location of maize root uptake activity moved down the profile with the development of the crop.

^{15}*N recovery in tree prunings*

The greatest N uptake by *Gliricidia* was from shallow ^{15}N placements (Table 4). *Peltophorum* took up relatively large amounts of ^{15}N from deep placements, and differences in *Peltophorum* uptake from the three depths were not significant. *Gliricidia* showed a more pronounced decline in uptake with distance from the application than did *Peltophorum* (Table 5). Large heterogeneity was observed. This heterogeneity was apparently not caused by differences in the size of trees; there was no relationship between the N yield and the ^{15}N recovery of individual plots (data not shown). It seems likely that, while the root distribution of hedgerows as a whole is fairly even, the distribution of roots of individual trees is more heterogeneous. This heterogeneity in the distribution of individual trees may explain the large variation in tree ^{15}N recovery observed, since tree recovery estimates are based on a smaller number of plants than maize recovery estimates.

Discussion

The zone of greatest ^{15}N enrichment of soil N extended some 20–30 cm beneath the ^{15}N placement depths (Figure 4). Root length density within this layer (Figure 3) gave some indication of patterns of ^{15}N uptake (Tables 2 and 4). *Gliricidia* ^{15}N uptake declined significantly with ^{15}N application depth, whereas *Peltophorum* recovered similar amounts of ^{15}N from all depths. This corresponded with the shallower root distribution of the former species. However, maize took up large amounts of ^{15}N from the deepest placements, despite low root length density at this depth. Factors other than root length density within a soil layer influence the amount of N uptake from that layer, such as the proportion of roots within other soil layers, the amount of plant N demand, and the timing of plant demand in relation to N availability in different soil layers. Both tree species had a similar root length density at 60–70 cm depth, but took up different amounts of ^{15}N from this depth. *Gliricidia*'s

capacity for N_2 fixation (50% N derived from N_2 fixation, Rowe et al. 1999) meant that overall it did not compete strongly with crop plants for N. However, *Gliricidia* may compete strongly for topsoil N during early crop establishment as indicated by its rapid enrichment following 5 cm depth placement (Figure 5). This may be disadvantageous during early crop growth when crop N demand is satisfied mainly from the topsoil (Figure 6). The relatively deep N uptake activity distribution in *Peltophorum* indicated that this species will not compete strongly with crop plants at least for topsoil N. *Peltophorum* recycles N from deeper soil layers more efficiently than *Gliricidia*, and may thus be more suitable than *Gliricidia* for use in agroforestry associations, particularly if uptake of water and other soil resources follows a similar distribution to N uptake. The pattern of soil drying (Figure 2) suggests that soil water was at least episodically depleted more by *Gliricidia* than by *Peltophorum*, though there is no evidence of differential depletion in different soil layers.

Root length density was not significantly affected by distance from the hedgerow in the *Gliricidia* and *Peltophorum* hedgerow intercropping systems. The hypothesis that tree root length density was smaller in the centre of the alley cannot therefore be supported. Ruhigwa et al. (1992) also noted that roots of some hedgerow intercropping tree species (*Alchomea cordifolia* and *Senna (Cassia) siamea*) were evenly distributed over the crop alley. In contrast, those of *Acioa* (*Dactyladenia*) *barteri* were concentrated close to the tree base, and it was concluded that the latter species was more promising for use in hedgerow intercropping. While the more even horizontal distribution of *Gliricidia* and *Peltophorum* roots may imply greater below-ground competition, such a distribution is likely to result in more efficient interception of leaching N, i.e., a safety-net. The even distribution of tree roots across the alley resulted in a similar recovery of ^{15}N by trees from different positions in relation to hedgerows (Table 5).

Maize root length densities in topsoil were greater than those of *Peltophorum*, and showed a more rapid decline with depth. Most of this difference was accounted for by relatively small *Peltophorum* L_{rv} and relatively large maize L_{rv} in the top layer of soil. The proportion of total *Peltophorum* root length in deeper soil layers was greater than the proportion of total maize root length. However, a small proportion of the root system may be capable of supplying all of a plant's N demand, if these roots are relatively well-supplied with N. The observed large uptake of ^{15}N by some maize plants from 65 cm depth placements during grain filling confirms this (Table 2, Figure 6).

Measured root length densities of maize and the two tree species were small in comparison to those observed by other workers (Schroth and Zech, 1995; van Noordwijk and Brouwer, 1991). This may be due to site (soil type with low pH and appreciable amounts of Al) or temporal specificity. It is also possible that the low root length densities observed here were partially due to some losses of fine roots at the root washing stage. The effect of sieve mesh size on the fraction of roots recovered was examined by Livesley et al. (1998); only 60% of the root length of *Grevillea robusta* was recovered using a 1 mm mesh, and using a 0.25 mm mesh (as in the current study) doubled the measured fine root length at some locations. Although the root length densities observed were low, relative density distributions reflect observations of other authors, and relative distributions of roots with depth and distance from hedgerows are valid.

The estimate of maize recovery was not much affected by including recovery from the outer sampling zone, indicating that lateral movement of ^{15}N and lateral scavenging by maize roots did not extend beyond 1 m radius, and it is unlikely that much ^{15}N was taken up beyond this radius. The sum of recovery from all three zones thus accurately reflects total maize recovery. Maize was able to recover a large proportion of the ^{15}N applied, even when application was made at 65 cm depth. The maize roots observed at or below this depth show that maize rooting depth in these soils was not as restricted as had been indicated by a previous study (Akiefnawati, 1995). It is possible that more spatial niche separation will occur on more acid soils where aluminium toxicity greatly restricts rooting depth. Niche separation was, however, observed early in the season; maize enrichment increased only slowly following ^{15}N application at 45 or 65 cm depth. The difference in the proportion of maize ^{15}N recovery derived from different plant parts following ^{15}N application at different depths may also be interpreted as being due to uptake at different growth stages (Gass et al., 1971). Maize root systems do not reach 45–65 cm depth until later in the growing season, when much of the N taken up is used in the filling grain. The proportion of recovered ^{15}N found in grain was greater following deep ^{15}N placements than following shallow placement, indicating that ^{15}N deeper in the soil became available later in the growth of the crop. This temporal separation shows the potential for tree

root systems to take up N which would otherwise have been leached, if they are active at depth before crop root systems have fully developed. However, trees take up little N immediately after pruning (Figure 5), so the timing of pruning in relation to N fertilizer application appears to be important to ensure efficient safety-net N uptake by the trees. There will obviously be a trade-off between the benefit of managing above-ground competition for light through pruning and the decrease in root activity that this causes.

The efficiency of recovery of ^{15}N by maize was high (44–62% from 5 cm depth placements) compared to the 16% observed by Akinnifesi et al. (1997) in a maize/*Leucaena leucocephala* hedgerow intercropping system following application of ^{15}N ammonium sulphate. This high efficiency was presumably caused by repeated application of small amounts of ^{15}N throughout the maize growing period. Recovery by trees, at 0.1–3% per tree, was similar to that observed in the previous experiment on this field (Rowe et al., 1999) and comparable to the 7% observed by Akinnifesi et al. (1997) if the total uptake from all trees on a plot is considered. Non-competitive N uptake by trees from the 'safety-net zone', i.e. the layer beneath the main crop rooting zone, appears to represent a large proportion of this recovery efficiency. Although maize was also shown to take up substantial amounts of ^{15}N from deep placements, this took place only later in the season and would probably not have prevented N leaching from previously applied N. The experiment demonstrated significant vertical separation between root distributions, and important temporal separation between vertical N uptake distributions. Nitrogen use efficiency appears thus to be greater in hedgerow intercropping systems than under monoculture, since N deeper in the soil, and at risk of being leached, is taken up by trees before crop roots reach this depth or at stages between plantings when no crop is present.

The study was successful in quantifying root length density distributions and ^{15}N recovery from different soil locations. Despite large variability in both of these, some relationship was revealed between root length density and ^{15}N recovery. Root length density distributions are, therefore, useful indicators of the location of potential N uptake, and thus the effects of trees and crop plants on nitrogen leaching.

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