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EFFECTS OF DEFOLIATION ON GROWTH CHARACTERISTICS AND N, P, K CONTENT IN AN ALDER/MAIZE AGROFORESTRY SYSTEM

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ABSTRACT

The effects of defoliation on the growth characteristics and N, P, K content of potted alder *(Alnus acuminata)* and companion maize (*Zea mays*) grown outdoors in sole and mixed cropping were examined. *Alnus* seedlings were subjected to 0, 25, 50 and 75% repeated artificial defoliation. Defoliation reduced the height and diameter, and stem, leaf, root and nodule biomass in *Alnus*. *Alnus* showed higher, albeit mostly not significant ($P > 0.05$), growth performance in mixed culture than in sole culture. However, the biomass of *Alnus* nodules was significantly lower in mixed compared to sole culture. Defoliation increased *Alnus* leaf N, P, K and nodule P and K concentrations, but decreased nodule N concentration and also significantly reduced both leaf and nodule total N, P, K content. In contrast, defoliation of *Alnus* increased the height, biomass and total N, P, K content in companion maize crop. The most severe defoliation treatment (75%) increased maize height by 57%, total biomass by 209%, and shoot total N, P, K by 209%, 238% and 208%, respectively compared to maize grown in association with non-defoliated trees. However, maize grown in sole culture showed significantly higher height, biomass and total shoot N, P, K content than did maize intercropped with *Alnus*. Results of this study indicate that defoliation of *Alnus* may not only influence the performance of the species, but it may also have significant effects on the performance of associated plants with important bearing in nutrient cycling in agroforestry.

Key Words: *Alnus acuminata,* companion crops, herbivory, nodulation, nutrient cycling

RÉSUMÉ

Les effets de la défoliation sur les caractéristiques de croissance et les contenues en N, P, K de l'aulne d'appartement *(Alnus acuminata)* et le compagnon de maïs *(Zea mays)* plantés dehors en monoculture et culture croisée étaient examinés. Les semis d'Alnus étaient sujets a 0, 25, 50 et 75% de défoliation artificielle répétée. La défoliation a réduit la hauteur et le diamètre, et la biomasse de tige, de feuille, de racine et de nodule en *Alnus*. L'Alnus a montré bien que principalement non significatif ($P<0,05$), la performance de croissance en culture croisée élevée qu'en monoculture. Cependant, la biomasse de nodules *d'Alnus* était significativement basse en culture croisée comparée à la monoculture. La défoliation a augmenté le N, P, K de feuille d'Alnus et les concentrations en P et K de nodule, mais a réduit la concentration en N du nodule et a aussi significativement réduit le contenu total en N, P, K de la feuille et du nodule. En contre parti, la défoliation d'Alnus a augmenté la hauteur, la biomasse et le contenu total en N, P, K dans le compagnon de plante de maïs. Le traitement le plus sévère de défoliation (75%) a augmenté la hauteur de 57%, la biomasse totale de 209%, et le N, P, K total de rejeton de 209%, 238% et 208%, respectivement comparé à l'association de plante de maïs avec des arbres non défoliés. Cependant, le maïs planté en monoculture a montré une hauteur significativement élevée, une biomasse et un contenu total en N, P, K de rejeton que le maïs en culture croisée avec *l'Alnus*. Les résultants de cette étude indiquent que la

défoliation d'Alnus peut non seulement influencer la performance des espèces, mais il peut aussi avoir des effets significatifs sur la performance des plantes associées avec de contenant important en substance en cycle en agroforesterie.

Mots Clés: *Alnus acuminata*, plantes compagnon, herbivore, nodulation, substance en cycle

INTRODUCTION

Agroforestry is regarded as a low-cost means for maintaining or improving the productivity of agricultural ecosystems while decreasing the requirement for external nutrients (Chuntanaparb and MacDicken, 1991). In a pot experiment to examine the growth characteristics and N content of *Leucaena leucocephala/Sorghum bicolor* agroforestry system, Avery and Rhodes (1990) observed that the height, dry weight and total N content increased significantly in sorghum grown with nodulated *L. leucocephala* over the control, sole sorghum. However, these authors noted that the gain in N content of the intercropped sorghum represented less than 1% of the N budget of *L. leucocephala* and was inadequate to sustain normal physiological development in sorghum. Similarly, Sprent (1983) observed that little, if any, N is transferred underground by actively growing legumes and suggested that N-fixing plants must be under some form of stress such as defoliation for significant N transfer to occur. Unfortunately, very little is known about the impact of herbivory on the growth characteristics of host and associated plants, and nutrient cycling in agroforestry.

Plant-herbivore interactions is important in agroforestry, especially in view of recent concerns over the risks of serious losses in agroforestry systems due to pest infestations (Schroth *et al.*, 2000; Rao *et al.*, 2000). Research studies have been conducted into the impact of insect herbivory on plants (Ericsson *et al.*, 1980; Reich *et al.*, 1993). Often, however, such studies have been concerned with plant responses in monocultures or natural plant communities. In some pioneering work on the interaction between damaged N fixing and non-N fixing plants, Gadjil (1971) demonstrated increased N uptake in *Pinus radiata* grown with damaged *Lupinus arboreus*. More recently, Bardgett *et al.* (1999) reported that low levels of white clover (*Trifolium repens* L.) root infection by clover cyst nematodes (*Heterodera trifolii* Goffart) increased root growth by 141% in the host plant and by 219% in the uninfected neighbouring grass (*Lolium perenne* L.). Thus herbivory may significantly influence the productivity and nutrient cycling in a system involving N fixing and non-N fixing plants.

Alder (*Alnus acuminata*) a N fixing tree species, has received considerable attention for use in highland agroforesty in several tropical countries, including Uganda (Russo, 1995; van Houten, 1997). Whereas extensive leaf perforations, largely attributed to honey bee (*Apis mellifera)*, have recently been reported on the species in Uganda (Roux, 1999; Nyeko *et al.*, 2002), information on the impact of this damage on the growth characteristics and nutrient status of this *Alnus* species and associated crops is lacking. Such information is important since defoliation can have a positive, negative, or neutral influence on plant growth (Prins and Verkaar, 1992) and is thus, essential for determining the pest status of damaging agents and planning for appropriate management strategies.

The objectives of this study were to (i) examine the effects of different levels of defoliation on the growth characteristics (height, diameter and biomass) and nutrient content of *A. acuminata*, (ii) assess the influence of a companion maize crop on the response of *A. acuminata* to different levels of defoliation, and (iii) assess whether defoliation of *A. acuminata* significantly affects the growth (height and biomass) and nutrient content of a companion maize *(Zea mays)* crop grown in the same season.

MATERIALS AND METHODS

Study area. This study was conducted at the World Agroforestry Centre (ICRAF) field station in Kabale district, Uganda. The district lies at latitude 0°16' S, longitude 29°57' E and approximately 2000 m above sea level. The rainfall pattern in Kabale district is bimodal with peaks in

March and April, and October and November averaging 1,000 mm - 1,480 mm per annum. A brief dry spell occurs in January and a drier period from June to August. The temperature averages 17.5 °C, which sometimes drops to about 10 °C at night.

Experimental materials and design. Nursery grown *A. acuminata* seedlings were transplanted outdoors into 8-litre plastic pots in May 1999. A pot-based experiment was used to enable measurements of root as well as shoot responses. In a field situation, reduced root growth may not be apparent, and possibly even disguised by more rapid growth of leaves and lateral branches. The pots were filled with a loamy forest soil-sand-compost manure mixture in the ratio 3:2:1, respectively to ensure that soil nutrients were not limiting. The forest soil was a mixture of soil collected from nearby plantations of rose gum *(Eucalyptus grandis)* and *A. acuminata* in the ratio 3:1, respectively. Soil from *A. acuminata* stands was used to provide more *Frankia* in order to facilitate nodulation of seedlings in addition to enhancing soil fertility in the pots. Because the companion maize crop was to be planted when defoliation treatments was expected to have exerted some impact on *A. acuminata*, sole maize pots were filled with the soil mixture and left bare until November 1999 when maize was planted. The maize seeds germinated within 10 days and the seedlings were thinned to 2 per pot a fortnight after planting.

Nine treatments were used in a split plot design, with each treatment in every plot randomly split over four harvests. The treatments comprised of 0%, 25%, 50% and 75% defoliated *Alnus* seedlings without (sole culture) and with (mixed culture) maize and a sole maize culture. The pots were arranged in 6 blocks (replicates), each plot initially comprised of 36 pots spaced 1 m within a row and 0.7 m between rows without extra space between plots. Without plant mortality, this experimental design allows equal number of plants per treatment to be assessed in all blocks at every sampling occasion. However, the between pot distance inevitably changes after every harvest. Therefore after every harvest, remaining pots were immediately moved to equalise the distance among them while maintaining their neighbours.

Treatment application. Defoliation treatments were applied beginning in July 1999 when *Alnus* seedlings were about nine months old and continued at 4-week intervals until the final harvest in April 2000. During every defoliation occasion the *Alnus* seedlings were subjected to four levels of artificial defoliation: 0%, 25%, 50% and 75% defoliation by excising with a pair of scissors, none, one-quarter, one-half and three-quarters of each leaf, respectively. For repeat defoliation, all new leaves were cut to the desired levels while those previously cut were not defoliated again. All pots were sprayed with a mixture of Benlate (benomyl) and Salut (chlorpyrifos and dimethoate) at 3-week intervals in order to prevent fungal and insect herbivory. The spray solution was prepared by mixing benomyl, Salut and water in the ratio of 4g:3ml:2 litres, respectively following the manufacturers' recommendations. Weeds appearing in the pots were hand-pulled immediately on emergence while those at the experimental site were hoed at 4-week intervals.

Determination of growth characteristics. Height and root collar diameter (RCD) of *Alnus* seedlings were measured at first defoliation and thereafter continued monthly until the final harvest in April 2000. Maize height was measured, on plants due for harvest, one day before each harvest. Beginning January 2000, six pots of each treatment were harvested monthly to determine plant biomass and N, P, K content. During each harvest, *Alnus* seedlings were separated into leaf plus petiole, stem plus branch, root, and nodule portions, and maize plants into shoot and root portions. All plant portions were oven-dried at 70 °C to constant weights and their biomass determined on an electronic scale. Plant samples were ground in Cyclotec 1093 sample mill while air-dried soil samples were pounded in a wooden motor to pass a 2 mm sieve for N, P, K analysis.

Determination of N, P, K concentration and content. Oven dried samples of *Alnus* leaves and nodules, maize shoot and soil were analysed for N, P, K concentration. The concentrations of N, P, K in every plant sample were multiplied by the respective dry weights of the samples in order to obtain their total N, P, K contents. Concentrations of N in plant and soil samples were determined

using the Kjeltec method (Anonymous, 1986). For each sample, 0.2g was weighed and transferred into a dry digestion tube. This was followed by addition of about 3.5g of Kjeltabs catalyst and 5ml of H_2SO_4 into the tube. The samples were digested in each run by putting a batch of 40 digestion tubes, placed in a digestion stand, in a preheated (420°C) digestion block until discoloration occurred (about 30 minutes). After digestion, the tubes were cooled using a fan and N concentration for each sample determined using Kjeltec Auto 1030 Analyser that directly gives the percentage N concentrations in sample solutions.

The concentrations of P and K were determined spectrophotometrically (Anonymous, 1986). For each plant sample, 0.2g was weighed into a crucible, ashed at 480°C in a Carbolite furnace and dissolved in 20 ml of 1M HCl to make sample solution for P and K analysis. For determination of P concentration, 5 ml of each sample solution was transferred into a 50 ml volumetric flask using a pipette, and 5 ml of 5M HCl and 5 ml of ammonium molybdate reagent were added. The solution was then diluted to 50 ml using distilled water and allowed to stand for 30 minutes, for complete colour development, before measuring P concentration. Standard solutions were prepared for every assay by pipetting 10 ml of each of 0, 10, 20, 30, 40, 50 $\mu g\ ml^{-1}$ P working standard solutions into a 50 ml volumetric flask. The flasks were filled to 50 ml by adding 5M HCl, 5 ml ammonium molybdate and distilled water, and allowed to stand for 30 minutes as for the plant sample solutions. The P concentrations in the standard and sample solutions were determined by measuring the absorbance at 400 nm, as a yellow phospho-vanado-molybdate complex, using grating spectrophotometer model CE303. A graph relating the absorbance to µg of P present in the standard solutions was constructed. The regression equation of the fitted line plot was then used to calculate the concentration of P in plant material as follows:

mg P kg^{-1} sample = {(sample absorbance - constant) ÷ slope} x 20; then,

% P = (mg P kg^{-1} sample) ÷ 10000

Available P in soil samples was extracted at room temperature (about 20°C) with a $NaHCO_3$ solution (Anonymous, 1986). For each sample, 2.5g was weighed into a wide mouth plastic bottle with a screw cap and 50 ml $NaHCO_3$ reagent of pH 8.5 added. The sample bottles were shaken on a shaking machine for 30 minutes, after which each bottle was immediately filtered into a conical flask through a 125 mm Whatman No. 2 filter paper and the filtrate (sample extract) transferred into 20 ml plastic bottles. From each sample extract, 5 ml was pipetted into a 100 ml conical flask and 1 ml of 1.5M H_2S0_4 added. The flask was then swirled to assist the release of CO_2, and 20 ml of 1.5% m/V ammonium molybdate reagent and 5 ml of ascorbic acid solution were added in tandem. The solution was allowed to stand for 30 minutes for complete colour development before determining P concentration by measuring absorbance at 880 nm. Concentration of P was calculated from the equation of the standard graph as: mgP/kg soil = {(sample absorbance - constant) ÷ slope} x 4.

Concentrations of K in plant and soil samples were determined using an aa/ae spectrophotometer (Anonymous, 1986). For plant samples, K concentration was measured from the sample solution in 1M HCl. From each sample solution, 5 µl was pipetted into 1 ml tubes and diluted 50 times using distilled water in order to make the K concentration readings fall within the photometer range. Standard working solutions containing 0, 1, 2, 3, 4 and 5 $\mu g\ ml^{-1}$ were prepared from a K stock standard solution (1 mg ml^{-1} of K) for every assay and the K concentrations in the standard and sample solutions were determined by flame photometry. A graph relating meter readings to $\mu g\ ml^{-1}$ of K in the standard solutions was constructed and the concentration of K in sample solutions calculated as:

mgK kg^{-1} sample = {(sample absorbance - constant) ÷ slope} x 5000; then % K = (mg K Kg^{-1} sample) ÷ 10000

Exchangeable K in soil samples was extracted with ammonium acetate pH 7.0. For each sample, 5g was weighed into a clean plastic bottle with a cap and 100 ml of 1M ammonium acetate solution

added. The content was then shaken for 30 minutes and filtered through No. 42 Whatman paper. To fall within the measurable range of the flame photometer, the soil extract was diluted 10 times. Then, 5 ml of each soil extract was pipetted into a 50 ml volumetric flask and 1 ml of 26.8% lanthanum chloride solution was added. The flask contents were diluted to the mark with ammonium acetate extraction solution and K concentration in the sample and standard solutions were determined by flame photometry. The concentration of K in the samples was calculated as: mg K $100g^{-1}$ soil = {(sample absorbance - constant) ÷ slope} x 10. This value was divided by the equivalent weight of K to obtain milliequivalent (me) K per 100g of soil.

Data analysis. Plant height, root collar diameter (RCD) and oven-dry weight, and plant and soil N, P, K content per pot were analysed for statistical significance using analysis of variance (ANOVA) in Minitab statistical package. Mean values of variables (height, dry weight and N, P, K content) for 2 maize plants grown in the same pot were treated as one observation. To determine whether *A. acuminata* compensated for the defoliation, leaf weight was standardised taking into account the percentage defoliation. Thus actual leaf dry weights in 0, 25, 50 and 75% defoliated seedlings were divided by 4, 3, 2 and 1, respectively, to obtain corrected leaf weight based on earlier procedures (Markkola, 1996) that was analysed using ANOVA. Treatment means were compared for level of significance by the least significance difference (LSD) at 5% probability level. Pearson correlation analysis in Minitab was used to determine the correlation between the dry weight of *Alnus* leaves and other growth variables of the species.

RESULTS AND DISCUSSION

***Alnus acuminata* height, root collar diameter (RCD) and dry weight.** At first defoliation, the height and RCD of *Alnus* in the 8 treatments ranged from 42.4 - 45.2 cm and 6.6 - 7.0 cm, respectively, and were not significantly different between treatments. Overall defoliation significantly reduced the height, RCD and dry weight of *Alnus* (Table 1). The effect of defoliation on the height, RCD and dry weight followed the order 0% < 25% < 50% < 75% defoliation. For example, mean total dry weight of 25%, 50% and 75% defoliated trees were 6%, 24% and 42% less

TABLE 1. Effect of defoliation on the height, root collar diameter (RCD) and dry weight of *A. acuminata* grown in sole and mixed cropping system

Factor	n*	Height (cm)	RCD (cm)	Oven-dry weight (g)							Root /shoot ratio
				Stem	Leaf	CLW*	Shoot	Root	Nodule	Total Plant	
Defoliation											
0%	48	118.0^{a}	2.7^{a}	86.9^{a}	62.5^{a}	15.7^{a}	150.0^{a}	63.1^{a}	3.5^{a}	217.8^{a}	0.45^{a}
25%	48	116.6^{a}	2.6^{a}	83.5^{a}	57.9^{a}	19.3^{b}	141.9^{a}	57.3^{b}	3.2^{a}	203.6^{a}	0.44^{a}
50%	48	108.0^{b}	2.4^{b}	67.6^{b}	47.4^{b}	23.7^{c}	115.7^{b}	47.5^{c}	2.8^{b}	166.5^{b}	0.43^{a}
75%	48	100.1^{c}	2.1^{c}	54.3^{c}	36.0^{c}	36.0^{d}	90.8^{c}	33.7^{d}	2.3^{c}	127.2^{c}	0.40^{b}
Harvest period											
January 2000	48	103.8^{a}	2.1^{a}	54.3^{a}	46.3^{a}	20.9^{a}	100.9^{a}	37.4^{a}	2.3^{a}	140.9^{a}	0.40
February 2000	48	108.5^{ab}	2.3^{b}	67.9^{b}	49.1^{ab}	22.2^{ab}	117.3^{b}	44.0^{a}	3.1^{b}	165.0^{b}	0.41
March 2000	48	112.3^{bc}	2.6^{c}	82.9^{c}	49.4^{ab}	22.3^{ab}	132.4^{bc}	54.5^{b}	3.3^{b}	190.4^{c}	0.44
April 2000	48	118.0^{c}	2.8^{d}	87.5^{c}	55.1^{b}	24.9^{b}	143.2^{c}	64.9^{c}	3.1^{b}	211.8^{c}	0.48
Cropping system											
Sole	96	109.0	2.4	70.9	47.98^{a}	21.8^{a}	119.5^{a}	48.4	3.1^{a}	171.6^{a}	0.44
Mixed	96	112.4	2.5	72.8	51.72^{b}	23.4^{b}	125.2^{b}	49.8	2.8^{b}	178.5^{b}	0.42

*n, number of observations; CLW, corrected leaf dry weight. For each of defoliation, harvest period and cropping system; means followed by the same letter within a column are not significantly different at 5% probability

than the total dry weight of non-defoliated trees. Conversely, there were generally significant increases in the height, RCD and dry weight of *Alnus* over the harvest period (Table 1). However, whereas the dry weight of nodules was significantly less at first harvest (January 2000) than at all other harvests, no significant difference was evident in nodule dry weight between subsequent harvests periods. Cropping system did not affect the height, RCD and dry weight of *Alnus* stem and roots, but the leaf, shoot and total plant dry weights were higher in mixed than in sole cropping (Table 1). In contrast, the dry weight of nodules was higher in the sole than mixed system (Table 1).

There were very strong positive correlations between leaf biomass and stem weight ($r = 0.997$, $P = 0.003$), root weight ($r = 0.999$, $P = 0.001$), nodule weight ($r = 0.999$, $P = 0.001$), height ($r = 0.997$, $P = 0.003$), and RCD ($r = 0.996$, $P = 0.004$). This indicates that *Alnus* reduced its growth and biomass allocation in all parts in response to defoliation. However, *Alnus* compensated for leaf loss, as the corrected leaf weight (CLW) was significantly higher in defoliated trees than in the control, and CLW increased significantly with increasing defoliation intensity (Table 1). Root/shoot ratio decreased with increasing defoliation intensity, but significant reduction was evident only at 75% defoliation (Table 1). This indicates that defoliation affected *Alnus* roots more than the shoots, thus stressing the importance of assessing the belowground response of plants under varying defoliation intensities.

Maize height and biomass. There were substantial effects of defoliation and cropping system on the height of maize (Table 2). However, the height of maize grown in association with 0%, 25% and 50% defoliation of *Alnus* was not significantly different. Sole maize was significantly taller than maize grown in association with *Alnus* at all harvest periods. This indicates that competition between *Alnus* and maize negatively affected the growth of the latter. The most severe defoliation (75%) of *Alnus* apparently reduced the competition to a level that benefited the height of maize (Table 2). Significant interactions occurred between defoliation treatment and harvest period, suggesting that the effect of *Alnus* defoliation on the height of maize was time dependent.

The dry weight of maize grown in association with 75% defoliated *Alnus* was higher than with 0%, 25% and 50% defoliated trees, albeit significantly less than the dry weight of sole maize crops (Table 2). For example, total (shoot plus root) dry weight of maize was up to 208% higher under 75% defoliation than 0% defoliation of *Alnus*. The root/shoot ratio of sole maize crops

TABLE 2. Effect of *A. acuminata* defoliation on the height and dry weight of companion maize

Factor	Number of pots	Height (cm)	Mean oven-dry weight (g)			Root/shoot ratio
			Shoot	Root	Total	
Defoliation						
0%	22	15.8 ^{a}	0.6 ^{ab}	0.2 ^{a}	0.8 ^{a}	0.45 ^{a}
25%	24	15.3 ^{a}	0.5 ^{a}	0.2 ^{a}	0.7 ^{a}	0.46 ^{a}
50%	24	17.6 ^{a}	0.7 ^{b}	0.3 ^{a}	1.0 ^{a}	0.59 ^{b}
75%	24	24.7 ^{b}	1.9 ^{c}	0.8 ^{b}	2.5 ^{b}	0.48 ^{a}
Sole maize	24	55.2 ^{c}	15.6 ^{d}	4.5 ^{a}	19.7 ^{c}	0.29 ^{c}
Harvest period						
January 2000	30	12.9 ^{a}	0.5 ^{a}	0.3 ^{a}	0.7 ^{a}	0.58 ^{a}
February 2000	30	17.9 ^{b}	1.5 ^{b}	0.8 ^{b}	2.0 ^{b}	0.52 ^{ab}
March 2000	29	24.9 ^{c}	2.6 ^{c}	1.1 ^{c}	3.4 ^{c}	0.43 ^{b}
April 2000	29	44.4 ^{d}	3.9 ^{d}	1.3 ^{c}	4.8 ^{d}	0.30 ^{c}

For each of defoliation and harvest period; means followed by the same letter within a column are not significantly different at 5% probability

was lower than those grown in a mixed system (Table 2), suggesting that the crop invests less in the shoot than in the root system when stressed by competition. There was a general decrease in root/shoot ratio of maize over the harvest period, indicating that the crop allocated relatively fewer resources for its root development with age.

N, P, K concentration and content in *A. acuminata*. Significant variations in N, P, K concentrations were caused by defoliation, harvest period and cropping system, but not the interactions between these factors. Generally, leaf N, P, K concentrations were higher in defoliated than in non-defoliated *Alnus*, and increased with increasing intensity of defoliation (Table 3). Compared to 0% defoliation, 75% defoliation increased N, P and K concentrations in *Alnus* leaves by 7.5%, 17.1% and 31.1%, respectively. Conversely, there was 7.7% decrease in nodule N concentration in 75% defoliated trees compared to 0% defoliated trees. The decrease in nodule N concentration (7.7%) approximated the 7.5% gain evident in the leaf N concentration of 75% defoliated *Alnus*. This suggests a flow of N from nodules to leaves to compensate for leaf N loss. The concentrations of P and K in *Alnus* nodules increased with increasing defoliation intensity although this was significant only at 75% defoliation (Table 3).

The concentrations of N, P, K in *Alnus* leaves and nodules varied markedly over time (Table 3). Generally, the concentrations of N, P, K decreased from January to March 2000 in both leaves and nodules. However, there was a general increase in leaf N, P, K and nodule K between March - April 2000. In contrast, the concentrations of nodule N and P were significantly lower ($P < 0.05$) in April 2000 than at all other harvest dates. Significant effect of cropping system on the nutrient concentrations was only evident on leaf K (Table 3).

Generally, total N, P, K content in leaves and nodules decreased with increasing defoliation intensity (Table 4). When compared to 0% defoliated trees, 75% defoliation reduced leaf total N, P and K content by 38%, 33% and 25%, respectively. In nodules, 75% defoliation reduced the total content of N, P and K by 40%, 24%, and 24%, respectively. Leaf and nodule total N, P, K

TABLE 3. Effect of defoliation and cropping system on N, P, K concentrations in *A. acuminata* leaves and nodules

Factor	Percent nutrient					
	Nitrogen		Phosphorous		Potassium	
	Leaf	Nodule	Leaf	Nodule	Leaf	Nodule
Defoliation						
0%	2.49 a	3.72 ab	0.16 a	0.30 a	1.25 a	2.12 a
25%	2.53 ab	3.98 a	0.17 ab	0.30 a	1.37 b	2.20 a
50%	2.59 b	3.69 bc	0.18 b	0.32 a	1.44 c	2.28 a
75%	2.68 c	3.43 c	0.19 c	0.36 b	1.65 d	2.46 b
Harvest period						
January 2000	2.66 a	3.95 a	0.18 a	0.39 a	1.49 a	2.53 a
February 2000	2.66 a	3.72 a	0.17 b	0.35 b	1.43 b	2.45 a
March 2000	2.46 b	3.95 a	0.17 b	0.35 b	1.32 c	1.96 b
April 2000	2.50 b	3.20 b	0.18 a	0.20 c	1.45 ab	2.12 b
Cropping system						
Sole	2.59	3.78	0.18	0.32	1.40 a	2.22
Mixed	2.56	3.63	0.17	0.32	1.45 b	2.31

For each of defoliation, harvest period and cropping system, means followed by the same letter within a column are not significantly different at 5% probability

content varied markedly over time (Table 4), perhaps reflecting the variability in the need for the nutrients as dictated by stress and growth requirements. Sole trees had lower total leaf N, P, K content than trees grown in mixed system (Table 4). Conversely, total nodule N, P, K content was higher in sole trees as compared to trees grown in mixed system.

N, P, K concentration and content in maize shoot. There were significant differences in maize N, P and K concentrations between defoliation treatments. Maize grown in association with 75% defoliated *Alnus* had 18.6%, 19.1% and 10.3% higher shoot N, P and K concentrations, respectively than maize grown with 0% defoliated *Alnus*. Similarly, shoot N, P and K concentrations were higher in maize grown with 75% defoliated trees than in sole maize. Whereas no significant difference occurred in shoot N and K concentrations between sole maize and maize intercropped with 0% defoliated trees, shoot P concentration was significantly higher in the former than in the latter. The concentrations of N, P, K in maize shoots decreased with time (Table 5). For example, N, P and K concentrations were 61%, 44% and 56% higher in January than in April, 2000, respectively.

There were substantial effects of *Alnus* defoliation on the total N, P and K content in maize shoots. Whereas 25% defoliation decreased, albeit not significantly, total shoot N, P, K content in maize, 50% and 75% defoliation showed marked increase in maize total shoot N, P, K content (Table 5). For example, total shoot N, P and K were up to 209%, 238%, and 208% higher in maize intercropped with 75% defoliated trees than in maize intercropped with 0% defoliated trees, respectively. However, sole maize showed substantially higher total shoot N, P, K content than maize intercropped with *Alnus*. Total shoot N, P, K content in maize increased with harvest period (Table 5), but significant interactions occurred between harvest period and defoliation. These interactions may be indicative of differential N, P, K requirements at different development stages of maize, which was possibly influenced by defoliation. For example, all sole maize plants

TABLE 4. Effect of defoliation and cropping system on N, P, K content in *A. acuminata* leaves and nodules

Factor	Nutrient content (mg/plant portion)					
	Nitrogen		Phosphorous		Potassium	
	Leaf	Nodule	Leaf	Nodule	Leaf	Nodule
Defoliation						
0%	1556.0 ^{a}	120.2 ^{a}	102.1 ^{a}	9.7 ^{a}	781.6 ^{a}	68.1 ^{a}
25%	1458.8 ^{a}	120.5 ^{a}	97.1 ^{a}	8.8 ^{ab}	785.2 ^{a}	67.1 ^{ab}
50%	1224.6 ^{b}	96.6 ^{b}	82.4 ^{b}	8.3 ^{bc}	679.2 ^{b}	59.2 ^{bc}
75%	961.6 ^{c}	73.0 ^{c}	68.6 ^{c}	7.4 ^{c}	590.2 ^{c}	52.5 ^{c}
Harvest period						
January 2000	1227.4 ^{a}	81.1 ^{a}	82.6 ^{a}	8.1 ^{a}	688.7 ^{a}	52.0 ^{a}
February 2000	1303.2 ^{b}	107.7 ^{b}	80.5 ^{a}	10.0 ^{b}	690.2 ^{a}	71.5 ^{b}
March 2000	1216.2 ^{a}	124.5 ^{c}	83.8 ^{a}	10.9 ^{b}	648.6 ^{b}	61.2 ^{c}
April 2000	1374.0 ^{b}	94.8 ^{b}	100.0 ^{b}	6.0 ^{c}	794.3 ^{c}	62.2 ^{c}
Cropping system						
Sole	1238.8 ^{a}	106.7 ^{a}	84.1 ^{a}	8.8 ^{a}	665.3 ^{a}	62.7 ^{a}
Mixed	1321.3 ^{b}	95.1 ^{b}	88.7 ^{b}	8.3 ^{b}	744.7 ^{b}	60.1 ^{b}

For each of defoliation, harvest and cropping system, means followed by the same letter within a column are not significantly different at 5% probability

tasselled between periods of March and April when most intercropped maize had not.

Soil N, P, K concentration. Overall, the concentrations of soil total N, available P and exchangeable K declined by 10%, 16% and 26%, respectively over the 4 months of harvest (Table 6). In contrast, soil N, P, K increased with increasing defoliation intensity. This indicates that defoliation reduced the ability of *Alnus* to utilise available soil N, P, K. However, only 75% defoliation exhibited significantly higher N concentration than 0% defoliation. The effect of cropping system on soil N concentration was not significant. In contrast, concentration of soil available P was higher and soil exchangeable K concentration was lower in sole maize pots than in pots that contained *Alnus* (Table 6).

Apart from obvious loss of photosynthetic area, defoliation negatively affects the availability of

TABLE 5. Effect of *A. acuminata* defoliation on the concentrations and total content of N, P, K in the shoots of companion maize

Factor	Number of pots	Nutrient concentration (%)			Nutrient content (mg/shoot)		
		N	P	K	N	P	K
Defoliation							
0%	22	1.10 ^{a}	0.40 ^{a}	3.98 ^{a}	5.9 ^{a}	2.1 ^{a}	19.6 ^{a}
25%	24	1.18 ^{ab}	0.39 ^{a}	4.02 ^{a}	5.3 ^{a}	1.9 ^{a}	16.9 ^{ab}
50%	24	1.29 ^{c}	0.46 ^{b}	4.22 ^{ab}	7.8 ^{b}	2.8 ^{b}	24.5 ^{ac}
75%	24	1.30 ^{c}	0.48 ^{b}	4.39 ^{b}	18.1 ^{c}	7.2 ^{c}	60.3 ^{d}
Sole maize	24	1.08 ^{a}	0.46 ^{b}	4.04 ^{a}	156.2 ^{d}	66.6 ^{d}	571.1 ^{e}
Harvest period							
January 2000	30	1.89 ^{a}	0.59 ^{a}	5.92 ^{a}	8.5 ^{a}	2.6 ^{a}	21.3 ^{a}
February 2000	30	1.35 ^{b}	0.46 ^{b}	4.74 ^{b}	13.6 ^{b}	5.2 ^{b}	47.2 ^{b}
March 2000	29	0.93 ^{c}	0.39 ^{c}	3.64 ^{c}	19.0 ^{c}	8.4 ^{c}	70.4 ^{c}
April 2000	29	0.74 ^{d}	0.33 ^{d}	2.58 ^{d}	24.3 ^{c}	11.6 ^{d}	84.0 ^{c}

For each of defoliation, harvest period and cropping system, means followed by the same letter within a column are not significantly different at 5% probability

TABLE 6. Concentrations of total N, available P and exchangeable K in soil used for growing maize and *A. acuminata* subjected to four defoliation intensities in sole and mixed cropping systems

Factor	Nutrient concentration		
	Total N (%)	P (mg P Kg^{-1} soil)	K (me $100g^{-1}$)
Defoliation			
0%	0.36^{a}	68.71 ^{a}	2.20 ^{a}
25%	0.37 ^{a}	68.71 ^{a}	2.19 ^{a}
50%	0.37 ^{a}	69.66 ^{a}	2.28 ^{a}
75%	0.39 ^{b}	71.78 ^{a}	2.22 ^{a}
Cropping system			
Sole *Alnus*	0.37 ^{a}	71.12 ^{a}	2.17 ^{a}
Sole maize	0.39 ^{a}	82.04 ^{b}	1.76 ^{b}
Mixed (*Alnus* + maize)	0.38 ^{a}	72.95 ^{a}	2.09 ^{a}

For each of defoliation, harvest and cropping system, means followed by the same letter within a column are not significantly different at 5% probability

essential growth elements such as carbohydrates, hormones, water and minerals by altering their synthesis, transport and allocation (Prins and Verkaar, 1992). This may explain the reduction in height, RCD and biomass of *Alnus* with increasing defoliation intensity observed in this study. The effect of defoliation was less severe on the height than on the RCD of *Alnus*, as was also observed by Wright *et al.* (1989) on red oak *(Quercus rubra* L.) and by Markkola (1996) on scots pine *(Pinus sylvestris* L.) seedlings. These results lend support to the suggestion by Ericsson *et al.* (1980) that alterations in the patterns of translocation might imply a shortage of carbohydrate at the normal sinks of the older foliage (stem, branches, and roots), whereas the formation of the new shoot might be well supplied with assimilates.

The very strong positive correlations evident between leaf biomass and stem, root and nodule biomass evident in the present study offer further support for the source-sink balance. Bassman and Dickman (1985) noted that carbohydrate translocation patterns were altered within 24 hours of defoliation with defoliated plants shunting more photosynthate into stems, leaves, and lateral branches developing subsequent to defoliation and less into roots than did control plants. The decrease in *Alnus* root/shoot ratio with increasing defoliation intensity may also indicate shifts in available photosynthate from roots to the shoot. Such reduction in root growth would not be apparent in field situations, but may render plants more susceptible to environmental stress and might also impair the uptake of mineral nutrients (Bassman and Dickmann, 1982).

The ability of *Alnus* to compensate for leaf loss was confirmed by the significant increase in net leaf weight with increasing defoliation intensity. Such growth-stimulating effects of partial defoliation may be attributed to intrinsic mechanisms involving enhanced photosynthesis following defoliation, favourable allocation of carbohydrate and biomass for growth, and increases in N or related protein concentrations (Reich *et al.*, 1993). Extrinsic mechanisms accompanying herbivory such as improved microclimate for remaining tissues, increased nutrient supplies and enhanced water status of remaining tissues may also result in plant compensation (McNaughton *et al.*, 1983). In the present study 50% and 75% defoliated *Alnus* compensated only partially in terms of height, RCD and dry weight, probably because modest stimulation of the compensatory mechanism(s) was unable to compensate in total carbon gain for the high loss of leaf area.

Reduction in N fixation following defoliation is widely cited in the literature (e.g., Sprent and Minchin, 1983; Huss-Danell and Sellstedt, 1985), but there has been no report on the effect of defoliation on nodulation and/or N fixation in *A. acuminata*. Huss-Danell and Sellstedt (1985) noted that nitrogenase activity in nodules of *A. incana*, measured as C_2H_2 reduction, nearly ceased only 5 hours after total defoliation. The present study did not examine N fixation, but significant reduction in nodule biomass was observed at 50% and 75% defoliation. Because N-fixing ability is affected by total nodule mass (Giller and Wilson, 1991), the observed decrease in nodule dry weight (Table 1) should be manifested as a decrease in N-fixing ability. However, caution is necessary when extrapolating this result to field conditions, as nodulation and N fixation may be influenced by variation in environmental conditions (Sprent and Minchin, 1983). For example, *Alnus* trees growing on N-poor soil (typical in field conditions) could be more dependent on symbiotically fixed N than those growing on N-rich soil (as used in this study). The effect of defoliation on the growth of *Alnus* may thus be greater in N-poor soils, because the reduction in N-fixing ability would have a greater impact on total N supply. Given the general lack of reports on the effect of defoliation on the N fixing ability of *Alnus* species in the tropics, attention should be given to differences between species, plant age as well as long-term impact of reduced N-fixing ability resulting from pest induced defoliation over a range of soil fertility levels and crop mixtures.

The present study showed positive effects of companion maize on the dry weight of *Alnus*. Similarly, Ta and Faris (1988) observed more alfalfa (*Medicago sativa* L.) biomass production from alfalfa grown in association with timothy (*Phleum pratense*) than from alfalfa monocultures, which the authors contend, was attributed to increased N fixation by alfalfa in mixed cultures. These authors suggested that the deletion of medium N by rapid uptake of timothy or the

excretion of substrates by timothy might have resulted in enhanced N fixation in their study. This explanation can hold true in the present study only if the significant reduction in nodule biomass in mixed cultures was compensated by increased rates of nitrogenase activity per nodule. Another reason for the positive effects of maize on *Alnus* growth could be that moderate competition between *Alnus* and maize stimulated root growth and nutrient absorption in the former.

Increases in foliar nutrient concentration following defoliation have been reported in some grass (e.g., McNaughton and Chapin, 1985) and woody species (e.g., Piene, 1980), but the literature on the effect of defoliation on nutrient concentration in nodules is scarce. In this study, 50 and 75% defoliation significantly increased the concentrations of *Alnus* leaf N, P, K and nodule P and K, but these defoliation levels decreased nodule N concentration. Explanations for the accumulation of N, P, K in the foliage of defoliated *Alnus* can only be speculative. One possibility is that there were fewer leaves on defoliated *Alnus* to accumulate a certain amount of nutrients, thus causing an increased accumulation in the remaining leaves (Piene, 1980). Alternatively, allocation of N, P, K to leaves might have been met by net export from the root tissue (Gadgil, 1971; Louahlia *et al.*, 1999) and/or stimulated uptake from the soil (McNaughton and Chapin, 1985). The observed increase of P in *Alnus* nodules may be indicative of increased nodule metabolism. Giller and Wilson (1991) noted that P is required for nodule metabolism and tends to be concentrated in nodules when the plant is deficient in the nutrient.

Defoliation *of Alnus*, particularly 75% defoliation, significantly increased the height and biomass of associated maize although these growth parameters were significantly lower in intercropped than in sole maize. Two possible reasons may account for this positive effect of *Alnus* defoliation on the growth of associated maize. First, since defoliation reduced the growth and total N, P, K content in *Alnus*, competition for resources such as light, water, and soil nutrients was possibly reduced with increasing defoliation intensity, thus leading to increased resource utilization and growth in maize. Secondly, defoliation of *Alnus* could have enhanced nutrient flux into the soil that was then taken up by the companion maize plants, leading to increased growth of the latter. However, whereas it is well established that herbivory enhances the transfer of fixed N from N-fixing plants to companion non-N fixers (Sprent, 1983; Ta and Faris 1987; Bardgett *et al.*, 1999), evidence on the transfer of other nutrients as result of herbivory is lacking. Mechanisms often suggested for the transfer of N from N-fixing trees to associated plants include secretion of N from nodules and roots of N fixing plants, root nodule decay, stimulation of non symbiotic N fixation, more efficient use of nutrients, light and water, and the N-sparing effect (Gadjil, 1971; Giller and Wilson, 1991).

In the present study, maize grown in association with defoliated *Alnus* showed highly significant increases in total shoot N, P, K content when compared with maize intercropped with non-defoliated *Alnus*. This suggests that defoliation can result in significant diversion of nutrients below ground, and can in turn alter the productivity in agroforestry system with important bearing in nutrient cycling.

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