Agroforestry Systems **30**: 301–313, 1995.

The influence of trees on nitrogen dynamics in an agrisilvicultural system in Sweden

M. BROWALDH
Department of Crop Production Science, Swedish University of Agricultural Sciences, P.O. Box 7043, S-750 07 Uppsala, Sweden

Key words: nitrogen mineralization, nitrification, respiration, organic matter, poplar

Abstract. During 1992 and 1993, nitrogen dynamics and microbial activity were investigated in an agrisilvicultural system consisting of oats or barley cultivated along the sides of a poplar plantation in Sweden. At each of three experimental sites (two silt loams and one silty clay loam), sampling for mineral nitrogen was carried out in three layers down to 90 cm at two distances from the trees, A (0.5–1.5 m) and B (4.0–5.0 m), two times each year (spring and autumn). Sampling of soil for organic matter, carbon and nitrogen, potential nitrification, N mineralization, basic respiration and substrate-induced respiration was carried out in the 0–10 cm layer at three distances from the trees: A (0.5–1.5 m), B (2.5–3.5 m) and C (4.0–5.0 m).

Significantly larger amounts of organic matter, total carbon and nitrogen at A than at B and C, indicated increased inputs from the trees through litter, decaying roots and root exudates. This could explain that the rates of nitrogen mineralization, potential nitrification and respiration were significantly higher at A than at B and C. The presence of trees resulted in a better utilization of nitrogen and moisture in the soil, reducing the potential for nitrate leaching and accumulating nitrogen close to the trees. The higher concentration of ammonium, lower concentration of nitrate and the consistently lower NO_3^-–N/NH_4^+–N-ratios observed at A than at C might be explained by a combined effect of increased nitrogen mineralization and efficient nitrate uptake by the trees.

Introduction

Accumulation of nutrients, conservation of organic matter and persistence through time are characteristics usually ascribed to natural ecosystems [Woodmansee, 1984]. Intensively cultivated soils, on the other hand, are characterized by considerable loses of organic matter and nutrients. Persson [1974] showed a decrease in humus content of 30% in the course of 20–30 years after land had been brought under cultivation. Consequently, many virgin soils accumulate greater amounts of mineralizable nitrogen than their cultivated counterparts [Smith and Young, 1975]. Partial imitation of natural tree-based ecosystems through agrisilvicultural practices, where trees and crops intentionally are mixed on the same land, is believed to enhance the long-term sustainability and productivity of agroecosystems. Benefits, such as maintaining organic matter, improving nutrient cycling efficiency and ameliorating microclimates, are generally attributed to the tree component of the system [Steppler, 1987]. More than half of the nutrients taken up annually by trees in temperate deciduous forests are returned to the soil by litterfall, through-

fall and stemflow [Duvigneaud and Denaeyer-De Smet, 1970]. Both carbon and nitrogen have been shown to accumulate underneath trees in natural ecosystems [McClaugherty et al., 1985; Boerner and Koslowsky, 1989]. According to Gersper and Holowaychuk [1971], stemflow could be responsible for higher inorganic nitrogen pool sizes close to trees.

In most forested ecosystems, ammonium is the dominant form of soil mineral nitrogen, whereas nitrate is more abundant in agricultural land [Rice and Pancholy, 1972; Robertson and Vitousek, 1981]. Various authors have suggested different mechanisms to account for a limitation of the nitrification in more mature ecosystems, such as allelopathic substances [Lodhi, 1977, 1978; Rice, 1964], low cation and phosphate availability [Vitousek et al., 1982], high C:N ratio [Johnson and Edwards, 1979] and limited availability of ammonium [Vitousek et al., 1982]. However, reports of actual nitrification rates are contradictory. Both an increase [Lamb, 1980; Robertson and Vitousek, 1981] and a decrease [Montes and Christensen, 1977] in nitrification rate with successional age of the ecosystem have been reported.

Nitrogen dynamics in natural forested ecosystems, as well as agricultural systems, have been investigated by many scientists, but relevant data on this matter from agrisilvicultural systems are very scarce. If trees play a central role in nitrogen transformations of natural ecosystems, the same might apply to agrisilvicultural systems. In this research it was reasoned that more carbon and nitrogen would accumulate close to than away from rows of trees in an agrisilvicultural system. Microbiological activity, including nitrogen mineralization, was postulated to be higher closer to than away from trees. It was further hypothesized that larger amounts of ammonium and lesser amounts of nitrate are present close to than away from trees resulting in lower NO_3^-–N/NH_4^+–N-ratios. Due to the length of time needed for trees to grow in temperate climates, this investigation utilizes plantations already existing. Agrisilvicultural systems were thus created by sowing oats or barley along rows of poplar trees.

Materials and methods

Study area

The study area is situated 5 km south of Uppsala, Sweden (50°49′ N and 17°39′ E). Weather conditions in the area during 1992 and 1993 are presented in Fig. 1. Three experiments (Sites 1, 2 and 3) were laid out along the sides of a poplar plantation (*Populus trichocarpa* Hook × *Populus deltoides* Marsh.), planted on former agricultural land where trees at Site 1 had been planted in 1988 and those at Sites 2 and 3 in 1987. The distance between trees is 1.5 m at Site 1 and 3.5 m at Sites 2 and 3. The layout of the experiments is shown in Fig. 2 and soil characteristics and crop yields are presented in Table 1. In 1992, only Site 1 was sown with oats (*Avena sativa* L.). Sites 2 and 3 were

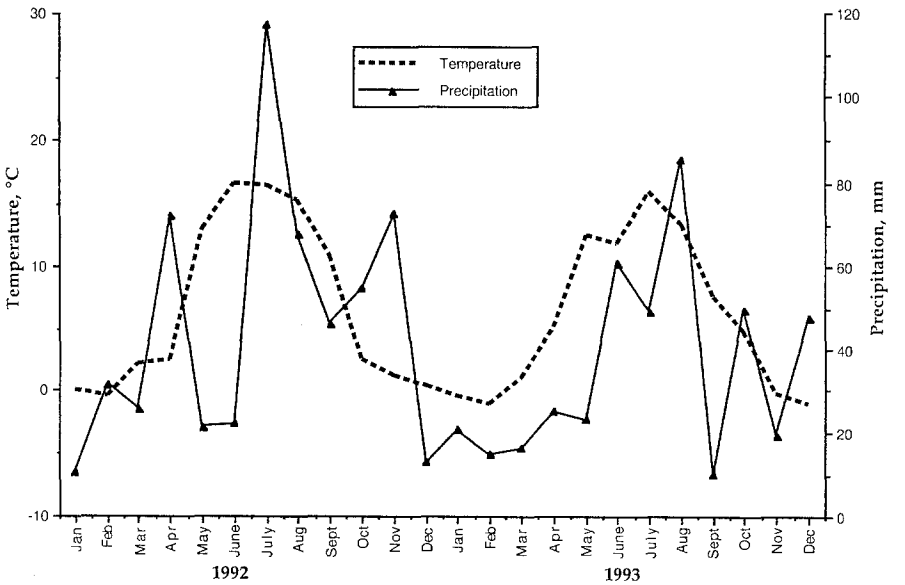

Fig. 1. Mean monthly temperature and rainfall for Ultuna in 1992 and 1993.

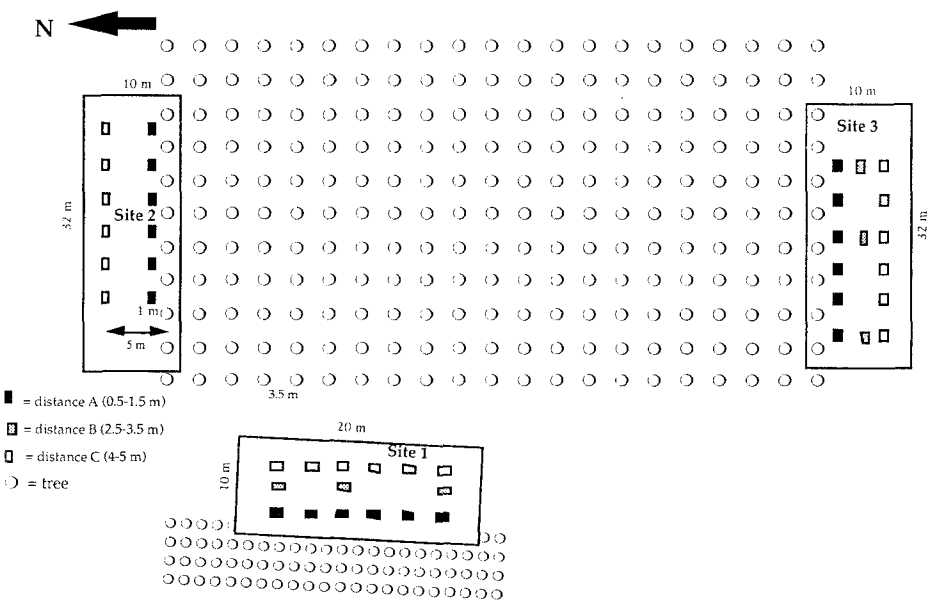

Fig. 2. Field plan for the experimental area with the three experimental sites and all the sampling plots (distances in 1993. In 1992, 3 sampling plots at all the distances (A, B and C respectively) were used at Sites 1 and 3.

Table 1. Soil characteristics of the three sites sampled in april 1992 and yields of grain and straw in 1992 and 1993. A and C refer to distance of 0.5–1.5 m and 4.0–5.0 m from the row of trees. Standard deviation for chemical characteristics in parenthesis.

	Site 1		Site 2		Site 3	
Soil Type						
0–30 cm	Silt loam (12% clay)		silt loam (18% clay)		Silty clay loam (36% clay)	
30–60 cm	Silt loam (16% clay)		Silt loam (22% clay)		Clay (60% clay)	
60–90 cm	Silty clay loam (36% clay)		Clay (64% clay)		Clay (65% clay)	
Chemical characteristics (n = 3)						
	A	**C**	**A**	**C**	**A**	**C**
0–30 cm						
pH(H_2O)	7.1 (0.06)	7.1 (0.1)	7.4 (0.1)	7.5 (0.1)	6.6 (0.08)	6.7 (0.1)
P-AL[a] (mg/100 g)	54.6 (2.3)	52.2 (5.6)	56.3 (2.5)	54.9 (2.2)	27 (1.5)	25 (2.1)
CEC (meq/100 g)	11.6 (2.0)	11.0 (1.9)	12.3 (1.1)	12.7 (0.9)	22.4 (1.6)	22.1 (1.2)
Total C (%)	1.28 (0.09)	1.22 (0.13)	1.27 (0.07)	1.23 (0.06)	1.42 (0.12)	1.32 (0.09)
Total N (%)	0.11 (0.008)	0.11 (0.013)	0.12 (0.02)	0.11 (0.04)	0.13 (0.01)	0.12 (0.009)
Yield (kg/ha)						
	A	**C**	**A**	**C**	**A**	**C**
1992						
Grain	500	1320	–	–	–	–
Straw	1336	3320	–	–	–	–
1993						
Grain	268	922	532	1856	993	1962
Straw	630	1845	1256	3898	1887	3928

[a] Available phosphorus extracted with acid ammonium acetate and lactate buffer solution of total concentration 0.5 N at pH 3.75 (Egnér et al., 1960).

kept weed-free by harrowing. In 1993, barley (*Hordeum distichum* L.) was cultivated at all three sites. Before sowing, the sites were harrowed. After harvesting the oats in 1992, the soil was prepared by a disc plough. Before this investigation was initiated, the sites had been fallowed and kept weed-free by harrowing as close to the trees as possible (30–50 cm from the trees). The trees at Site 1 had been fertilized with a total of 60 kg N/ha (NPK (18–4–10) micro) during the period of 1988 to 1991 (equivalent to 2.5 mg N, 0.54 mg P and 1.38 mg K/100 g dry soil). The trees at Sites 2 and 3 were given approximately 5 kg of N/ha in 1989, 10 kg/ha in 1990, 60 kg/ha in 1991 and 1992 (NPK (18–4–10) micro) (equivalent to 5.6 mg N, 1.21 mg P and 3.11 mg K/100 g dry soil). The trees were not fertilized thereafter and crops were not fertilized.

Sampling plots and sampling

Sampling plots of 1 × 2 m for determination of chemical and microbiological parameters were selected at three distances from the rows of trees, 0.5–1.5 m (A), 2.5–3.5 (B) and 4.0–5.0 m (C). Randomization of the sampling plots was carried out pairwise (A and corresponding B and C). In 1992, three sampling plots were selected at each distance at Sites 1 and 3, six others were selected at all three sites in 1993 (Fig. 2).

Sampling for mineral nitrogen was carried out only at distances A and C, three times in both years: in the spring, at crop maturity (development stage 85 (DC 85), soft dough, of the decimal code according to Tottman [1987]) and in late autumn (exact dates are given in Tables 3 and 4). In 1992, only Site 1 was sampled for mineral N. At crop maturity, most mineral nitrogen had been taken up by the vegetation. Since nitrogen uptake was not analyzed (and to make the presentation more clear) the data on soil mineral N from sampling at crop maturity is not presented here. On each sampling occasion, 8 soil cores were collected randomly in each plot from the 0–30 cm layer (using an auger with 33 mm diameter) and 5 soil cores from the 30–60 cm and 60–90 cm layers (using an auger with 26 mm diameter) and mixed separately for each layer. In 1993, the number of soil cores collected was reduced to 5 from the 0–30 cm layer and 3 from the 30–60 cm and 60–90 cm layers of each plot at all three sites. The concentration of mineral nitrogen is presented from the 0–30 and 30–90 cm layers, even though three layers were analyzed separately.

On September 25, 1992, the 0–10 cm layer in plots A, B and C at Sites 1 and 3 was sampled for determination of organic matter (OM), soil carbon and nitrogen and for microbiological analysis, using an auger with a diameter of 33 mm. The 0–10 cm layer, at positions A and C, of Site 1 and 2 was sampled on September 21, 1993. All the above parameters were analyzed in 1993 from Site 1 but only carbon and nitrogen from Site 2. All soil samples were put into a freezer at a temperature below –20 °C within 3 hours after sampling.

Sample preparation and analyses

For the analysis of mineral nitrogen, the samples were ground in frozen condition, and 100 g was immediately mixed with 250 ml of 2 M KCl and shaken overnight. The extract was then filtered by centrifugation and 100 ml was kept for analysis. The amount of ammonium and nitrate was determined colorometrically, using a TRAACS autoanalyzer. Measurement of the total microbial activity, determined as the basic rate of respiration, was done according to Palmborg and Nordgren [1993], and the rate of substrate-induced respiration (SIR) for estimation of microbial biomass according to Anderson and Domsch [1978]. Both were measured with the equipment designed by Nordgren [1988]. Potential nitrification was measured according to the method of Belser and Mays [1980], modified by Torstensson [1993], a method where the accumulation of nitrite is measured. Nitrite oxidation was inhibited through the addition of chlorate (15 mM) and the oxidation of ammonium was optimized through addition of ammonium sulphate (4 mM). Nitrogen mineralization was determined according to the method of Waring and Bremner [1964], where the production of ammonium is measured after incubation of soil under waterlogged conditions. All microbiological analyses were determined in duplicates.

After drying and grinding (in a porcelain mill until it passes a 250 μm aperture sieve to get a representative sample) of subsamples from the 0–10 cm layer, the total amount of C and N was determined (in duplicates) using a Carlo Erba Elemental Analyzer. The amount of organic matter was determined through ashing in furnace (loss of weight after drying to 500 °C expressed as % of dry soil (105 °C), then substracted with a correction factor of 1.0 to compensate for weight losses other than organic matter [Ekström, 1927]). All data comparing A and C were subjected to Student's *t*-test. All data comparing A, B and C (OM, carbon, nitrogen, and microbiological data at Sites 1 and 3) were subjected to analysis of variance and the means were compared using Tukey's Multiple Range Test at the 5% level. Statistical analyses were computed using SYSTAT version 5.2 [SYSTAT, 1992].

Results

Soil organic matter, total carbon and nitrogen

Significantly larger amounts of OM, total carbon and nitrogen were present at A than at B and C at Sites 1 and 3 in 1992, but no differences in the C/N ratio were found. In 1993, when 6 sampling plots were used, the differences were highly significant at Site 1, but not at Site 2 (only total carbon and nitrogen was analyzed at Site 2). The amounts of OM, carbon and nitrogen were larger at Site 3 than at the other sites (Table 2).

Table 2. Total carbon and nitrogen, C/N-ratio and microbiological parameters in the top soil to a depth of 10 cm of the soils at Sites 1 and 3 in 1992 (n = 3) and at Site 1 and 2 in 1993 (n = 6). A, B and C represent distances of 0.5–1.5 m, 2.5–3.5 m and 4.0–5.0 m from the row of *Populus*.[a]

Parameter	1992						1993			
	Site 1			Site 3			Site 1		Site 2	
	A	B	C	A	B	C	A	C	A	C
OM(ash furnace)	2.7 a	2.3 b	2.4 b	3.7 a	3.2 b	3.2 b	2.6	2.3***	nd	nd
C %	1.49 a	1.30 b	1.28 b	1.75 a	1.56 b	1.50 b	1.53	1.34***	1.35	1.33
N %	0.14 a	0.12 b	0.12 b	0.16 a	0.14 b	0.14 b	0.12	0.11*	0.12	0.11
C/N-ratio	10.9	10.7	10.9	11.0	11.0	10.8	12.7	12.2	11.3	12.1
Pot. nitrif.(µg NO_2/100 g DW × h)	7.1 a	5.7 b	5.9 b	13.0 a	9.7 b	9.1 b	6.2	4.8**	–	–
N-mineral.(µg/g DW)	11.5 a	6.2 b	6.7 b	9.4 a	6.3 b	5.5 b	–	–	–	–
Basic resp. (mg CO_2/100 g × h)	0.09 a	0.07 ab	0.06 b	0.11 a	0.09	0.09 b	0.20	0.17	–	–
SIR (mg CO_2/100 g × h)	1.7 a	1.2 ab	1.1 b	2.4 a	1.6 b	1.4 b	1.95	1.43***	–	–

[a] Comparisons are made horizontally for each parameter within each site. In 1992: Means in each row followed by the same letter are not significantly ($p \leq 5\%$) different. In 1993: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$ (student's t-test) for comparison horizontally within each sampling occasion (– = no data; nd = not determined).

Microbiological analyses

Potential nitrification, N mineralization, basic respiration and SIR were all significantly higher close to than away from trees (except for the rate of basic respiration at Site 1 in 1993) (Table 2). No significant differences were observed between B and C in any of the microbiological parameters analyzed in 1992. Comparing the sites, potential nitrification, basic respiration and SIR were higher at Site 3, but N mineralization was greater at Site 1. Comparing the years at Site 1, basic respiration and SIR were higher in 1993 than in 1992.

Mineral nitrogen

Amounts of mineral nitrogen at Site 1 on sampling occasions in the spring and autumn of 1992 and 1993 are shown in Table 3, and at Site 2 and 3 in 1993 in Table 4. Mineral N dynamics were similar for different sites and years in many respects.

Larger amounts of ammonium (except in the 30–90 cm layer at Site 1, October 1992) and consistently smaller amounts of nitrate were present at position A than at C throughout the soil profiles in bother years. In the 0–30 cm layer, the differences were significant, except in the autumn of 1992 at Site 1 and in the autumn of 1993 at Site 3. In the 30–90 cm layer, the differences were all significant for nitrate but for ammonium only significant in the spring at Site 1 in 1992 and in the spring at Site 3 in 1993. The overall

Table 3. Soil mineral nitrogen (kg/ha) and the ratio of NO_3^-–N to NH_4^+–N at Site 1 on two sampling occasions, in the spring and autumn of 1992 (n = 3) and 1993 (n = 6) at distances of 0.5–1.5 m (A) and 4.0–5.0 m (C) from the row of *Populus*.

Parameter	1992				1993			
	May 4		October 26		April 27		October 26	
	A	**C**	**A**	**C**	**A**	**C**	**A**	**C**
0–30 cm								
NH_4^+–N	6.7	2.3***	3.5	2.9	7.0	4.2***	6.3	4.0***
NO_3^-–N	1.9	3.1*	0.7	1.0	1.7	5.5***	0.3	0.5*
Total Min. N	8.6	5.4**	4.2	3.9	8.7	9.7	6.6	4.5***
NO_3^-–N/NH_4^+–N	0.3	1.4***	0.2	0.3	0.2	1.3***	0.04	0.1***
30–90 cm								
NH_4^+–N	3.4	1.2*	2.4	5.0	3.5	2.8	2.4	2.2
NO_3^-–N	4.3	36.9*	2.8	14.9*	0.8	9.5***	0.03	1.6*
Total Min. N	7.8	38.1*	5.2	19.9*	4.3	12.3***	2.5	3.8*
NO_3^-–N/NH_4^+–N	1.2	31.8*	1.4	3.3	0.3	4.0***	0.01	0.9*

* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$ (student's t-test) for comparison horizontally within each sampling occasion.

Table 4. Soil mineral nitrogen (kg/ha) and the ratio of NO_3^-–N to NH_4^+–N at Site 2 and site 3 on two sampling occasions, in the spring and autumn of 1993 at distances of 0.5–1.5m (A) and 4.0–5.0 m (C) from the row of *Populus*. $n = 6$.

Parameter	Site 2				Site 3			
	April 28		October 26		April 29		October 26	
	A	C	A	C	A	C	A	C
0-30 cm								
NH_4^+–N	6.4	3.2***	5.4	3.2***	7.7	5.3***	5.9	5.6
NO_3^-–N	3.9	12.4***	0.7	1.3***	6.3	12.3***	2.1	2.7
Total Min. N	10.3	15.6***	6.1	4.5**	14.0	17.6**	8.0	8.3
NO_3^-–N/NH_4^+–N	0.6	4.0***	0.1	0.4***	0.8	2.4***	0.4	0.5*
30–90 cm								
NH_4^+–N	5.6	4.0	4.3	3.4	9.1	5.4**	7.5	6.2
NO_3^-–N	15.7	87.6***	4.0	17.5**	33.8	69.8**	8.5	18.0*
Total Min. N	21.3	91.5***	8.3	21.0**	42.8	75.2*	16.0	24.2*
NO_3^-–N/NH_4^+–N	3.3	23.3***	1.0	5.2**	3.9	12.7***	1.2	3.1*

* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$ (student's *t*-test) for comparison horizontally within each sampling occasion.

differences in nitrate content between A and C were much more pronounced, and varied more than the differences in ammonium content. The concentration of nitrate in the 0–30 cm layer was between 3 and 10 times greater in spring than in autumn and between 3 and 5 times greater in the 30–90 cm layer. The concentrations of nitrate were very much higher at Site 2 and 3 than at Site 1, especially in spring. Significantly more total mineral nitrogen was present at C than at A below the top soil at all sites and sampling occasions. Greater amounts of mineral nitrogen were present at Site 1 in 1992 than in 1993, the difference being particularly pronounced at C.

The NO_3^-–N/NH_4^+–N-ratios were consistently lower at A than at C in all samples analyzed in both years. The differences were highly significant, except in the autumn of 1992 at Site 1. Comparing the season, the highest ratios at C were found in the spring.

Discussion

The significantly greater amounts of organic matter and total carbon found in the 0–10 cm layer of A should mainly be attributed to the organic matter inputs through litterfall and from the roots of the trees, since soil tillage was the same at all three distances from the trees. Roots of trees may play an important role in the build-up of organic matter. Nadelhoffer et al. [1985] estimated that the fine root biomass pool is replaced 0.5 to 2.2 times a year.

One of the weaknesses of this investigation is the fertilization of trees

during the establishment of the plantation, which naturally has improved conditions in A compared to B and C. Most probably, however, the effect of added N, P and K did not overshadow the effect of trees. Earlier fertilizations at Site 1 were quite low compared to the other sites (44% compared to Site 2 and 3), but the differences between A, B and C were just as pronounced (see Table 2). Furthermore, one may argue that it would have been desireable to have data on amounts of carbon from the year of establishment. This is true, but the data presented here still point towards an increase of organic matter close to poplar trees. At Site 2, no significant differences in total carbon and nitrogen were found between A and C. A small experiment with poplar clones had earlier been carried out close to this site and sampling plots C. Even though these trees were harvested some years before the start of the present investigation, they certainly could have influenced the results at that site.

The larger amounts of total carbon (the readily available fraction) close to the trees would favour overall bacterial activity [Stotzky and Norman, 1963], as was shown through increased respiration and N mineralization. Significantly higher rates of basic respiration and SIR at A than at C clearly indicate a larger microbial biomass close to the trees (Table 2). The direct supply of carbonaceous material from tree roots may partly explain this difference. Material such as sugars, aminoacids, and organic acids exudated from living roots, are important in supplying maintenance energy and determining growth of microbial populations [Bowen and Rovira, 1991].

The consistently greater amounts of ammonium at position A (Tables 3 and 4) and the higher rate of N mineralization at A than at B and C (Table 2) may indicate more favourable conditions for production of NH_4^+ close to the trees. If plant roots stimulate N mineralization, as indicated by many authors [Clarholm, 1985; Haider et al., 1987] a higher stimulation would be expected close to the trees, where more roots are present.

The higher total N content at A than at B and C could partly be the result of a concentration of nitrogen below the trees through stemflow and throughfall [Gersper and Holowaychuk, 1971], and the subsequent incorporation of some mineral N into the organic phase. The most probable reason for an increased total N content close to the trees may be uptake by roots, scavenging a great volume of soil for nitrogen, thus concentrating nitrogen below the trees through litterfall. Naturally, one could not exclude earlier fertilization with nitrogen as an explanation. However, fertilization at Site 1 ended in 1991 and the total quantity of N received between 1988 and 1991 did not exceed 60 kg/ha.

Before continuing the discussion of mineral nitrogen, it is important to point out that the pool sizes of mineral nitrogen are only instantaneous representations of the surplus in the balance of inorganic N production versus uptake by crops, immobilization and losses. The results of this investigation are in agreement with the observation that nitrate concentration fluctuates more widely than level of ammonium [Schmidt, 1982; Riha et al., 1986]. The lower

total concentration of mineral nitrogen, especially nitrate, below the top soil (30–90 cm) at A than at C should be principally attributed to the efficient uptake of nitrogen by the trees. The peaks of mineral nitrogen in spring were probably a result of larger amounts of decomposable material and increased soil moisture. Furthermore, the lack of active roots before the growing season starts and a possible stimulation of N mineralization after thawing of frozen soil might have led to a build-up of the mineral nitrogen pool in the soil. Freezing and thawing could cause a disruption of the structure of organic matter, thus facilitating mineralization [Focht and Martin, 1979].

The low NO_3^-–N/NH_4^+–N-ratios observed close to the trees in this investigation may be a combined effect of an efficient nitrate uptake by the trees and an enhanced N mineralization. In the present experiments, potential nitrification was significantly larger close to the trees than further away (Table 2). This is only an indication of ammonium oxidation per unit of time under optimal conditions and is not the actual rate of nitrification. However, if nitrification was limited, the most probable reason would be competition for and not limited availability of ammonium. Plants and heterotrophs are considered to be better competitors for ammonium than nitrifiers [Vitousek et al., 1982; Gosz and White, 1986], especially when the availability of easily degradable carbon is not limited. Furthermore, the drying out of the soil close to the trees might have reduced nitrification periodically.

The higher values of potential nitrification and respiration at Site 3 than at Site 1 might be attributed to the higher clay and carbon content at Site 3. As NH_4^+-ions are adsorbed to the clay mineral surfaces, such places are colonized by nitrifiers [Kunc and Stotzky, 1980]. The greater amount of mineral nitrogen at Site 1 in 1992 than in 1993 could partly be caused by the incorporation of straw in the autumn of 1992. Furthermore, the temperature and moisture conditions might have been more favourable for nitrogen mineralization and nitrification in 1992 than in 1993 (Fig. 1). In April and July, 1992, the precipitation was higher than in the same months in 1993.

In conclusion, the introduction of trees into the agricultural system seems to have a clear effect on nitrogen dynamics. The roots of the trees obviously scavenge mineral nitrogen efficiently, as well as water from the soil profile, thus probably reducing the total loss of nitrogen from the system. A build-up of both carbon and nitrogen compounds, through litterfall, decaying roots and root exudates, close to the trees was shown. This may explain the increased microbiological activity, including nitrogen mineralization and potential nitrification. The low NO_3^-–N/NH_4^+–N-ratios found close to the trees might be explained mainly by a combined effect of increased nitrogen mineralization and efficient uptake by the trees.

Acknowledgement

The present work was made possible by financial support from the Swedish council for Forestry and Agricultural Research.

References

Anderson JPE and Domsch KH (1978) A physiological method for the quantitative measurement of microbial biomass in soils. Soil Biology and Biochemistry 10: 215–221

Belser LW and Mays EL (1980) Specific inhibition of nitrite oxidation by chlorate and its use in assessing nitrification in soils and sediments. Applied Environmental Microbiology 39: 505–510

Boerner REJ and Koslowsky SD (1989) Microsite variations in soil chemistry and nitrogen mineralization in a beech-maple forest. Soil Biology and Biochemistry 21: 795–801

Bowen GD and Rovira AD (1991) The rhizosphere. The hidden half of the hidden half. In: Waisel Y, Eshel A and Kafkafi U (eds) Plant Roots. The Hidden Half, pp 641–669. Marcel Dekker Inc, New York

Clarholm M (1985) Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. Soil Biology and Biochemistry 17: 181–187

Duvigneaud P and Denaeyer-De Smet S (1970) Biological cycling of minerals in temperate deciduos forests. In: Reichle DE (ed) Analysis of Temperate Forest Ecosystems, pp 199–225. Springer-Verlag, New York

Egnér H, Riehm H and Domingo WR (1960) Untersuchungen über die chemische Bodenanalyse als Grundlage für die Beurteilung des Nährstoffzustandes der Böden Ann Roy Agric Coll Sweden 26: 199–215

Ekström G (1927) Klassifikation av svenska åkerjordar. In: Sveriges Geologiska Undersökningar (SGU), pp 130–135. Serie C, årsbok 20:6, nr 345, Stockholm

Focht DD and Martin JP (1979) Microbiological and biochemical aspects of semi-arid agricultural soils. In: Hall AE, Canell GH and Lawton HW (eds) Agriculture in Semi-Arid Environments Ecological Studies 34, pp 119–147. Springer-Verlag, New York

Gersper PL and Holowaychuk N (1971) Some effects of stemflow from forest canopy trees on chemical properties of soils. Ecology 52: 691–702

Gosz JR and White CS (1986) Seasonal and annual variation in nitrogen mineralization and nitrification along an elevational gradient in New Mexico. Biogeochemistry 2: 281–297

Haider K, Mosier A and Heinemeyer O (1987) The effect of growing plants on denitrification at high nitrate concentrations. Soil Science Society of America Journal 51: 97–102

Johnson DW and Edwards NT (1979) The effects of stem girdling on biogeochemical cycles within a mixed deciduous forest in eastern Tennessee. II: soil nitrogen mineralization and nitrification rates. Oecologia 40: 259–271

Kunc F and Stotzky G (1980) Acceleration by montmorillonite of nitrification in soil. Folia Microbiology 25: 106–125

Lamb D (1980) Soil nitrogen mineralization in a secondary rainforest succession. Oecologia Berlin 47: 257–263

Lodhi MAK (1977) The influence and comparison of individual forest trees on soil properties and possible inhibition of nitrification due to intact vegetation. American Journal of Botany 64: 260–264

Lodhi MAK (1978) Allelopathic effects of decaying litter of dominant trees and their associated soil in a lowland forest community. American Journal of botany 65: 340–344

McClaugherty CA, Pastor J, Aber JD and Melillo JM (1985) Forest litter decomposistion in relation to soil N dynamics and litter quality. Ecology 66: 266–275

Montes RA and Christensen NL (1977) Nitrification and succession in the Pidmont of North Carolina. Forest Science 25: 287–297

Nadelhoffer KJ, Aber JD and Melillo JM (1985) Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. Ecology 66: 1377–1390

Nordgren A (1988) apparatus for the continuous long-term monitoring of soil respiration rate in large number of samples. Soil Biology and Biochemistry 20: 955–958

Palmborg C and Nordgren A (1993) Soil respiration curves, a method to test the abundance, activity and vitality of the microflora in soils. In: Torstensson L (ed) Guidlines. Soil Biological Variables in Environmental Hazard Assessment, pp 149–156. Swedish EPA, Rep 4262

Persson J (1974) Humusbalans i odlad jord. Journal of the Scientific Agricultural Society of Finland 46: 247–263

Rice EL (1964) Inhibition of nitrogen-fixing and nitrifying bacteria by seed plants. I. Ecology 45: 824–837

Rice EL and Pancholy SK (1972) Inhibition of nitrification by climax ecosystems. American Journal of botany 59: 1033–1040

Riha SJ, Campbell GS and Wolfe J (1986) A model of competition for ammonium among heterotrophs, nitrifiers and roots. Soil Science Society of America Journal 50: 1463–1466

Robertson GP and Vitousek PM (1981) Nitrification potentials in primary and secondary succession. Ecology 62: 376–386

Schmidt EL (1982) Nitrification in soil. In: Stevenson FJ (ed) Nitrogen in Agricultural Soils, Agronomy 22: 253–288

Smith SJ and Young LB (1975) Distribution of nitrogen forms in virgin and cultivated soils. Soil Science 120: 354–360

Steppler HA (1987) Agroforestry: a decade of development. In: Steppler HA and Nair PKR (eds) ICRAF and A Decade of Agroforestry Development, pp 13–21. International Council for Research in Agroforestry (ICRAF), Nairobi, Kenya

Stotzky g and Norman AG (1963) Factors limiting microbial growth activities in soil. III. Supplementary substrate additions. Canadian Journal of Microbiology 10: 143–147

SYSTAT (1992) Statistics. Version 5.2 Edition. SYSTAT, Inc, Evanston, Illinois

Torstensson L (1993) Ammonium oxidation, a rapid method to estimate potential nitrification in soils. In: Torstensson L (ed) Guidlines. Soil Biological Variables in Environmental Hazard Assessment, pp 40–47. Swedish EPA, Rep 4262

Tottman DR (1987) The decimal code for the growth stages of cereals, with illustrations. Ann Appl Biology 110: 441–454

Vitousek PM, Gosz JR, Grier CC, Melillo JM and Reiners WA (1982) A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecological Monographs 52: 155–177

Waring SA and Bremner JM (1964) Ammonium production in soil under waterlogged conditions as an index of nitrogen availability. Nature 4922: 951–952

Woodmansee RG (1984) Comparative nutrient cycles of natural and agricultural ecosystems: a step toward principles. In: Lowrance R, Stinner BR and House GJ (eds) Agricultural Ecosystems. Unifying Concepts, pp 145–156. John Wiley and Sons, New York