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Primary production and nitrogen allocation of field grown sugar maples in relation to nitrogen availability

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Abstract. Above ground net primary production (NPP), nitrogen (N) allocation, and retranslocation from senescing leaves were measured in 7 sugar-maple dominated sites having annual net N mineralization rates ranging from 26 to 94 kg · ha^{-1} · yr^{-1}. The following responses were observed: (1) Green sun leaves on richer sites had higher N mass per unit leaf area than sun leaves on poorer sites; (2) Total canopy N varied much less than annual net mineralization, ranging from 81 to 111 kg · ha^{-1}; (3) This was due to the existence of a large and relatively constant pool of N which was retranslocated from senescing leaves for use the following year (54 to 80 kg · ha^{-1}); (4) The percentage of canopy N retranslocated by sugar maple was also relatively constant, but was slightly higher on the richer sites. Percent N in leaf litter did not change across the gradient; (5) Above ground NPP increased linearly in relation to N allocated above ground. Therefore, N use efficiency, expressed as above ground NPP divided by N allocated above ground was constant; (6) N use efficiency expressed as (NPP above ground/total N availability) was a curvilinear function of N availability; and (7) This pattern reflected a decreasing apparent allocation of N below ground with decreasing N availability.

Introduction

Nitrogen (N) is generally considered to be the limiting nutrient in most northern temperate forest ecosystems (Mitchell and Chandler, 1939; Cole et al., 1967, Auchmoody and Filip, 1973). It produces the largest increases in forest production in fertilizer trials and is often the only element that causes an increase (Tamm, 1975; Lea et al., 1979).

Responses to added N include increased foliar N concentration (Mitchell and Chandler, 1939; Brix, 1971; Miller et al., 1976; Fagerstrom and Lohm, 1977), increased total mass of foliage (Mitchell and Chandler, 1939; Tamm, 1975; Miller and Miller, 1976), and decreased retranslocation from senescing leaves (Turner, 1977). Total above ground production generally shows a 'declining return' in response to fertilization (Mitchell and Chandler, 1939; Miller et al., 1976; Turner, 1976), implying declining N use efficiency (Production/N availability) at high levels of addition.

It is difficult to extrapolate from fertilizer trials to unfertilized stands because: (1) not all fertilizer is taken up by plants (Mead and Pritchett, 1975a, b); and (2) the response in a fertilized stand represents a dynamic condition as the stand adjusts first to higher, then rapidly decreasing, N availability following a pulse nutrient addition. These responses may not be the same as for natural stands that have reached a steady state condition at constant, higher N availability.

For naturally occurring N availability gradients, Vitousek (1982) showed that nitrogen use efficiency in leaf production was highest at low levels of availability and declined as N cycling increased. Pastor et al. (1984b) documented a pattern of declining returns in above ground production with increases in N mineralization for a mixed species sequence. Nadelhoffer et al. (1983) showed increased leaf production with increasing N mineralization. In all of these studies, data from multi-species stands with variable composition were used. Thus, the resulting patterns could be due to changes in the responses of the dominant species and/or to changes in species composition along the gradients examined. In a study of individual species along a qualitative fertility gradient, Zimka and Stachurski (1976) found large differences in the plasticity of different species with regard to nutrient retranslocation from senescing leaves.

The purposes of the present study were (1) to examine the relationship between soil N availability, total above ground production and the allocation of production in sites dominated by a single species (sugar maple, *Acer saccharum*, Marsh.), and (2) to examine the efficiency of retranslocation and the relative importance of retranslocatable N in proportion to the total pool of N available to plants (mineralization + retranslocation) as a function of N mineralization.

Methods

Study sites

The seven study sites are all dominated by sugar maple and lie within the University of Wisconsin Arboretum, Madison, Wisconsin. The climate is characterized by warm, humid summers and cold winters (July mean temperature = 21.2 °C; January = −5.2 °C). Mean annual precipitation is 95.3 $\mathrm{cm\,yr^{-1}}$, of which about 70% falls as rain between April and October (Wisconsin State Climatological Laboratory Data, Madison, Wisconsin, 1971–1980).

The sites are 15 m x 15 m (0.0225 ha) plots in a single large stand approximately 500 m long by 100 m wide. The stand was established on an old field site by heavy plantings of sugar maple in 1946, 1953, and 1955. Lighter plantings continued until 1959. Minor amounts of basswood (*Tilia americana* L.) and white ash (*Fraxinus americana* L.) were also planted. Other dominant or co-dominant trees include quaking aspen (*Populus tremuloides* Michx.), black cherry (*Prunus serotina* Ehrh.), butternut (*Juglans cinerea* L.), and silver maple (*Acer saccharinum* L.). Records of the University of Wisconsin Arboretum show no of plantings of these species.

The soil is derived from glacial deposits overlain by a loess cap. The soil in six plots (plots 1–4, 6–7) is a Typic Hapludalf, fine silty, mixed, mesic; the soil in the remaining plot (5) is a Typic Haplaquoll, fine silty, mixed, mesic, with a seasonally high water table (U.S.D.A. 1978). The soil in all plots shows evidence of past plowing. The forest floor is a mull. In all plots earthworms fragment and incorporate the previous year's leaf litter into the mineral soil by mid-July. There is little topographical variation within the stand.

Soil analyses

The depth of the Ap horizon was measured with a soil probe at 10 randomly selected points within each plot. The cores were oven-dried to constant weight at 100 °C and ground to pass through a 2-mm sieve. Subsamples were digested in hot concentrated sulfuric acid plus 30% hydrogen peroxide (Miller and Miller, 1948) and analyzed for total N (Technicon, 1977b). Additional subsamples were ashed in a muffle furnace at 500 °C for >8 h to determine organic matter content.

Volumetric cores were taken at five randomly located points in each plot for the determination of bulk density. Bulk density was estimated in two successive 15 cm deep layers; the lower boundary of 30 cm was chosen because all Ap horizons were less than 30 cm deep.

Nitrogen mineralization

Net N mineralization was measured by an *in situ* polyethylene bag incubation method (Eno, 1960; Ellenberg, 1977; Melillo, 1977; Nadelhoffer et al., 1983; Pastor et al., 1984) from May 1982 to May 1983. A transect was established along a diagonal through each plot. Eleven 6.0-cm diameter by 15-cm deep sample cores were removed from the soil profile at regular intervals along the transect, placed into 0.04-mm thick polyethylene bags, and reinserted into the profile. Seven of these cores were from the 0–15 cm soil layer; four contained soil from 15–30 cm. At the same time 11 paired samples were removed for analysis of pre-incubation NO_3–N and NH_4–N pools. Incubation periods were 25–37 days in May through August (approximately the calendar months), followed by a 75-day autumn and a 162-day winter incubation. The transect was moved laterally approximately 0.25 m at each sampling.

Samples were homogenized and subsamples extracted for 48 h with 1 N KCl (Nadelhoffer et al., 1983; Pastor et al., 1984). Extracts were analyzed for NH_4–N and NO_3–N (Technicon, 1978, 1977a). Soil moisture content was determined by drying soil subsamples at 100 °C for >48 h.

Organically bound N is released initially as NH_4 by microbial decomposers and can be oxidized to NO_3; therefore, net N mineralization over an incubation period is estimated by summing observed changes in NH_4–N plus NO_3–N. Nitrification is estimated as the observed change (incubation – initial) in NO_3–N alone. Multiplying observed concentration changes by sample depth, bulk density, and factors accounting for volume of extractant and sample dry weight yields an estimate of net N mineralization on a kg/ha basis.

Annual aboveground production

In 1981 leaf litter production was measured using four 0.25-m^2 litter traps in each plot. In 1982 a fifth trap was added in each. Data from 1981 represent total litter production during September to December. In 1982 litter collections took place weekly in September and November, and twice weekly in October (the period of heaviest litterfall). Sugar maple litter was sorted from that of other species.

Litter was dried to constant weight at 65 °C. In 1982 all litter was composited by trap within each plot and ground in a Wiley mill to pass a 0.08 cm mesh. Subsamples were subjected to a sulfuric acid/hydrogen perioxide digest (Miller and Miller, 1948) and analyzed for total N (Technicon, 1977b). Additional subsamples were ashed at 500 °C for >6 h for determination of percent ash.

Reproductive tissues were not collected. Few or no sugar maple samara were observed in any of the plots in 1982. Basswood and butternut seed production was light in plots in which these species were present. Fairly heavy seed production of ash was noted in Plot 6 in 1982.

Understory (<1.0 m tall) production was measured on September 16, 1982, in seven randomly selected 0.25-m^2 quadrats per plot. The current year's understory growth was clipped from the volume extending 1.0 m above a 0.5 m x 0.5 m frame placed on the forest floor. Samples, including both wood and leaves, were dried to constant weight and weighed.

Production of overstory perennial tissues was estimated by allometric regression. Diameter at breast height (DBH) was measured on all stems $>=$ 5 cm DBH on each plot. Increment cores taken in winter from the stems (1 from small stems, 2 from larger individuals) allowed an estimate of five years' DBH increment. Allometric equations were used to convert the current and five year previous DBH values to total aboveground biomass. One fifth of the difference between these is the estimate of annual woody production above ground. The summary allometric regressions reported by Pastor et al. (1984a) were used for sugar maple, aspen, red maple, and yellow birch. The regression for black cherry was that of Wiant et al. (1977); white spruce (*Picea glauca* (Moench) Voss), that of Baskerville (1965); hornbeam (*Ostrya virginiana*), that of Reiners (1972); ash, that of Monteith (1979); butternut, that suggested by Monteith (1979). The red maple regression was used for silver maple and basswood. Biomass values were increased by 13% to estimate woody biomass and production below ground (Whittaker and Marks 1975).

Green tissue samples

Green sugar maple leaves were collected from all plots between July 20 and 28, 1982. Using an extension pruner and climbing ladders, we cut six branches with sun leaves and six with shade leaves in each plot. Sun leaves were defined as those clearly projecting above the canopy and continuously exposed to direct sunlight. Shade leaves were collected from lower canopy positions from trees that were canopy dominants or co-dominants. The six samples of both sun and shade leaves were collected from different stems; sun and shade samples were not paired to represent the same six stems.

The green leaves were dried and ground. Subsamples were digested in acid and analyzed for total N, and other subsamples were ashed in a muffle furnace, following the procedures reported above for litter.

Data on the percent N in green leaves and in leaf litter allow an estimate of retranslocation of N prior to litterfall. The calculation of (green leaf %N – litter %N)/(green leaf %N) yields an estimate of retranslocation as a percent of the green leaf N pool. This calculation is valid if weight loss during leaf senescence is minimal. To verify this we calculated the specific weights (g/cm^2 of leaf surface) of green shade leaves and of subsamples of maple litter. Dried and weighed samples of shade leaves (20–60 leaves, six samples per site) were run through a LiCor Model 3100 Leaf Area meter. Specific weight was calculated as total weight/total area. The procedure was repeated with samples of maple leaf litter. Specific weight of green leaves was not greater than that of fallen leaves.

Throughfall

N can be lost from leaves during senescence by leaching in throughfall as well as by retranslocation. We collected throughfall during leaf senescence in two plots – those with the highest and the lowest 1981 leaf litter production – to estimate the magnitude of this N flux. Throughfall was collected from September 27 to November 8, 1982. This period bracketed >97% of total leaf litterfall in both plots. Throughfall was collected in seven polyethylene jugs per site through funnels of radius 8.0 cm, each with an insert of nylon screen (1.5 mm mesh) to exclude solid materials. Bulk rainfall was collected at a single point in the open approximately 0.5 km from the study plots. Samples were collected biweekly (if rain had fallen). Phenyl mercuric acetate (0.5 ml; $1\,g \cdot l^{-1}$) was placed in each jug before each collection period to prevent microbial activity. Samples taken to the lab were stored at 3 °C until they were analyzed for NH_4–N and NO_3–N (Technicon 1978, 1977a).

Results

Vegetation and soils

Despite a uniform age and history, the stand shows considerable variation in several structural characteristics among plots (Table 1). Stem density (>2 cm DBH) varied by a factor of 2.78, from 1501 to 2677 stems $\cdot$ ha^{-1}. Basal area (stems > 2 cm DBH) varied by a factor of 1.80, from 16.7 to 30.0 m^2 $\cdot$ ha^{-1}.

Table 1. Vegetation and soil characteristics of seven sugar maple dominated sites in the University of Wisconsin Arboretum

	1	2	3	4	5	6	7
Density (stems > 2 cm DBH • ha^{-1})	2222	2267	2677	2400	1689	1511	1501
Basal area (stems > 2 cm DBH • ha^{-1})	16.7	23.3	19.1	22.6	27.3	30.0	22.5
Biomass (T/ha) (stems > = 5 cm DBH)	97	150	116	148	207	232	150
Total canopy height (m)	19	19	15	18	22	22	22
Depth of Ap (cm)	18.6	26.4	23.2	21.4	27.9	22.5	29.9
Bulk density (g • cm^3)							
0–15 cm	1.035	1.032	1.024	1.011	0.972	0.992	0.927
15–30 cm	1.339	1.141	1.177	1.165	1.101	1.192	0.892
Percent organic matter (in Ap)	5.3	4.6	5.5	5.4	7.7	5.6	6.2
Percent nitrogen (in Ap)	0.23	0.17	0.20	0.19	0.28	0.20	0.19
N mineralization (kg • ha^{-1} • yr^{-1}, 0–30 cm)	26	34	41	41	64	84	94

Biomass (stems > = 5 cm DBH) varied by a factor of 2.38, from 97 to 232 Mg ha^{-1}. Maximum canopy height ranged from 15 to 22 m.

The depth of the Ap horizon ranged from 18.6 to 29.9 cm. Percent soil organic matter in the Ap ranged from 4.6 to 6.2 in the Alfisols. It was higher, 7.7%, in the Mollisol in Plot 5.

Nitrogen mineralization

Net nitrogen mineralization ranged from 26 to 94 kg • ha^{-1} yr^{-1} (Table 1). In Plots 3 and 4, 51% and 35% respectively of mineralized N was nitrified. In the remaining plots nitrification represented > = 100% of observed mineralization.

Green leaf and total canopy N

Mean sugar maple sun leaf %N was 2.42% (Table 2). Mean shade leaf %N was 2.53%. This difference was not statistically significant ($P > 0.10$). Analysis of variance indicated a significant difference between plots for both sun and shade leaf %N (Sun leaves; $f(6,35) = 4.37$, $P < 0.01$. Shade leaves: $f(6,35) = 3.41$, $P < 0.01$), but no systematic change in %N in either sun or shade leaves was observed across the N mineralization gradient.

Nitrogen per unit leaf area in sugar maple sun leaves varied significantly among plots (Table 2; $f(6, 35) = 3.87$, $p < 0.01$) and was significantly related to N mineralization (Figure 1; $R^2 = 0.734$; $f(1,5) = 13.8$; $p < 0.025$). For shade leaves, no significant differences were found.

Total nitrogen in green sugar maple leaves in each site was calculated as the mean %N of the sample of sun and shade leaves in each plot times sugar maple litter fall. Values range from 42 to 100 kg • ha^{-1} (Table 2).

Table 2. Green leaf, total canopy and leaf litter characteristics for the seven study sites

		1	2	3	4	5	6	7
Green leaves – sugar maple								
Sun leaves ($n = 6$)								
%N	Mean	2.35	2.47	2.40	2.10	2.48	2.42	2.70
	S.D.	0.16	0.20	0.19	0.17	0.20	0.23	0.29
mg-N · cm^{-2}	Mean	0.0887	0.1141	0.1132	0.1031	0.1137	0.1275	0.1289
	S.D.	0.0140	0.0116	0.0252	0.0172	0.0219	0.0148	0.0109
Shade leaves ($n = 6$)								
%N	Mean	2.49	2.46	2.24	2.52	2.89	2.56	2.57
	S.D.	0.16	0.29	0.29	0.20	0.40	0.14	0.23
mg-N · cm^{2}	Mean	0.0667	0.0641	0.0644	0.0661	0.0723	0.0675	0.0690
	S.D.	0.0094	0.0051	0.0064	0.0152	0.0116	0.0061	0.0094
Total N in green sugar maple leaves (kg · ha^{-1})		65	69	42	50	100	62	85
Total canopy N (kg · ha^{-1})		87	97	81	84	104	89	111
Litter								
Sugar maple leaf litter ($n = 5$)								
%N	Mean	0.67	0.69	0.71	0.61	0.69	0.62	0.65
	S.D.	0.03	0.05	0.02	0.02	0.07	0.04	0.02
Non-maple leaf litter ($n = 5$)								
%N	Mean	0.97	1.11	1.08	1.03	0.94	1.02	1.10
	S.D.	0.07	0.08	0.07	0.06	0.09	0.05	0.08

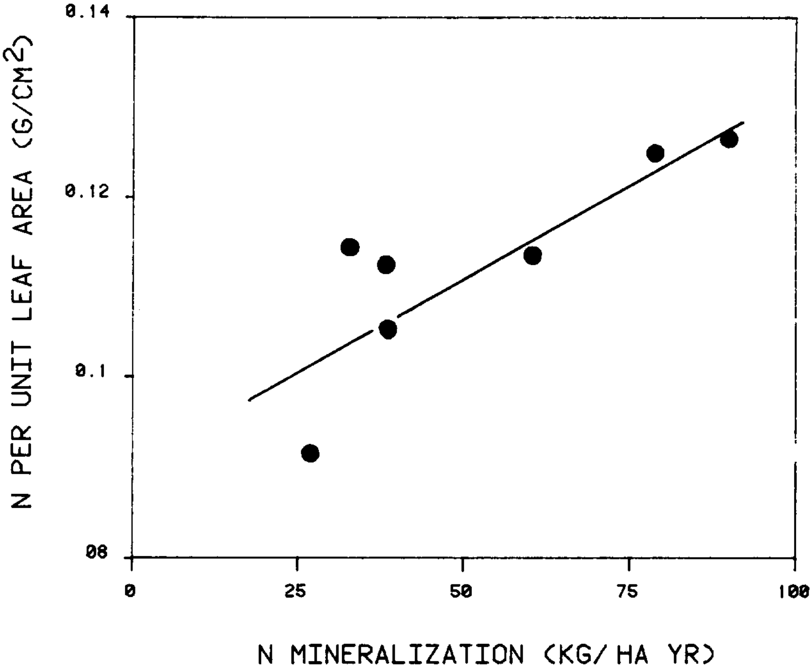


Figure 1. Nitrogen per unit leaf area in sun leaves of sugar maple as a function of N mineralization.

Calculating total canopy N required an estimate of green leaf N for non-maple species. We assumed that retranslocation for these species was 60%, so that green N equalled (litter N/0.4). Available data on %N in green leaves of other species on the plots (Pastor and Bockheim, 1984; von Althen, 1973; Likens and Bormann, 1970; Mitchell and Chandler, 1939; McHargue and Roy, 1932) are in general agreement with these calculations. The subsequent calculations on total canopy N and retranslocation are not sensitive to these values because sugar maple provides most of the litter fall in our plots. Total canopy N ranged from 81 to 111 kg • ha^{-1} (Table 2).

Litter nitrogen

Mean nitrogen concentration in sugar maple leaf litter ranged from 0.61% to 0.71%. The mean of 35 trap samples was 0.66% (Table 2). Non-maple litter was consistently higher in %N than sugar maple litter. The observed range was 0.94% to 1.11%.

Throughfall

Throughfall in plot 7 did not differ from bulk rainfall in either ammonium or nitrate concentration. Significant canopy leaching did occur in plot 3 ($P < 0.05$) but totalled only 1.05 kg N • ha^{-1}. This is less than 2% of the

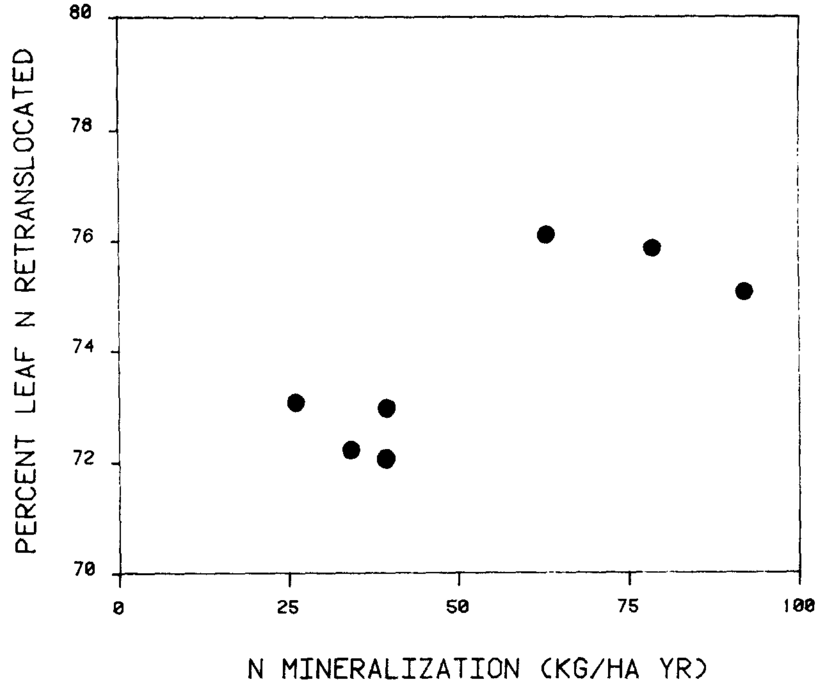


Figure 2. Percent retranslocation of N from individual leaves of sugar maple as a function of N mineralization.

$54 \, kg \cdot ha^{-1}$ removed from leaves in this plot prior to abscission. Similar results are reported by Ryan and Bormann (1982).

Retranslocation

The percentage of N in green sugar maple leaves retranslocated during senescence decreases slightly at low levels of soil N availability (Figure 2). A Newman-Keuls analysis of variance separated a group of Plots 5, 6, and 7 (highest retranslocation; also the highest N mineralization) from a group of Plots 1, 2, 3, and 4. There was no overlap between these groups ($p < 0.05$).

Total retranslocation for the entire canopy in each site was calculated as the total green canopy N minus total N in litter fall. This ranged from 54 to $80 \, kg \, N \cdot ha^{-1}$ (Table 3) and was not related to N mineralization. Adding this value to N mineralization for each plot yields the total N available for plant growth from both soil and internal plant pools. This varies from 86 to $174 \, kg \, N \cdot ha^{-1}$ (Table 3). The percentage of total canopy N provided by retranslocation decreased linearly with increasing net N mineralization (Figure 3).

Table 3. Retranslocation and N return in leaf litter for the seven study sites

		1	2	3	4	5	6	7
% Retranslocation from individual sugar maple leaves		73.1	72.0	71.8	72.8	76.1	75.8	74.7
N available from retranslocation (kg • ha^{-1} • yr^{-1})[a]	maple	46	48	29	35	71	45	65
	other	14	18	25	20	5	17	15
	total	60	66	54	55	76	62	80
Total N available (N mineralization + retranslocation; kg • ha^{-1} • yr^{-1})		86	100	96	95	140	146	174
% of Total N available supplied by retranslocation		69.8	66.0	56.8	57.3	54.3	42.5	46.0
N returned to forest floor in leaf litter (kg • ha^{-1} • yr^{-1})		26.9	31.2	28.7	27.1	28.1	26.4	30.9

[a] Retranslocation for sugar maple calculated directly from sugar maple green leaf and litter %N. Retranslocation for other species (values in parentheses) estimated as 60% of green leaf %N

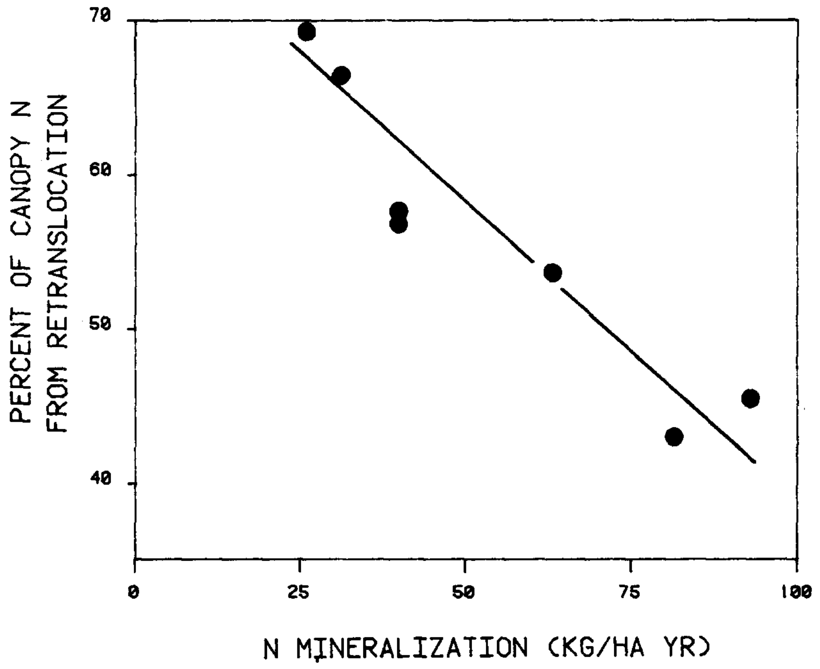


Figure 3. Percentage of total N in green leaves which is derived from retranslocation as a function of N mineralization.

Table 4. Net primary production above ground for sugar maple and for all species in the seven study plots

	1	2	3	4	5	6	7
All species							
Leaf production (1981–82 mean) $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$)	3.60	3.79	3.23	3.55	3.96	3.55	4.17
Woody tissue production $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$	2.37	3.72	3.36	3.56	3.85	4.14	3.29
Total production $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$	5.97	7.51	6.59	7.11	7.81	7.69	7.46
Sugar maple							
Leaf production (1982) $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$	2.64	2.70	1.68	2.24	3.57	2.43	3.29
Woody tissue production $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$	1.44	2.87	2.27	2.32	2.89	2.19	1.98
Total production $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$	4.08	5.57	3.95	4.56	6.46	4.62	5.27
Maple as % of total	68.3	74.2	59.9	64.1	82.7	60.1	70.6
Understory							
1982 $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$	0.062	0.029	0.011	0.009	0.000	0.003	0.030

Production

Mean leaf production ranged from 3.23 to 4.17 $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$ (mean of two years data, differences between years on a given plot ranged from + 10 to − 620 $\mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$; overall mean was 260 $\mathrm{kg \cdot ha^{-1}}$ less in the second year of collection). Production of perennial tissues ranged from 2.37 to 4.14 $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$ (Table 4). Neither leaf nor woody production showed a significant relationship with N mineralization.

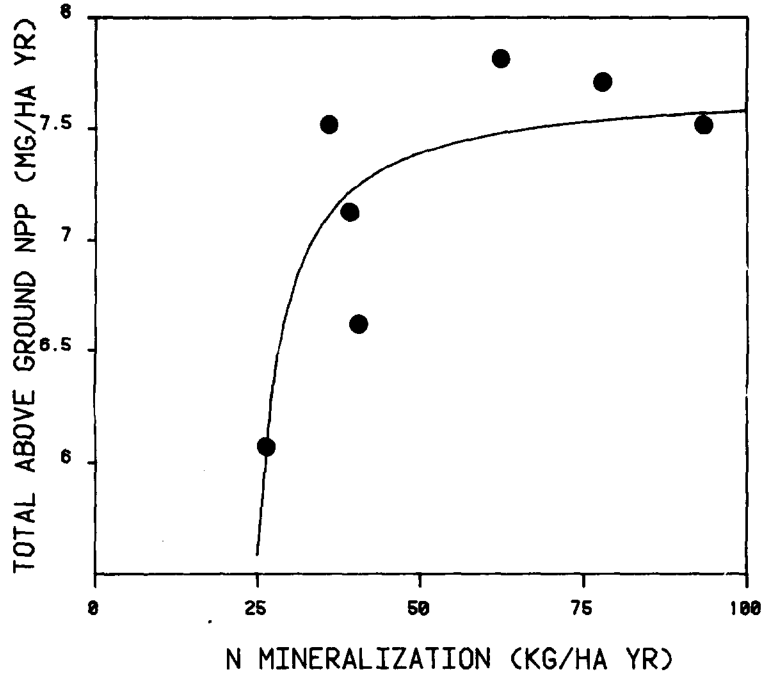
Total above ground NPP increases with increasing N mineralization (Figure 4a) and increasing total N availability (mineralization + retranslocation, Figure 4b). Several different functions could be used to describe these patterns. Each equation has a different theoretical underpinning and suggests different interactions between N availability and production. We fit four different equations for both sets of data: (1) a simple linear function, (2) a quadratic function, (3) an asymptotic (modified Michaelis-Menten) function, and (4) a double linear or linear to asymptote (Blackman curve) function. For both sets, the Michaelis-Menten function describing progressively smaller increases in productivity with increasing N availability, was the best and only statistically significant fit. The equations are:

$$Y = 7.87[1.0 + (1.82/(\mathrm{TOTN}\text{-}80.0))] \qquad R^2 = 0.87,\ p < 0.05,\ \mathrm{SEE} = 0.247$$

and

$$Y = 7.69[1.0 + (1.13/(\mathrm{NMIN}\text{-}22.0))] \qquad R^2 = 0.73,\ p < 0.05,\ \mathrm{SEE} = 0.346$$

where Y is total above ground NPP ($\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$), TOTN is total N



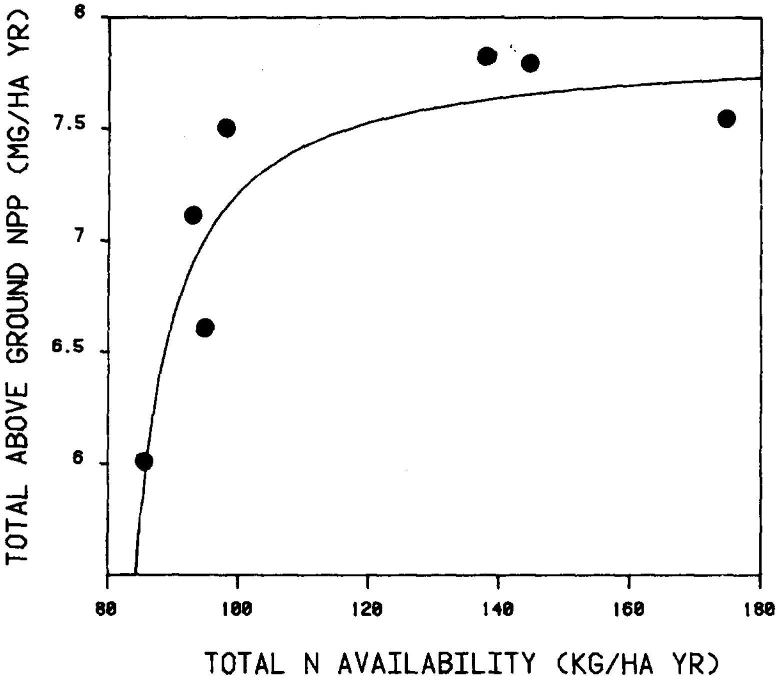


Figure 4a. Total above ground NPP as a function of N mineralization. Line is best fit for the Michaelis-Menten equation with non-zero X intercept (see text).

Figure 4b. Total above ground NPP as a function of total N availability (mineralization + retranslocation). Line is best fit for the Michaelis-Menten equation with non-zero X intercept (see text).

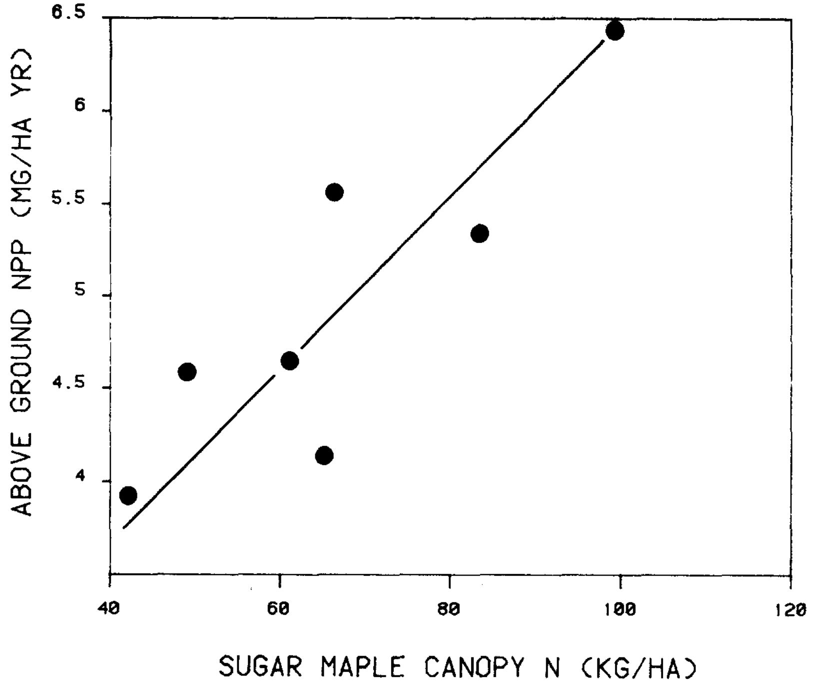


Figure 5. Total above ground NPP by sugar maple as a function of total N in green laves of sugar maple.

availability (kg • ha^{-1} • yr^{-1}) and NMIN is N mineralization (kg • ha^{-1} • yr^{-1}). The total N availability relation is the better of the two predictors of productivity, reflecting the more accurate estimate of the N status of the dominant plants. Both regressions were improved significantly by allowing predicted productivity to go to zero well above zero N availability (the 80. and 22. coefficients).

Total above ground production by sugar maple alone is strongly and linearly related to total N in sugar maple leaves (Figure 5). Over this range, each additional kg of N moved to the canopy adds about 38 kg to total above ground production.

Understory production (Table 4) varied from 0 to 0.062 Mg • ha^{-1} • yr^{-1}. A Newman-Keuls analysis of the data separated plot 4 from the other plots in a comparison of groups of six means ($p < 0.05$).

Discussion

The gradient

It is surprising to see such extreme variation in N mineralization over such a short distance in a stand with little variation in topography and soil texture.

The most distinctive visual difference between soils in these sites is the depth of the Ap horizon, which leads to significant differences in total soil organic matter and N. We hypothesize that sheet erosion during the period of cultivation may have caused the movement of topsoil along the slight elevational gradient that does exist and resulted in the gradient in depth of Ap and indirectly to the differences in N mineralization. This difference should have relatively little effect on the total water holding capacity of the sites.

Leaf and canopy nitrogen

The only significant alteration in leaf characteristics that we measured was an increase in the amount of N per unit leaf area for sugar maple sun leaves in sites with high N mineralization. Since the concentration of the carboxylating enzyme is strongly correlated with N content (Mooney and Gulmon, 1982), leaves in the most favorable light environments apparently respond to increased N availability by increasing the amount of photosynthetic tissue beneath each square centimeter of leaf surface. Mooney et al. (1978) and Gulmon and Chu (1981) have found the ratio of N/leaf area correlates well with maximum photosynthetic rate. As soil N availability increases, we infer that sugar maple responds not by increasing leaf production, but by increasing the photosynthetic capacity of leaves in the crown positions most favorable for photosynthesis. Advantages of this response over that of increasing leaf production might include minimizing the cost in carbon of adding photosynthetic tissue, since entire new leaf skeletons need not be constructed, and increased water use efficiency (net photosynthesis/g water transpired), as photosynthetic capacity is increased without adding to transpiring leaf surface area (Mooney et al., 1978; Field et al., 1983).

Aboveground production increases linearly with canopy N (Figure 5a). However, this regression does not pass through the origin ($p < 0.05$). It predicts positive above ground production (of about $2\,\mathrm{Mg} \cdot \mathrm{ha}^{-1}$) when canopy $N = 0$. Therefore, over a range starting with zero production and zero canopy N, the curve would show a pattern of declining returns (cf. Mooney and Gulmon, 1979).

Retranslocation

We found no evidence that retranslocation increases as soil N availability declines. Percent retranslocation from individual sugar maple leaves was greatest in plots with the greatest N mineralization (Figure 2), due to a slightly greater green leaf %N in these plots coupled with a fixed lower bound to which N was withdrawn at senescence. This finding is in marked contrast to results from fertilization studies, in which percent retranslocation generally declines with increasing fertilizer additions (Turner, 1977; Miller et al., 1976). Zimka and Stachurski (1976) noted that different species had very different retranslocation characteristics along a qualitative site quality gradient, with

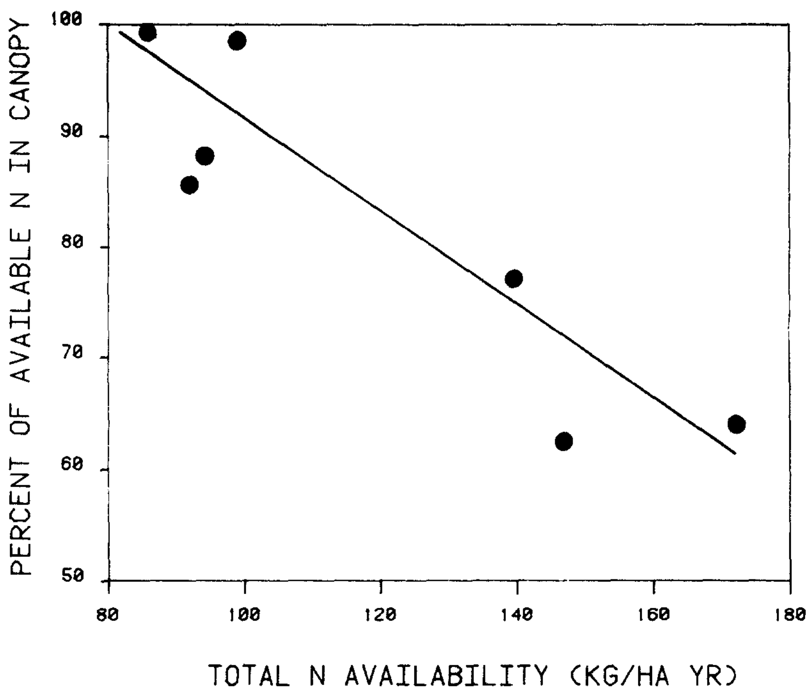


Figure 6. Percentage of total available N (mineralization + retranslocation) allocated to green leaves as a function of total N availability.

some species showing variable efficiency of retranslocation and others not. Flanagan and Van Cleve (1983) show variable retranslocation for several taiga species. Chapin's (1980) analysis concluded that increased retranslocation from individual leaves is not common at low levels of nutrient availability.

Retranslocation contributes a much greater proportion to total N available for plant use when N mineralization is low than when N mineralization is high. Retranslocated N represents 70% of total N availability (mineralization + retranslocation) in our poorest plot; this figure falls to about 40% as N mineralization increases. As a result, total canopy N (range 81 to 111 kg $\cdot$ ha^{-1}) is much less variable than N mineralization (range 26 to 94 kg $\cdot$ ha^{-1} $\cdot$ yr^{-1}). Thus retranslocation serves to dampen environmental variability and allow full canopy closure even under conditions of very low soil N availability.

The 70% of total N available represented by retranslocated N on our poorest plot nearly matches percent retranslocation from individual leaves. This suggests that nearly all N dropped in litter each year is recycled back to leaves, with little available for woody tissue and root production. Our data for this plot are 26 kg-N $\cdot$ ha^{-1} $\cdot$ yr^{-1} mineralization, 27 kg-N $\cdot$ ha^{-1} $\cdot$ yr^{-1} returned in leaf litter. Expressed in a different way, the percentage of total N availability accounted for in the canopy increases with decreasing N mineralization, and approaches 100% on the poorest plot (Figure 6).

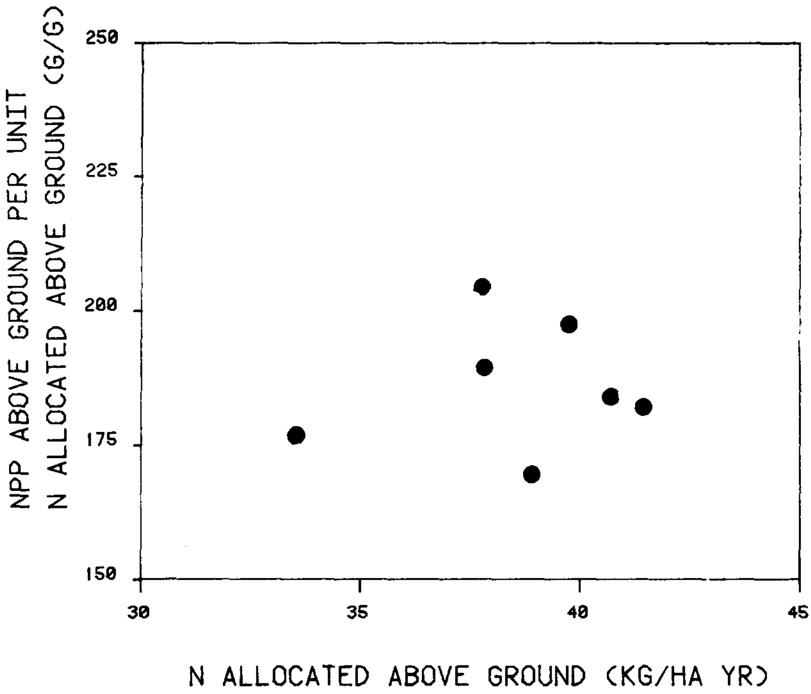


Figure 7. Nitrogen use efficiency above ground based on N allocated above ground.

Net primary production and N cycling

There is a linear relationship between total sugar maple canopy N (kg • ha^{-1}) and total aboveground production (Figure 5). The relationship between total N availability (mineralization + retranslocation) and total aboveground production (Figure 4) is strongly curvilinear and asymptotic. Thus the declining rate of return in aboveground production as N availability increases is due primarily to the fact that the 'extra' N available is not moved into the canopy on the richer sites. We infer that as N availability increases the relative availability of other resources (e.g., light, water), limits the photosynthetic contribution that could be gained from additions to canopy N. This conclusion is in accord with the theoretical basis of the Michaelis-Menten function, which describes the saturation of a process in terms of substrate availability. For sugar maple, leaf area, canopy N, and aboveground production on our sites are related to soil N availability only when availability is low (less than about 50 kg^{-1} ha^{-1} yr^{-1}); as N availability increases, these parameters are apparently determined by the availability of other resources, and plant response is uncoupled from soil nitrogen status.

In the range over which aboveground production is directly related to N availability, production drops rapidly toward zero as N availability declines. Leaf production and canopy N are maintained, however, even when soil N

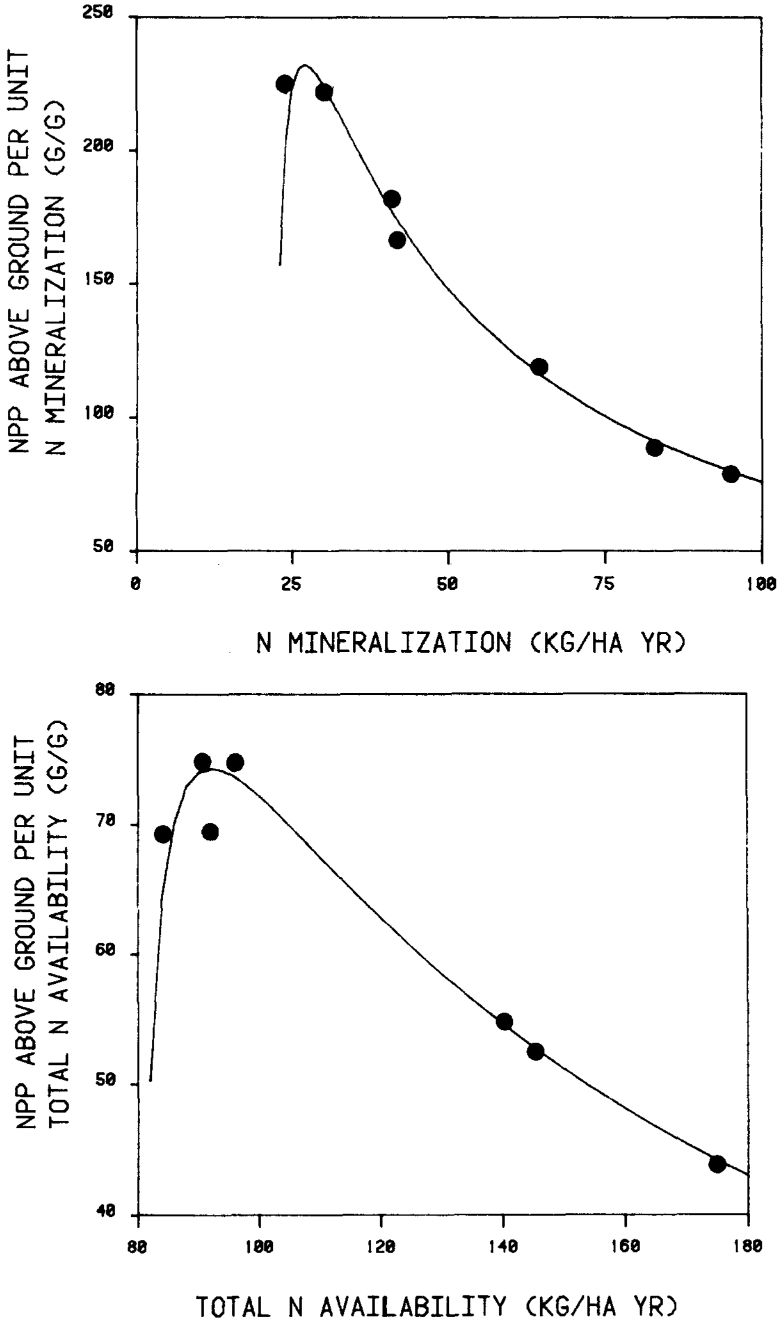


Figure 8a. Nitrogen use efficiency above ground based on N mineralization (Note: line generated from equation derived in Figure 4a, not fit to points on this graph, see text). Figure 8b. Nitrogen use efficiency above ground based on total N availability (mineralization + retranslocation, Note: line generated from equation derived in Figure 4b, not fit to points on this graph, see text).

availability drops to very low levels; the maintenance of photosynthetic tissue apparently has the highest priority for sugar maple across a broad range of N availability.

This finding has implications for stand maintenance at critically low levels of N availability. If available N is moved preferentially into leaves, little must remain available for woody tissue and root growth on the poorest sites. N mineralization in our poorest plot may be barely sufficient to support stand maintenance; any perturbation that serves to reduce present N availability (e.g., removal of yearly litterfall, experimental application of carbohydrates) should result in the deterioration of the present forest cover.

Nitrogen use efficiency

The concept of nutrient use efficiency has emerged as an important method of expressing carbon-nutrient interaction and response to nutrient stress (Vitousek, 1982; Chapin, 1980; Turner, 1977). Increasing efficiencies of nutrient use are generally reported with decreasing nutrient availability.

For our plots, two patterns are of interest. Efficiency of N use aboveground only (total aboveground production per unit N in annual aboveground production) does not vary systematically (Figure 7). However, efficiency of N use based either on N mineralization or on total N availability does increase with declining N availability (Figures 8a, 8b. Note that the lines in these figures are not fit through these data points, but are calculated from the Michaelis-Menten functions in Figures 4a and 4b).

A theoretical consequence of constructing a Michaelis-Menten function with a positive x-intercept is that the efficiency of N use is predicted not to climb indefinitely as N availability declines, but rather to peak and fall toward zero at a positive value for N availability. Our poorest plot appears to confirm this result (Figure 8b), again suggesting that this stand is barely being maintained at the present level of N availability.

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