Can Intensively Managed Forest Ecosystems be Self-Sufficient in Nitrogen?

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ABSTRACT

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A simple input-output model was constructed to evaluate the long-term net nitrogen (N) gain or loss or N self-sufficiency of several silvicultural systems. In general, short-rotation, whole-tree-harvest systems are not self-sufficient in N. If they include an active biological nitrogen fixation (N_2 fixation) component, however, they are highly N self-sufficient even when they sustain large losses of N in harvested biomass. Forestry systems, with or without substantial N_2 fixation, appear to be greatly superior in this respect to most annual agricultural crops with or without N_2 fixation. All N inputs and outputs must be measured in field experiments, however, before N self-sufficiency can be accurately evaluated. Better estimates of loss through harvest removal, and gain through N_2 fixation and atmospheric inputs, over more than one rotation are particularly needed.

INTRODUCTION

Nitrogen limits the productivity of many forest ecosystems (see, e.g., Gessel et al., 1973), in large part because of high vegetative N requirements, generally low N inputs, and potential losses of N through leaching and denitrification. Short-term productivity of many silvicultural systems may be increased at the expense of greater loss of N from the production site. This loss occurs when a greater proportion of total biomass is harvested, when rotation length is reduced, or when biological productivity is increased through higher planting densities or the use of fast-growing species and varieties.

Tree utilization standards greatly affect the quantity of nutrients removed from a site. Whole-tree harvesting, which removes most of the above-ground portion of the tree (usually not the leaves), removes 1.5–4 times more nutrients than does bole-only harvesting (Kimmins, 1977). Decreasing the number of years a forest crop occupies the site usually results in harvest at a time of more rapid growth and thus a higher above-ground N content (Wells and

Jorgensen, 1975), and can lead to increased N losses from the soil associated with harvest disturbance (Armson, 1977). Nitrogen uptake occurs more rapidly in highly productive stands (McColl and Powers, 1984), regardless of the reason for increased productivity.

Increased loss of N through economic optimization may be offset by including or enhancing N_2-fixing species in the silvicultural system. The rapid early growth of many of these species makes short rotations possible from a wood-production point of view. The N_2-fixing species grown for short rotations, however, accumulate N more rapidly than do non-N_2-fixers, leading to greater N removal during harvest (Dawson and Gordon, 1979). Increased nitrification under N_2-fixers also causes greater leaching losses (Van Miegroet and Cole, 1984). Thus, that continuous rotation of N_2-fixing species will lead to N self-sufficiency remains to be demonstrated. Further, no current model predicts the minimum time and space that must be allocated to the N_2-fixing component of alternate or mixed-cropping systems to insure N self-sufficiency. This analysis is particularly important because of the current high interest in agroforestry systems, one component of which is often a tree capable of N_2 fixation.

The purposes of this paper are: (1) to develop a simple model to evaluate N self-sufficiency of intensively managed ecosystems; (2) to evaluate the importance of N_2 fixation in maintaining N levels in intensively managed ecosystems; (3) to compare self-sufficiency for several temperate-zone silvicultural systems; and (4) to discuss factors that may influence rates of N_2 fixation and N self-sufficiency of these systems.

EVALUATION OF N SELF-SUFFICIENCY

We evaluated N self-sufficiency using a rotation-based N budget in which all inputs and outputs on an annual basis are averaged over an entire rotation (kg N ha^{-1} year^{-1}). Thus, the relative importance of individual inputs and outputs can be compared within a system, net change in N capital can be compared between systems with different rotation lengths, and changes in site and crop N can be directly related to biomass or economic yields averaged over the rotation. Average annual net gain or loss in the ecosystem is determined by a simple input-output model:

Net N gain or loss $= (I_{nf} + I_{ad}) - (O_{hl} + O_{ol})$

where I_{nf} is the annual input of biologically (symbiotically and non-symbiotically) fixed N averaged over the entire rotation period (kg ha^{-1} year^{-1}); I_{ad}, annual atmospheric deposition of N in rain, cloudwater, and dust (kg ha^{-1} year^{-1}); O_{hl}, the average annual harvest lost, the amount of N in biomass removed during harvesting divided by the rotation length (kg ha^{-1} year^{-1}) — a value similar to the forestry concept of mean annual increment; and O_{ol} accounts for other ecosystem losses (kg ha^{-1} year^{-1}) including erosion, denitri-

fication, volatilization, leaching beyond the rooting zone, and long-term immobilization in organic matter.

This model simply describes long-term changes in N capital. Our premise is that decline in N capital over successive rotations will result in reduced long-term site productivity. Data are inadequate to test the generality of this premise, but it seems reasonable given that N limits plant growth on most sites (Gessel et al., 1973). Processes affecting N availability and uptake can vary during a rotation, but these are usually site and species-specific and cannot be generally modeled for all situations. Our empirical approach could be used to follow changes in N sufficiency during a rotation if model components are measured periodically. The original purpose of the model, however, was to quantify changes averaged over the entire rotation.

METHODS

We report on N accumulation and N_2 fixation in a 5-year-old red alder plantation in northwest Oregon and include the few data from the literature on cumulative N_2 fixation and N accumulation by N_2-fixing species.

A red alder plantation spacing trial was established in 1974 on a 12-ha tract about 10 km south of Apiary, Oregon. Five growing seasons later, productivity, nutrient content, and N_2 fixation were assessed (Bormann, 1981; Bormann and Gordon, 1984). Biomass of the components was estimated by use of dimension-analysis techniques (Whittaker and Marks, 1975), and samples collected for dimension analysis were analyzed for total (Kjeldahl) N content. Five branches were sampled from each of three trees by a stratified-random method on each of three spacing treatments and two replicates for a total of 18 sample trees. Nitrogenase activity was measured by acetylene-reduction techniques and used to estimate N_2 fixation (Bormann and Gordon, 1984). Five-year cumulative N_2 fixation was calculated by linear interpolation between N_2 fixation in the 5th year and time zero. Depressed N_2 fixation was observed during the 5th year in the densely spaced stands because of intense intraspecific competition. Depressed N_2 fixation was unlikely during the 4th growing-season due to more open conditions, so N_2 fixation during the 4th year in the densely spaced stands was assumed to be the same as that of the intermediately spaced stands during the 5th growing-season. We then interpolated to calculate N_2 fixation in the earlier years of the dense stands. An ethylene:nitrogen ratio of 3:1 was used to estimate N_2 fixation in this study (Silvester, 1983), a ratio less than that indicated by the general stoichiometry of the chemical equations for the nitrogenase-catalyzed reduction of N_2 to NH_3 and C_2H_2 to C_2H_4; however, because empirical estimates of the ratio of *Frankia*-nodulated plants have been close to 3 (Silvester, 1983), we have retained it here. Rates of N accumulation predicted with this model are less than the rate measured

in a study of N accretion in red alder stands in western Washington (Bormann and DeBell, 1981).

The relative N self-sufficiency of this system and a lupin/pine system (Gadgil, 1971a) were compared with several non-N_2-fixing systems. Data from the literature on non-N_2-fixing systems were accepted if most model components had been estimated and if no N_2-fixing component was known.

For a more general evaluation of N self-sufficiency on a wide variety of systems, data on N accumulation in vegetation (Fried and Broeshart, 1967; Freedman, 1981) are entered into the model. Model assumptions, based on available literature, are: (1) no N_2 fixation occurs if there is not a known N_2-fixer in the system; (2) atmospheric deposition averages 8 kg ha^{-1} year^{-1}; and (3) other losses average 2 kg ha^{-1} year^{-1}. Because of inaccuracies in biomass and nutrient data and site specificity of atmospheric deposition and other losses, to predict sufficiency level for individual stands is inappropriate. If these inaccuracies are randomly distributed within the data, to look at general trends among all the systems is appropriate.

RESULTS

Nitrogen self-sufficiency of N_2-fixing systems

Nitrogen accumulated rapidly in a red alder plantation as a result of rapid growth and N_2 fixation (Table 1). Dense and intermediate stands accumulated

TABLE 1

Nitrogen accumulation (kg ha^{-1}), current and cumulative N_2 fixation, and estimated annual N_2 fixation and harvest losses in a 5-year-old red alder plantation

Component	Density (trees ha^{-1})		
	1240	4068	10091
Foliage	54.2	72.2	64.5
Branches	63.5	90.8	77.2
Stem	19.7	39.9	75.0
Roots	10.8	19.9	11.5
Branches + stem	83.2	130.7	152.2
Aboveground	137.4	202.9	216.7
Total	148.2	222.8	228.2
N_2 fixation, 5th year	62	88	57
Est. cumulative N_2 fix.	185	264	277
I_{nf}[1]	37	53	55
O_{hl}[2] (stem + branches)	17	26	30

[1]I_{nf} = model N_2 fixation (kg N ha^{-1} year^{-1}).
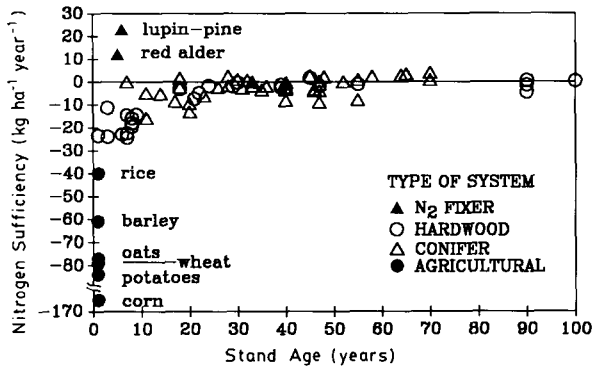[2]O_{hl} = model harvest losses (kg N ha^{-1} year^{-1}).

Fig. 1. Annual net nitrogen gain or loss (self-sufficiency) of forest, N_2-fixer, and agricultural systems based on potential harvest loss data (Fried and Broeshart, 1967; Gadgil 1971b; Freedman 1981); a whole-tree harvest is assumed.

the most total N. In intermediate-density stands, most N is held in branches, whereas in dense stands relatively more N is in the stem. If only stems and branches were harvested, average annual harvest loss would be 17–30 kg N ha^{-1} $year^{-1}$; losses would increase by about 1.5 times if all above-ground biomass were harvested.

Estimated cumulative N_2 fixation exceeds N accumulation by 16–20%. This N presumably can be accounted for in soil reserves, or has been lost through leaching or volatilization. Estimated N_2 fixation exceeds average annual harvest loss by 20–27 kg ha^{-1} $year^{-1}$. Because atmospheric deposition and other N losses are estimated to be 2 kg ha^{-1} $year^{-1}$, a 5-year alder rotation with a stem-plus-branch harvest will still accumulate N, although the rate will be about half that of N_2-fixation inputs.

Comparison of N_2-fixing systems with non-N_2-fixing systems

Silvicultural systems with an N_2-fixing component appear to be self-sufficient in N, with annual gains of 20–27 kg ha^{-1} (Table 2), even when N exports in harvested biomass are dramatically high.

Silvicultural systems without an N_2-fixing component are less sufficient, ranging from -10 to 2 kg ha^{-1} $year^{-1}$. Short-rotation cottonwood culture with branch-and-stem harvest (White, 1974) appears to deplete the soil more than does short-rotation culture of conifers with a stem-only harvest (Cole et al., 1968; Wells and Jorgensen, 1975). Depletion of N during cottonwood rotations greatly exceeds that of conifers if stands are whole-tree harvested.

Trends in nitrogen self-sufficiency

Information is inadequate for an accurate assessment of N self-sufficiency of most ecosystems, but we can compare patterns of N self-sufficiency among different silvicultural and agricultural systems if we make several assumptions

TABLE 2

Nitrogen sufficiency of eight short-rotation silvicultural systems

Harvest system	Inputs[a]		Outputs[a]		Sufficiency or net change
	I_{nf}	I_{ad}	O_{hl}	O_{ol}	
Alder dense, 5 year[b]	55	2	30	2	+25
Alder intermediate, 5 year[b]	53	2	26	2	+27
Alder open, 5 year[b]	37	2	17	2	+20
Lupin/pine, 2,4 year[c]	28	5	5	5	+23
Cottonwood, 8 year[d]	0	8	17	1	−10
Douglas-fir, 37 year[e]	0	1	3	1	−3
Loblolly pine, 20 year[f]	0	11	7	2	+2
Loblolly pine, 16 year[g]	0	11	9	2	0

[a]$I_{nf} = N_2$ fixation; I_{ad} = atmospheric deposition; O_{hl} = harvest losses; O_{ol} = other losses; all values in kg ha^{-1} year^{-1}.

[b]This paper. N in atmospheric deposition (Abee and Lavender, 1972). Other losses are rough estimates.

[c]Data on N_2 fixation rates in *Lupinus arboreus* from Gadgil (1971a), supported by Sprent and Silvester (1973); data on *Pinus radiata* rotation on same soil type from Gadgil (1971b). All stems and branches are assumed to be harvested. Other losses are rough estimates.

[d]Data from White (1974). Average of eight stands of *Populus deltoides* grown in southern Alabama. All stems and branches are assumed to be harvested. Other losses are rough estimates.

[e]Data from Cole et al. (1968). Assumption is that only stems are harvested.

[f]Data from Sweitzer and Nelson (1972). Assumption is that only stems are harvested. Other losses are rough estimates.

[g]Data from Wells and Jorgensen (1975). Assumption is that only stems are harvested. Other losses are rough estimates.

about the model components I_{ad}, I_{nf}, and O_{ol} (Table 3). In general, N self-sufficiency is higher in conventional harvest systems compared with whole-tree harvest systems (average difference, 8 kg ha^{-1} year^{-1}). Sufficiency of non-N_2-fixing hardwood systems appears to average 1.4–6.2 kg ha^{-1} year^{-1} less than that of conifer systems. Plantations appear to be about 1.9 kg ha^{-1} year^{-1} less sufficient than are natural stands. The N-sufficiency level is sharply decreased in whole-tree harvesting systems with rotations of less than 25 years (Fig. 1), presumably because young stands accumulate N more rapidly. Most young stands in this data set, however, are plantations that may contain genetically improved stock. The least N-self-sufficient class of forest system (hardwood plantations) is 2.5–11 times more N-sufficient than are agricultural crops.

Optimizing time or space given to N_2-fixers in mixed or rotational culture

The N self-sufficiency model can be rewritten to calculate the minimum allocation of time or space needed by the N_2-fixing component to achieve N self-sufficiency for the stand. The rewritten model becomes:

TABLE 3

N self-sufficiency level[a] for silvicultural and agricultural systems in the temperate zone

System	Number of stands	Age (years)	Productivity (t ha^{-1} year^{-1})	Harvest losses (kg ha^{-1})		Nitrogen sufficiency (kg ha^{-1} year^{-1})	
				C-H	W-H	C-H	W-H
Forestry crops							
Hardwood – Nat.	14	47	2.5	163	340	2.1	−1.5
Hardwood – Pltn.	14	11	3.1	65	182	0.7	−16.2
Hardwood – Avg.	28	30	2.7	136	266	1.7	−8.6
Conifer – Nat.	3	53	1.7	58	167	4.8	2.5
Conifer – Pltn.	38	37	3.6	104	289	3.0	−2.8
Conifer – Avg.	41	38	3.5	101	280	3.1	−2.4
Agricultural crops							
Wheat	1				56		−79
Potatoes	1				90		−84
Corn	1				174		−168
Barley	1				67		−61
Rice	1				46		−40
Oats	1				83		−77

[a]Based on potential harvest-loss data (Fried and Broeshart, 1967; Freedman, 1981) and assumed values for other model components (see 'Methods'). C-H: conventional harvest (stem only); W-H: whole-tree harvest (above-ground biomass); Nat: natural stands; Pltn: plantations.

$$P = (-I_{ad} + O_{hl2} + O_{ol}) / (I_{nf} - O_{hl1} + O_{hl2})$$

where P is proportion of time or space given to the N_2-fixer; I_{ad}, atmospheric deposition; O_{hl1}, harvest loss of the N_2-fixing component; O_{hl2}, harvest loss of the non-N_2-fixing component; I_{nf}, N_2 fixation; and O_{ol}, other losses.

If the cottonwood and alder rotations (Table 2) grew on the same site at the rates described, then alder would have to occupy the site about one-third of the time for this system to be N self-sufficient. The model in its current form would apply only to mixed stands when the species were compatible enough that interspecific competition did not affect N uptake rate. Also, because woody plants capable of symbiotic N_2 fixation may take several years to develop appreciable N_2-fixation capacity on some sites (Silvester, 1983), the N_2-fixing-component occupancy time (rotation cropping) or space (mixed cropping) must be modified to adjust for this lag.

DISCUSSION

Given adequate information, this simple input-output model can be used to assess the potential N self-sufficiency of a silvicultural system. Pure rotations

of N_2-fixers and at least some alternate-cropping schemes will probably remain N self-sufficient; however, in many situations, culture of an N_2-fixing crop would not be N self-sufficient. The presence of a species capable of N_2 fixation does not ensure that active fixation occurs. Alder, as well as all other tested woody perennials capable of nodulation, will grow well in an un-nodulated condition with sufficient substrate N (Bajnk et al., 1978). In off-site plantings, or when nutrients are deficient or levels of inoculum that limit nodulation are low, N_2 fixation may not occur. Also, because some inocula are more effective than others (Carpenter et al., 1984), the presence of nodules does not indicate what level of N_2 fixation is occurring. Direct measurement (such as acetylene reduction, ^{15}N assay, or N accretion) is required for verification of actual N_2 fixation. We have observed 'claimed' N_2-fixing tree plantations that seem to be poorly nodulated or un-nodulated.

Nitrogen fixation is an energy-expensive process, requiring about 18.8 g carbon g^{-1} N fixed (Gutschick, 1978). In small alders, N_2 fixation rates were proportional to photosynthesis rates for a range of clonal genotypes (Gordon and Wheeler, 1978). Clearly, N_2 fixation will be minimal in plants growing in deep shade. It may be possible for understory plants to fix N in measurable quantities if plants occupy the site during early stand establishment or after heavy thinning (Gadgil, 1976).

Although N sufficiency may not often be a problem for stands of pure N_2-fixers, the effect of harvest removal of nutrients other than N is of considerable concern. The N_2 fixers are generally thought to have particularly high requirements for phosphorus, suggesting that harvest removal of P may be higher in N_2-fixing crop species.

Nitrogen self-sufficiency appears to be achievable within some silvicultural systems; however, until the N dynamics of a variety of systems are measured over several rotations on the same site, conclusions will be incomplete. In the interim, N dynamics of existing planted and natural systems including N_2-fixers should be measured over a wide range of sites and species composition to rigorously test the sufficiency hypothesis, because it is central to the concepts of sustainable silviculture and 'sustained yield'.

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