

## Chapter (non-refereed)

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# Nitrogen cycling in a *Quercus/Fraxinus* (oak/ash) woodland in northern England, examined using the computer model FORTNITE

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## Abstract

Nitrogen cycling in a mixed deciduous woodland (Meathop Wood, a UK International Biological Programme research site) is considered in 2 ways: (i) through the presentation of a 'static' annual nitrogen cycle, and (ii) by dynamic modelling using the computer model FORTNITE. In the 'static' cycle, the nitrogen content of forest components and annual transfers are quantified in terms of kg N ha<sup>-1</sup> and kg N ha<sup>-1</sup> yr<sup>-1</sup> respectively. Data required for the dynamic modelling are presented, as are predictions (model outputs) of changes in tree growth, forest floor and available nitrogen parameters over 100 years following the 1939 coppicing of the woodland. Predictions for the years 1962, 1967 and 1972 closely match estimates derived from field measurements. The modelling also suggests that the woodland is unlikely to change its species composition during the next 50 years, except that the *Betula* (birch) may die out. The effects of removing one tree species, *Acer pseudoplatanus* L. (sycamore), on the growth of the woodland, and the F+H layer and available nitrogen were also simulated using the dynamic model. Both approaches to the study of nitrogen cycling are discussed with respect to their value for integrating scientific research and for developing scenarios on the effects of environmental factors and management practices on forest structure and productivity.

## 1 Introduction

If both the short- and long-term changes in the forest as it develops, and the consequences of forest management practices on the environment and on forest site quality are to be predicted with any satisfactory degree of accuracy, the biological functioning of the forest ecosystem needs to be properly understood. The complexity and dynamic nature of forests make difficult any long-term predictions, particularly when they comprise several interacting tree species. Though many research studies can be usefully carried out on component parts of forests, it is only when the forest is viewed as an integrated unit that the complex interplay of environmental factors and the biological processes can be fully visualized. As part of the International Biological Programme of the late 1960s and early 1970s, a semi-natural woodland ecosystem, Meathop Wood, in northern England, was chosen for such a study, and many papers have been published describing aspects of the research (eg Bunce 1968; Frankland 1982; Gray *et al.* 1974;

Harkness *et al.* 1986; Harrison 1979, 1985; Mosse 1978; Satchell 1971; Satchell *et al.* 1971; Spink 1975; Swift 1977; Swift *et al.* 1976; Sykes & Bunce 1970; White & Carlisle 1968; White & Harrison 1987).

## 2 Study site

The site is a mixed deciduous coppice-with-standards woodland, located on the northern edge of Morecambe Bay at 54°12'N and 2° 53.5'W, with an oceanic climate. The tree species comprise *Quercus petraea* Mattuschka (Liebl.) (sessile oak), *Fraxinus excelsior* L. (common ash), *Betula pubescens* Ehrh. (downy birch) and *B. pendula* Roth (silver birch), and *Acer pseudo-platanus*, with an understorey of *Corylus avellana* L. (hazel). The site was last fully coppiced in 1939, and its tree age structure partially reflects the effect of this management. The soil is an acid (pH 4.3–7.0) brown earth, averaging 13.5 cm in depth, derived from Silurian slates and shales, overlying Carboniferous limestone.

## 3 Static model of nitrogen cycling

Nutrient cycling processes were a central theme in the study of this woodland. In the nitrogen cycle of the woodland (Figure 1), all the values presented are derived from measurements made in the woodland, except for estimates of (i) direct assimilation of nitrogen as ammonia from the atmosphere by the tree canopy from Eriksson (1966), and (ii) N fixation, which has been calculated on the assumption that the nitrogen capital within the soil remains constant with time, by the formula used by Bormann *et al.* (1977):

$$N_{\text{fix}} = N \text{ in net annual tree production} \\ + N \text{ lost from the soil} - N \text{ in rainfall and aerosols} \\ + \text{gaseous uptake by tree canopy.}$$

The value of such a budgetary cycle is that it provides information on the amounts and distribution of nitrogen capital within the forest ecosystem. It shows clearly that the trees' nitrogen requirements far exceed the amounts needed for annual increments in tree growth, for much of the nitrogen taken up each year is subsequently lost, being recycled to the soil in organic debris. It indicates, too, that the trees conserve nitrogen by withdrawing over 60% of the element from the leaves prior to leaf-fall; whether there is an equivalent conservation of nitrogen prior to root death is unknown. We can also obtain an estimate of the amounts of nitrogen gained (though the input

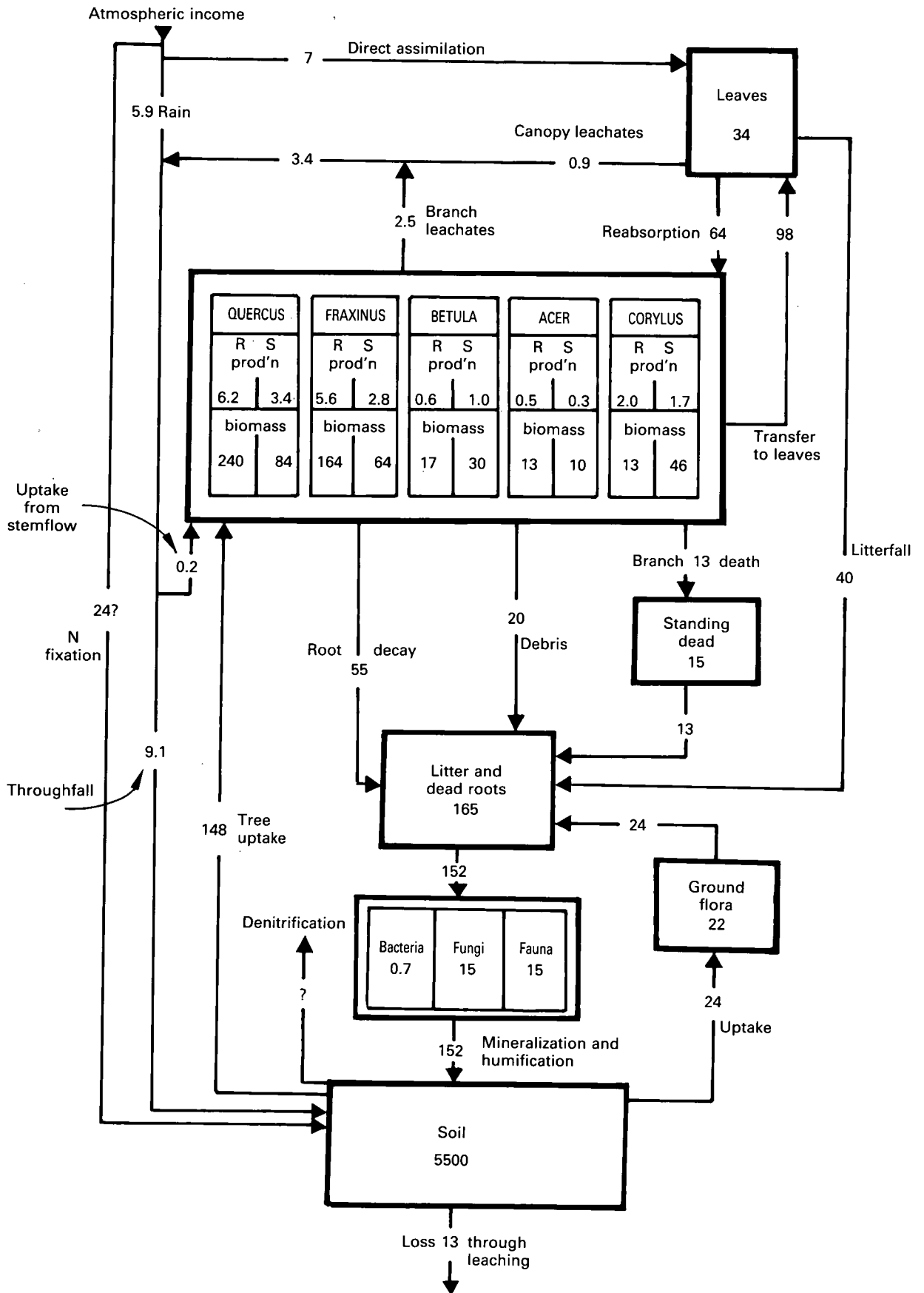


Figure 1. The nitrogen cycle of the mixed deciduous woodland in Meathop Wood, UK; nitrogen contents in kg ha<sup>-1</sup> and annual net transfers in kg ha<sup>-1</sup> yr<sup>-1</sup>

from N fixation is uncertain) and lost from the ecosystem. The forester can ascertain the approximate amount of nitrogen which would be removed in timber, and this amount can be roughly equated with the known capital within, and inputs to and losses from, the ecosystem. Unfortunately, the research forester cannot use this type of 'model' to understand the consequences of the various management practices, how they may influence future forest productivity, and which of the practices are most important in this respect.

#### 4 Dynamic model of nitrogen cycling

Full integration of research data, such that the influences of different environmental factors and the interactions of the various dynamic biological processes in the forest ecosystem, and possible outcomes of specific forest management strategies, can all be examined, is really only possible through the use of computer simulation models. The forest computer model called FORTNITE, published by Aber and Melillo (1983), is, to our knowledge, the most comprehensive model that is suitable for a multi-species, uneven-aged forest ecosystem, and which integrates tree growth parameters, environmental factors and nitrogen cycling elements. It also gives the potential to 'manipulate' the forest in a variety of ways, and to indicate the consequences in the outputs. Validation runs show that the model accurately predicts successional changes in tree growth, species composition, leaf production, forest floor biomass and dead wood biomass following clearfelling, for some North American forests.

Details of the data required to run the model are given by Aber and Melillo (1983). In summary, 4 classes of data are required: (i) environmental factors, (ii) tree growth parameters, (iii) tree nitrogen response data, and (iv) forest floor decomposition and nitrogen variables. The environmental factors are (i) the heat sum (degree days) for the global distribution limits (DMIN and DMAX) of each tree species, calculated by the formula given by Botkin *et al.* (1972), (ii) the actual evapotranspiration levels (WMIN and WMAX) for the same distribution limits, calculated by the method given by Thornthwaite and Mather (1957), and (iii) the responses of each species to varying light intensities—first, an estimate of the lowest percentage of full light intensity (LMAX) below which the species fails to grow and reproduce itself, and, second, regression constants (A1) and coefficients (A2 and A3) for the so-called light-demanding and shade-tolerant groups of species (Aber *et al.* 1979). The tree growth parameters are the constants and coefficients from equations relating the tree diameter at breast height or 1.3 m (dbh) to tree height (B2 and B3), stem dry weight (SA and SB), branch dry weight (BA and BB), root biomass dry weight (RA and RB), and the constant and coefficient for the regression relating crown width to stem dbh (SLTA and SLTB) for all species (see Whittaker *et al.* 1974). Maximum leaf dry

weight (LFWT) produced 100 m<sup>-2</sup> area canopy, the root/stem biomass ratio (RTST), the maximum likely stem dbh (DIMX) and age (AGMX) and the numbers of regenerating saplings 100 m<sup>-2</sup> (SAPN) under optimum conditions in the site are also required for each tree species. The tree nitrogen response data are the constants and coefficients (N1–N5) from regressions of tree responses on available soil nitrogen based on fertilizer trials, for 3 groups of tree species classed according to their nitrogen requirement (Mitchell & Chandler 1939; Aber *et al.* 1979). For the decomposition module, the model requires information for up to 6 leaf litter types, 10 size classes of above-ground woody material, woody roots, fine roots, twigs and forest floor material. These data are (i) the fraction of the initial litter weight as nitrogen, (ii) the fractional weight loss per year, (iii) the amount of nitrogen immobilized per gram weight loss, (iv) the fraction of weight as nitrogen when litter cohort transfers to the

Table 1. Data file: tree variables required for FORTNITE model (data structured as input file)

MEATHOP RAW DATA		NO CLEARFELL					
		NRVAR=		4			
KTMS=	25.	NYR=	100.	KPNT=	3.	FRPT=	1.
NSPP=	5	NSVAR=	33				
SPNM	Q PE	F EX	B PE	A PS	C AV		
G	1.40	1.40	1.70	0.65	1.60		
B2	.0053	.0043	.0043	.0048	.0058		
B3	.0007	.0007	.0007	.0008	.0003		
LFWT	302.	209.	360.	237.	180.		
DMIN	1755.	1755.	735.	1755.	1251.		
DMAX	7375.	7375.	6590.	7375.	6590.		
WMIN	510.	510.	382.	510.	455.		
WMAX	682.	682.	682.	682.	682.		
RTST	0.75	0.67	0.23	0.57	0.33		
DIMX	170.	170.	50.	80.	25.		
AINC	.01	.01	.01	.01	.01		
AGMX	300.	200.	90.	120.	50.		
SAPN	4.	3.	1.	1.	8.		
LMAX	.20	.30	.20	.20	.05		
A1	1.00	1.00	1.00	1.00	1.00		
A2	-4.640	-4.640	-4.640	-4.640	-4.640		
A3	.05	.05	.05	.05	.05		
TC	1.	2.	3.	5.	4.		
SA	74.7	64.5	72.5	165.5	91.7		
SB	2.38	2.39	2.388	2.123	2.144		
BA	12.5	17.5	21.76	26.5	55.3		
BB	2.72	2.67	2.393	2.459	2.047		
RA	66.8	52.6	22.03	100.2	50.86		
RB	2.45	2.50	2.389	2.228	2.104		
SLTA	1.13	1.18	1.67	1.63	3.02		
SLTB	.219	.222	.106	.199	.081		
N1	2.79	2.99	2.94	2.94	2.94		
N2	-.00175	-.00175	-.00234	-.00234	-.00234		
N3	219.77	207.43	117.52	117.52	117.52		
N4	-0.6	-5.0	-1.2	-1.2	-1.2		
N5	1.0	2.9	1.3	1.3	1.3		
DGRO	1.	1.	1.	1.	.1.		
NPLOT=	1	NTREE=	12				
SPECIES	1.	DBH	16.				
	1.		1.				
	2.		3.				
	3.		3.				
	4.		2.				
	5.		1.				
	5.		1.				
	5.		2.				
	5.		2.				
	5.		3.				
	5.		3.				

next compartment, (v) the destination compartment for the litter cohort, and (vi) the litter type.

To run the model, a simulated starting plot of 100 m<sup>2</sup> is described as the number of trees occurring, their species identity, and their dbh in cm. A further input file is required containing data for the study site, namely the accumulated degree days (°F), actual annual evapotranspiration rate, a relative solar energy input factor, the timing and degree of harvesting intensity required, and an estimate of the nitrogen available from precipitation, mineral soil and fertilization. The structure, development and functional rationale, together with a listing of the model program written in FORTRAN 66, are presented by Aber and Melillo (1983).

We have recently started to examine the research data for Meathop Wood, using this model. Our first objectives were to examine (i) the possible time-course of woodland development since the last full coppicing of the woodland, when the stems of *Fraxinus*, *Corylus*, *Acer*, *Betula* and all but the largest *Quercus* were removed, and (ii) the possible effects of a management practice in which the *Acer* trees were removed at 52 years after regrowth; this is an invasive species, and the timber is of little commercial value. We would have liked to investigate the influences of thinning and coppicing the woodland, but the computer program as written does not allow these aspects to be investigated.

To study the long-term development of the woodland, the model was run (using a VAX 8600 computer) for 100 years, with an initial plot of trees representative of the situation which would have been present a year or so after the coppicing. The sapling numbers (SAPN) were taken as the relative numbers of each species which grew up following the coppicing; these figures were derived from tree age distribution data for the woodland. The relationships between heights of trees and dbh (1.3 m) for the species studied do not follow the parabolic function described by Aber and Melillo (1983); instead, they were related linearly by an equation in the form:

$$\frac{1}{h(\text{cm})} = f \left( \frac{1}{\text{dbh}} + k \right)$$

so the program and B2 and B3 in Table 1 were adjusted accordingly. Values for LFWT for each species were calculated in grams of leaf material m<sup>-2</sup> of tree crown area (incorrectly quoted as g 100 m<sup>-2</sup> of crown area in the original document—J D Aber, pers. comm.), based on litterfall data. Because specific details on the sensitivity of growth and seed generation to light intensity and on the general growth responses to nitrogen fertilization, as determined by Mitchell and Chandler (1939), are not available for these tree species, the appropriate equations were selected (Aber *et al.* 1979) based on published information on generalized tree responses (Evans

Table 2. Data file: decomposition and nitrogen variables required by FORTNITE model (data structured as input file)

NCMPAR=	7	NFVAR=	20				
FNM1	F+H	FFLR	LRGE	ROOT	FINE	LEAF	TWIG
FNM2	LAYR	WOOD	WOOD	WOOD	ROOT		
0.	.013	.200	.000	.020	1.	6.	
0.	.019	.495	.000	.019	1.	6.	
0.	.013	.292	.000	.020	1.	6.	
0.	.019	.331	.000	.019	1.	6.	
0.	.013	.495	.000	.020	1.	6.	
0.	.007	.420	.000	.019	1.	6.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.008	.595	0.00	.020	1.	5.	
0.	.009	.120	0.00	.015	1.	7.	
0.	.005	.370	0.00	.010	1.	2.	
NCOHRT	7						
16.	.186	.310	-.025	5.	0.	1.	
2.14	.047	.363	.00	.02	1.	6.	
4.7	.014	.095	.00	0.005	2.	3.	
4.8	.017	.095	.00	0.006	1.	4.	
2.70	.015	.595	0.00	.020	1.	5.	
1.33	.007	.370	0.00	0.005	2.	2.	
2.70	.023	.120	0.00	.015	1.	7.	
DDEC1	1.00	DDEC2	1.00				
IHARV	1						
DLIM	0. 0. 0. 0. 0.						
REGEN	0. 0. 0. 0. 0.						

1984, 1986). The model was run with 7 classes of litter cohorts initially defined in terms of biomass, nitrogen content and decomposition rates (Table 2), a sophistication provided for, but not used, by Aber and Melillo (1983). The decomposition rates of organic matter in the F+H layer and of twig material on the soil surface were estimated by modelling the rate of incorporation of  $^{14}\text{C}$ -bomb carbon from the atmosphere (Harkness *et al.* 1986). The turnover rate of the fine roots used is very similar to the initial  $k$  values found by experimentation elsewhere (McClaugherty *et al.* 1984). The woodland degree-day sum and actual evapotranspiration values, with net available N input from the mineral soil ( $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ), are given in Table 3.

During the testing of the model, the decomposition rates of the fine roots and the F+H layer on the soil surface, and the tree responses to light and available nitrogen, were found to be very sensitive parameters, and hence these factors require particular attention in research studies.

The computer simulation of the woodland resulted in a close match between the predicted biomass values for all the 5 species and the biomass estimates derived for the woodland during the period 1962–72 (Table 4). It also showed that the total biomass may increase to about  $280 \text{ tonnes dry matter ha}^{-1}$  (Figure 2), with

Table 3. Data file: site variables required for the FORTNITE model (data structured as input file)

NPVAR= YEAR	DEGD	AET	PHI	CUT	N IN
1	3350.00	595.00	1.00	0.00	0.1600
2	3350.00	595.00	1.00	0.00	0.0100
3	3350.00	595.00	1.00	0.00	0.0100
4	3350.00	595.00	1.00	0.00	0.0100
5	3350.00	595.00	1.00	0.00	0.0100
6	3350.00	595.00	1.00	0.00	0.0100
7	3350.00	595.00	1.00	0.00	0.0100
8	3350.00	595.00	1.00	0.00	0.0100
9	3350.00	595.00	1.00	0.00	0.0100
10	3350.00	595.00	1.00	0.00	0.0100
.	.	.	.	.	.
50	3350.00	595.00	1.00	0.00	0.0100
.	.	.	.	.	.
80	3350.00	595.00	1.00	0.00	0.0100
.	.	.	.	.	.
90	3350.00	595.00	1.00	0.00	0.0100
.	.	.	.	.	.
100	3350.00	595.00	1.00	0.00	0.0100

*Quercus* and *Fraxinus* forming the majority of the biomass (Figure 3). Thereafter, there will be a short-term decline in the live biomass, due to a short-term increase in tree mortality. *Betula* will show a significant decline, and this genus may well die out (Figure 3); this is a realistic prediction in that *Betula* is a short-lived



Figure 2. Trends in the biomass of all tree species combined and tree components in Meathop Wood, predicted using FORTNITE (— total; --- basal area; ··· stems & branches; - · - roots; - - - leaves)

Table 4. Comparison of predicted (P) and measured (M) biomass values for Meathop Wood

	1962		1967		1972	
	P	M	P	M	P	M
<i>Quercus</i>	58	68	74	78	100	88
<i>Fraxinus</i>	56	46	61	53	69	63
<i>Betula</i>	20	16	16	18	13	20
<i>Acer</i>	8	5	12	6	15	7
<i>Corylus</i>	15	10	10	18	7	19
Total tree	158	146	173	173	204	198
Stem + branch	97	88	104	108	121	124
Roots	57	58	65	65	79	74
Basal area	23	18	22	23	24	25

Measured data provided by J M Sykes and R G H Bunce  
Biomass is expressed as  $t\ ha^{-1}$  and basal area as  $m^2\ ha^{-1}$

tree and individuals can now be seen in the woodland to be rotting and falling over. *Corylus* may show some slight decline, but death in some coppice stools will probably be matched by new recruitment. *Acer*, the invasive species, may not become a major component of the woodland, and could even show a decline after 80 years. Apart from these minor changes, the model predicts that the woodland will probably remain in a similar state as at present.

The computer simulation also shows that the inputs of leaf, root and branch litters increase only slowly as the woodland ages, following the last coppicing (Figure 4).

The predicted values, perhaps with the exception of the dead rootwood biomass, agree well with the estimates from field measurements. The dead wood remaining within the woodland canopy increases with time, as trees age; this result is as expected.

The model also predicts a slow increase in the F+H layer material on the soil surface; this prediction is consistent with the known tendency for organic matter to accumulate in soils under woodland (Van der Drift 1971). The so-called available nitrogen shows a significant increase, along with the organic matter in the F+H layer, as the woodland ages; again, this prediction is consistent with known accumulation of nitrogen in soils under woodland (Jenkinson 1971).

The computer simulation of the removal of all the *Acer* trees 52 years after coppicing suggests that this would result in significant increases in the growth of *Fraxinus* and *Quercus* (Figure 5), due partly to increases in the amount of available nitrogen (Figure 6). The prediction is in agreement with the well-known effects of thinning on the growth of trees in forest ecosystems (Evans 1984; Carey *et al.* 1982). It is all the more interesting, as conservationists often wish to remove *Acer* from British woodlands, because it is considered a non-native species. Its removal could result in larger

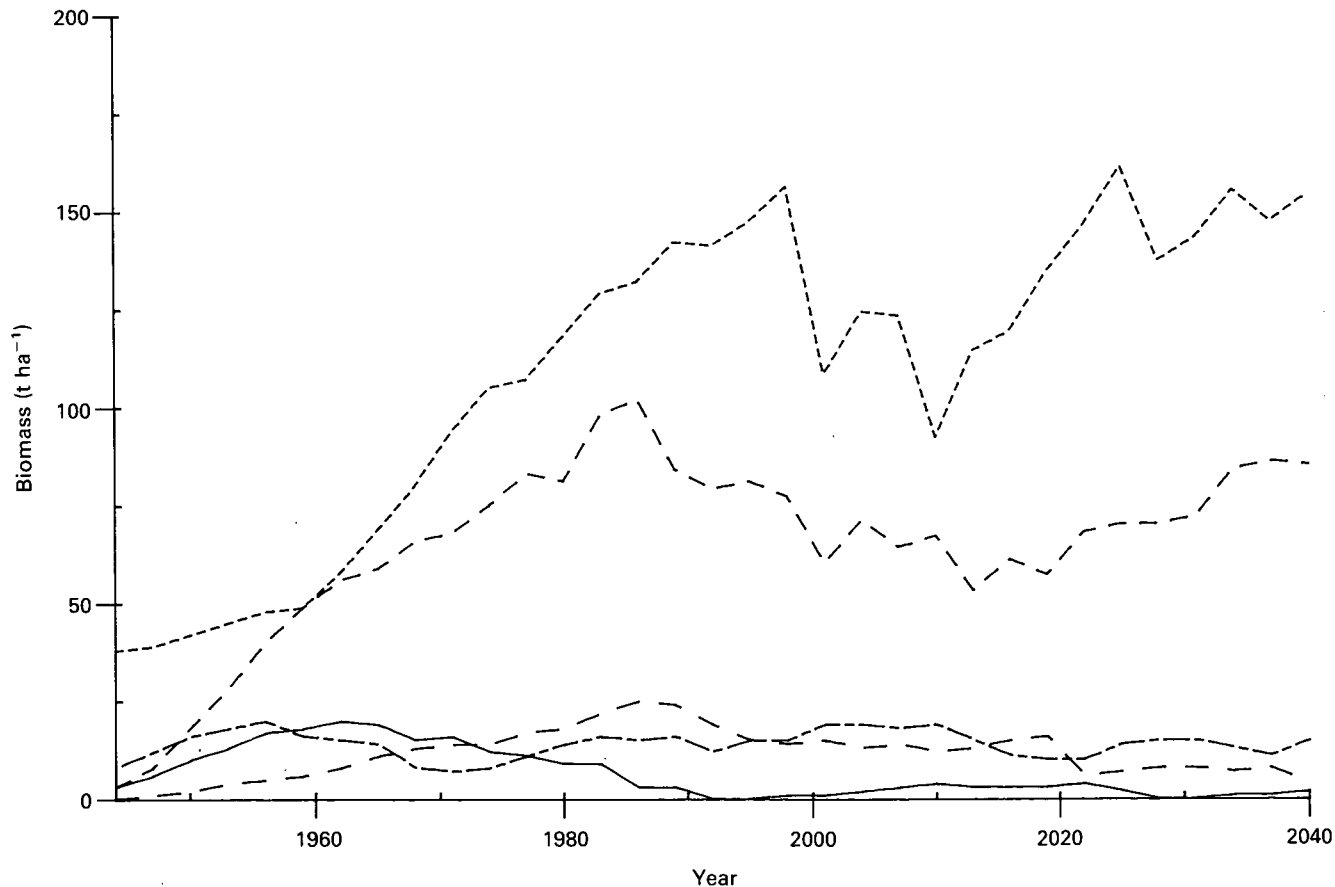


Figure 3. Trends in total biomass of each tree species in Meathop Wood, predicted using FORTNITE (---- *Quercus*; - - - *Fraxinus*; ——— *Betula*; - - - *Acer*; - · - · *Corylus*)

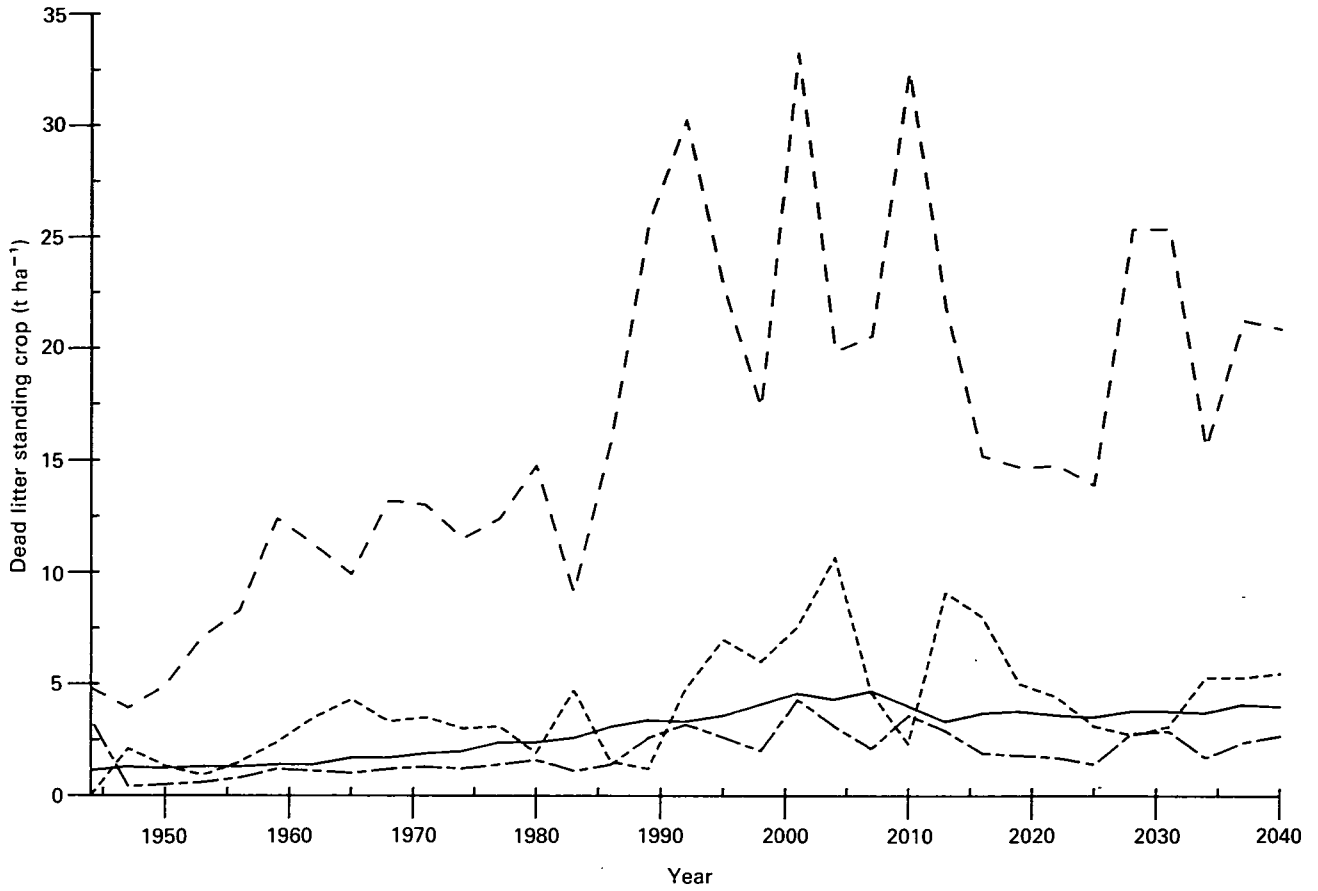


Figure 4. Trends in forest floor components and dead wood in the canopy of Meathop Wood, predicted using FORTNITE

(... wood on forest floor; --- large wood in canopy; - - - rootwood; — fine roots)



Figure 5. Effects on the biomass of Quercus and Fraxinus, predicted using FORTNITE, of the removal of Acer stems

(— Quercus; ... Fraxinus; - - - Acer; --- after removal of Acer)



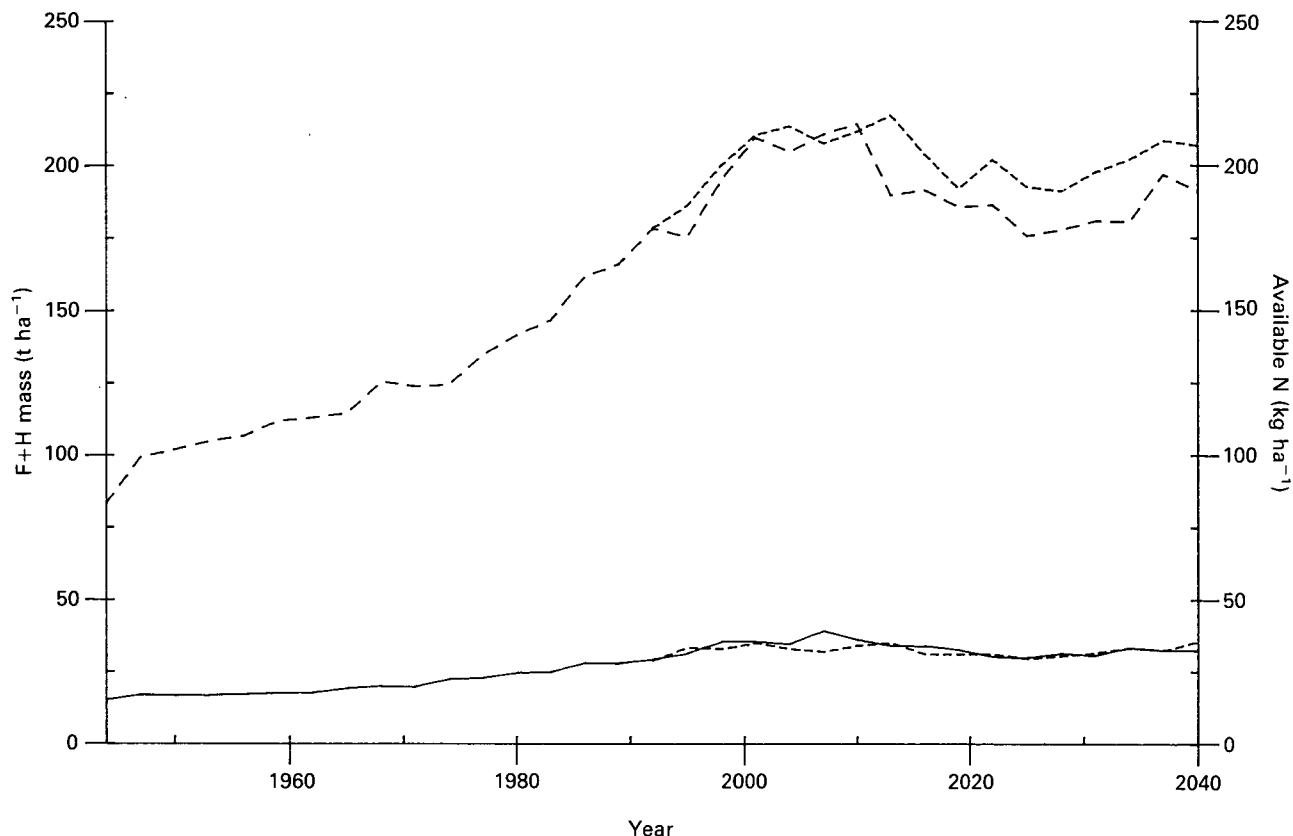


Figure 6. Effects on the amounts of F+H layer material and available nitrogen in the soil, predicted using FORTNITE, of the removal of Acer stems (— F+H layer; - - - available N; - · - after removal of Acer)

*Fraxinus* and *Quercus* trees, thus improving the potential yield of the more important timber.

### 5 Conclusions

From this limited application of the simulation model FORTNITE to the Meathop woodland data, our conclusions are that it has considerable potential. Not only can it be used to integrate data from various forest studies in a dynamic way, thus enabling a more thorough examination of the research information, but it can also be applied, as Aber and Melillo (1983) indicate, to predict the potential long-term effects of forest management practices on forest ecosystems.

We would recommend that this model is considered as a means for (i) integrating the research data, and (ii) developing scenarios on the effects of various management practices in the Changbai Mountain Reserve.

### 6 Acknowledgements

We are particularly grateful to J M Sykes and R G H Bunce of the Institute of Terrestrial Ecology, for providing basic data on the tree growth parameters from which the relationships with dbh were derived, and in addition the tree production data (Table 4) for comparison with the model outputs.

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