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Investigations of the ecosystem energetics of an English woodland

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Investigations of the Ecosystem Energetics

of an English Woodland

by

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ACKNOWLEDGMENTS

SUMMARY

INVESTIGATIONS OF THE ECOSYSTEM ENERGETICS OF AN ENGLISH

WOODLAND

1. Energy flow and accumulation in the aboveground parts of an

    alder-birch woodland in County Durham were studied between

    April 1966 and April 1968.   Dry matter transfers and accumulations

    were measured and converted to energetic data by the use of

    calorific equivalents.   It was shown that only calorific values

    appropriate to a particular category of material and season

    provide adequate calorific equivalents.

2. Tree net aboveground primary production was $3574Kcal/m^2/year$.

    $2417Kcal/m^2/year$ (68.0%) was wood, $901Kcal/m^2/year$ (25.0%)

    canopy leaves, $232Kcal/m^2/year$ (6.4%) other parts, and

    $24Kcal/m^2/year$ (0.6%) loss to herbivores.

3. Tree litter fall was approximately $1450Kcal/m^2/year$ in both study

    years.   66.0% was alder and birch leaves, 19.2% small wood, and

    14.3% other litter.   Seasonal changes in canopy biomass,

    biocontent and Leaf Area Index were demonstrated.

4. Ground vegetation net aboveground primary production was $1016Kcal/$

    $m^2/year$ in 1966-7 and $1142Kcal/m^2/year$ in 1967-8.   Ground

    vegetation litter was 40% to 50% of total litter production.

    This component was measured by a modified Paired Plots Technique.

5. Forest Floor Litter disappearance was normally 2500Kcal/m^2/year.

6. Total ecosystem plant biocontent (without roots) was near 86,000Kcal/m^2, 54% was stored as wood, 42% as litter and soil organic matter. Net accumulation of energy was established only in tree wood (+2,200Kcal/m^2/year).

7. Insolation was measured by Monteith solarimeters and an integrator developed in this study. Incident shortwave radiation was 818,490Kcal/m^2/year. Net photosynthetic efficiency (aboveground) was 0.58%. The tree stratum fixed 0.64% of energy incident in its growth season; lower strata fixed 0.52% of the energy reaching them.

8. Net Primary Production (aboveground) was approximately 4750Kcal/m^2/year. Net Ecosystem Production was normally near 2300Kcal/m^2/year (48.9% of NPP).

9. The methods used were critically appraised and perspectives for future work outlined.

CONTENTS

Chapter III.   Ground Vegetation and the Forest Floor

Chapter IV.   Ecosystem Energetics

CHAPTER I

INTRODUCTION AND BASIC DATA

Section I   Introduction

1. Ecosystem Energetics

The processes by which biological systems retain their integrity are energy-requiring.   Ecosystems are the most complex level of biological organization, representing the totality of the myriad interrelationships between and within the biota and physical environment in a given area.   The quantitative study of energy fixation, partition and dissipation by ecosystems is thus of fundamental importance and interest to biology.

In particular, an understanding of the energetics of long-term change in ecosystems is essential for the development of a predictive theory of environmental management.   The development of such a theory depends not only on information on natural successions, but also on those chains of events starting with catastrophe or management.   In fact the evidence presented by Raup (1964) suggests that rarely, if ever, does the ecosystem standing on any substantial tract of land or water reach or maintain a state which may be described as a climax.   The reason for this is the irregular but frequent (on an ecological time-scale) occurrence of natural catastrophes such as hurricane, fire and pestilence.   Man's actions often seem to act in a similar way, for example in shifting cultivation.

Thus real ecosystems do not usually represent a simple time-series of successional stages from a pioneer to a climax ecosystem. Rather they represent the interaction between the causal relationships implied by ecosystem energetics and the consequences of the latest natural catastrophe or management practice, in terms of mineral supply, radiation climate and viable species available within the relevant area.

With the advent of global pollution it seems unlikely that any real situation with which ecology will be concerned will not be either the product of a 'natural' catastrophe or of 'management'. Therefore it is important to obtain data for energy fixation, partition and dissipation in real ecosystems at various stages of development from various starting points. Only when such data are available can the causal relationships implied by the energetics of the ecosystem be elucidated.

In order to understand the changes taking place in the trophic energetics of an ecosystem it is necessary to define its important components and to measure their contributions to energy accumulation and flow (both to other parts of the ecosystem and to the heat sink). This is because the stresses imposed on the ecosystem by catastrophe or other changes are rarely equal in their impact on all parts of the ecosystem (e.g. fire in the Brookhaven Forest, Whittaker & Woodwell 1969). It is reasonable to predict that the resilience of an ecosystem will depend, at least in part, on the availability of energy and nutrients from

its stores and on the time-scale of this availability. Therefore,
the various forms in which energy and nutrients are stored in the
several components of an ecosystem are of fundamental relevance
to a theory of ecosystem development.

The problem is, how are the parameters relating to
energy accumulation and flow to be measured?

I.2 The basic approach

It is clear that methods for the measurement of energy
flow and accumulation must depend on the nature of the system
concerned. Thus the methods adopted for a nannoplankton system
(Odum et al 1959) differ widely from those for a woodland
(Whittaker & Woodwell 1969). However, certain considerations
derived from woodland studies (Whittaker & Woodwell, op cit) are
of general relevance. Thus considering first the plant community

$$NPP = GP - Rs_A \qquad (Kcal/m^2/yr)(1)$$

where NPP is net primary production,

GP is gross primary production

and Rs_A is respiration of the plant community.

For the entire ecosystem

$$NEP = GP - (Rs_A + Rs_H) \quad (Kcal/m^2/yr) \quad (2)$$

where NEP is net ecosystem production

and Rs_H is respiration of heterotrophs.

Hence,

$$NEP = NPP - Rs_H \qquad (Kcal/m^2/yr)$$

NEP is a measure of ecosystem energy accumulation. The sum $(Rs_A + Rs_H)$ is a measure of rate of energy dissipation. Whilst Rs_A will vary with ecosystem bulk and radiation climate, Rs_H relative to NEP is a measure of the relative importance of dissipation of stored energy in the trophic scheme. Therefore it is valuable to differentiate between Rs_A and Rs_H. In fact, the basis of an ecosystem energetics study must be the measurement of rate of storage (NPP), net rate of accumulation (NEP) and heterotroph respiration (Rs_H). Autotroph respiration (Rs_A) is more difficult to measure and it is possible to construct a preliminary sketch of energy-flow relevant to ecosystem development theory without it. It must eventually be measured, but its measurement will not figure in this thesis.

The currently accepted basis for the calculation of NPP, NEP and Rs_H is the measurement of dry matter production and loss and the subsequent conversion of this data to energy terms by the use of caloric equivalents. This approach was used here, and its validity will be re-examined in Section XI.

I.3 The choice of study ecosystem

It is a commonplace observation that steady-state ecosystems are difficult or impossible to find, even if a satisfactory definition of them is thought to be available. More important are ecosystems representative of commonly existing types, or of types likely to increase in importance. The practice

of sustained coppicing of woodland in England has existed for
several hundreds of years.   Consequently considerable areas of
woodland exist which are still being managed in this way, or
have recently been so.   It was of interest to examine a woodland
where this practice had stopped and where there was no evidence
of previous cultivation other than coppice management.   Thus a
coppice woodland standing on a soil profile showing no evidence
of tillage, but rather of a low moor succession before forestry
(Hornung, pers.comm.), was chosen.   This woodland was also the
site of intensive studies of the energetics of forest floor and
soil invertebrates being carried out concurrently by members of
the Zoology Department.   This afforded opportunities for common
environmental observations and collation of data on an ecosystem
basis.

I.4 The plan of this thesis

        The thesis contains four chapters.   The first contains
this Introduction and basic data relating to the Study Area and
the caloric content of plant material.   Chapter Two gives the
data for tree biomass and net production, Chapter Three for
ground vegetation and the forest floor;   Chapter Four is a summary
of the ecosystem energetics of this system as far as the data
obtained allow and an assessment of the validity of the conclusions
reached.

SectionII   The Study Area

II.1 Position and Topography

The study area, on Lord Londonderry's Estate at Wynyard, 19km southeast of Durham City, County Durham, was located in the section known as Newton Hanzard Plantations (National Grid Reference NZ425288).   This land belonged to the Wynyard Estate for at least 120 years.   Since 1952 a large part of the estate, including Newton Hanzard, has been managed by the Forestry Commission, although the Estate retains overshooting rights.   Most of the 4,940 hectares managed by the Forestry Commission comprises mixed woodland, much of it, including the Study Area, managed solely as shooting cover.   The Study Area was some distance from the public roads and was thus free from unwanted human interference.

The Study Area was bounded on two sides by a forest ride, on another by a boundary fence next to arable land, and on the fourth side by a 20 year old plantation of birch.   Its area was approximately 2ha.   A grid of eight 20 by 20m squares (area 0.32ha) was marked out near the northern end of the Study Area.   The squares were separated and surrounded by 2m wide paths.   Within this grid much of the destructive and other sampling was carried out, both in this study and in those on various animal populations.

The Study Area was at approximately 67.1 metres (220ft) above O.D. and lay in a slight hollow in the undulating landscape

of southeast Durham with a slight eminence 1km to the W.N.W. and a deep ravine running N.S. 300m to the east. A stream ran down the ravine. Fig.1 shows the topography of the Grid giving 0.2m contours upwards from an arbitrary level (0.0) near its southern edge. The ground sloped gently down from the north-eastern corner of the Grid towards the south. A drainage ditch cut through the Study Area, just southwest of the Grid, and flowed most of the former's length, and joined the ditch which drained the ride forming the southern boundary of the Study Area. A few metres from 'H', a 13m high scaffolding tower was erected; this is described in Section IX.

On all sides the Grid was buffered by a belt of Study Area. This belt was 70m wide to the west, where the outer boundary was with arable land. To the south it was 150m wide, to the east it was only 14-20m wide, but the boundary here was only a narrow forest ride separating the Study Area from a very similar vegetation. To the north the belt was 23m wide, and again no great edge effects were expected as the plantation of young birch was 5 to 6m high and extremely dense.

II.2 Geology, soil and forest floor

Magnesian limestone formed the rock layer beneath the thick deposit of boulder clay which is characteristic of the region. To determine the extent of soil structure variation within the Grid, pits were dug to a depth of approximately 1m

Figure 1.

Topography of the Grid. Contours at 0.2m upwards from an
arbitrary level (0.0).

NEWTON HANZARD STUDY AREA

20 M

N

R
I
D
E

TOWER → X

DITCH

1.2
1.0
0.8
0.6
0.4
0.2
0
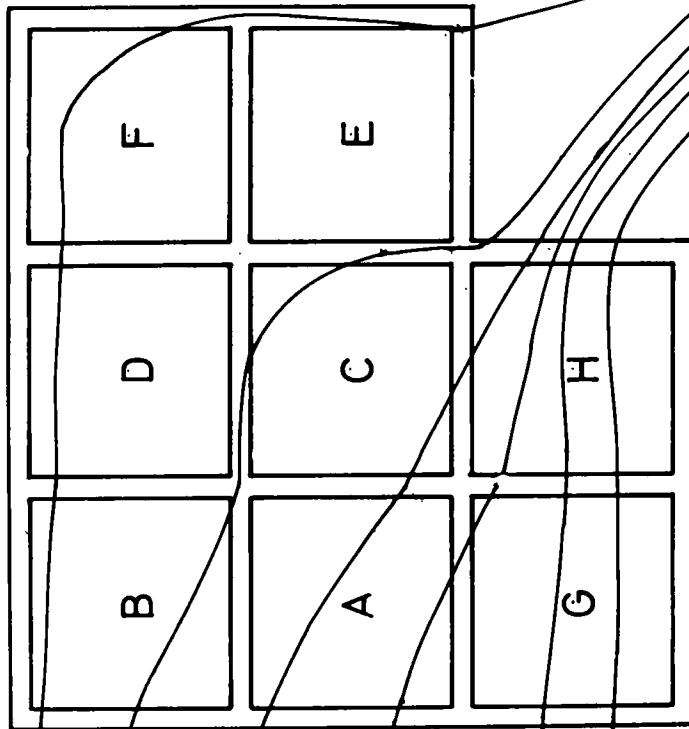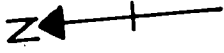
A B C D E F G H

to expose the soil profiles beneath the main vegetation types.
For this purpose the types were 'Dryopteris/Rubus' under
predominantly alder cover, and 'Dryopteris/Rubus', 'Grassy' and
'Pteridium' under predominantly birch cover.   Although 'Pteridium'
was not widespread in the Study Area, this soil profile was
described because of its differences from the others investigated.
Using the classification of Taylor & Pohlen (1962) the profiles
are characterized in Table I.

Depths were measured from the surface of the discernable
maximum litter cover.   The soil profile for 'Dryopteris/Rubus'
under predominantly birch tree cover was similar to that under
alder although the A_1 horizon was a lighter coloured soil of
higher clay content.   The Grassy type under birch cover did not
show a distinct O_2 horizon, the dead grass material forming a
dense matt along with bryophytes, upper roots and birch debris.
The 'Pteridium' type showed well-developed O_1 and O_2 horizons
lying directly on a heavily gleyed boulder clay.

The water table lay between 15 and 30cm below the soil
surface for most of the year (P.J. Bolton, pers.comm.) although
during the wetter periods, particularly in winter, it often reached
the surface.   This may account for the total lack of an A_2 horizon
on the Grid.

In summary, throughout most of the Grid the soil was
largely an upper clay or clayey loam lying on a gleyed boulder
clay.   A more exhaustive description of the soils of the Grid

TABLE I. SOIL PROFILES

ALDER COVER

DRYOPTERIS/RUBUS TYPE

LAYER	DEPTH	COMMENTS
O_1 or L	: 0 to 0/1.5cm;	depth varies according to season. Plant debris.
O_2(F+H)	: 0/1.5cm to 1.5cm;	Variable depth, never extensive
A_1	: 1.5cm to 14/16cm;	Dark clay loam
A_2	: ABSENT	
$A_3 + B_1$	: 14/16cm to 20/22cm;	Transitional
B_2	: 20/22cm + ;	Gleyed Boulder clay

BIRCH COVER

DRYOPTERIS/RUBUS TYPE

LAYER	DEPTH	COMMENTS
O_1 or L	: 0 to 0/1.5cm;	depth varies according to season. Plant debris.
O_2(F+H)	: 0/1.5cm to 1.5cm;	Variable depth, never extensive
A_1	: 1.5cm to 14/16cm;	Lighter coloured clay soil
A_2	: ABSENT	
$A_3 + B_1$	: 14/16cm to 20/22cm;	Transitional
B_2	: 20/22cm + ;	Gleyed Boulder clay

BIRCH COVER

GRASSY TYPE

LAYER	DEPTH	COMMENTS
$O_1 + O_2$	: 0 to 4/7cm;	Dead grass material and sparse Birch debris
A_1	: 4/7cm to 14/16cm;	Lighter coloured clay soil
A_2	: ABSENT	
$A_3 + B_1$	: 14/16cm to 25/30cm;	Transitional
B_2	: 25/30cm + ;	Heavily gleyed Boulder clay

BIRCH COVER

PTERIDIUM TYPE

LAYER	DEPTH	COMMENTS
O_1	: 0 to 4cm;	Dead fronds of Pteridium
O_2	: 4cm to 9/12cm;	Slowly decomposing fronds
A_1	: ABSENT	
A_2	: ABSENT	
$A_3 + B_1$	: ABSENT	
B_2	: 9/12cm + ;	Heavily gleyed Boulder clay

was made by P.J. Bolton (1969) with whom the soil profile
studies were carried out.

The Forest Floor (Ovington 1954) was rather complex,
being composed of the decaying remains of the various parts of
several dozen plant species.   As in a mull, the tree leaf
litter disappeared almost completely within one year.   As in a
more, the dead parts of several species, and fallen wood,
persisted for several years.   Whilst somewhat patchy, the forest
floor could be described as a mor, consisting of a dense carpet
of plant remains.   There was a more or less marked boundary
between the organic material and the mineral soil.   This boundary
was intermittently interrupted by mull-like patches, where an
intricate mixture of humus and mineral soil was observed, but
such patches were neither common nor extensive.

Samples of the Forest Floor from each soil type were
taken to the laboratory so that the pH determinations might be
made.   The measurements were made on a pulp consisting of 100gms.
Forest Floor material and 50mls distilled water.   Ten replicates
were used for each soil _kind_ ~~type~~.   Table II shows the mean pH $\pm$ 1 SE,
for each soil _kind_ ~~type~~.   The Forest Floor under 'Pteridium' was most
acid;   under the predominant 'Dryopteris/Rubus' type throughout
the grid it was only slightly less acid, and under grass cover
it was markedly less acid.

II.3 Climate

Complete meteorological records were not available for

TABLE II. FOREST FLOOR   pHs

FOREST FLOOR TYPE	Means of 10 pH detns. $\pm$ 1 S.E.
1. DRYOPTERIS/RUBUS (ALDER COVER)	4.70 $\pm$ 0.04
2. DRYOPTERIS/RUBUS (BIRCH COVER)	4.75 $\pm$ 0.02
3. GRASSY (ALDER COVER)	5.00 $\pm$ 0.06
4. GRASSY (BIRCH COVER)	5.50 $\pm$ 0.05
5. PTERIDIUM (BIRCH COVER)	4.50 $\pm$ 0.05

the Study Area. However, measurements of incident short-wave radiation were made from 1st May 1967 to 1st May 1968 and these are described in Section X. Rainfall records kept by the Hartlepool Water Company at the Crookfoot Reservoir 2km distant from Wynyard were used to supplement the more complete records kept by the Durham University Observatory. The Durham University Observatory is 102.4m (336ft) above O.D.; the rain gauge at Crookfoot 89.3m (293ft) above O.D.; and the Study Area 67.1m (220ft) above O.D. Table III summarizes the meteorological data for 1966 and 1967 and compares them with the long term averages. These averages of temperature, rainfall and sunshine refer to the standard period 1906-1935. Average wind speeds are for 1938-1947. Figures show mean temperature, sunshine and rainfall at Durham in 1966 and 1967 (after DUO Daily Meteorological Observations, 1966 and 1967).

The climate of central and southeastern County Durham is much as one would expect in the cool temperate zone. The region lies to the east of the Pennines, so that rainfall at Durham and Crookfoot is relatively low. The two stations showed similar rainfalls and extreme conditions rarely occur; it thus seems reasonable to assume that even the fluctuations in conditions noted at the meteorological stations will be less marked within the woodland vegetation of the Study Area.

TABLE III.   SUMMARY OF METEOROLOGICAL DATA FOR THE YEARS 1966 & 1967 COMPARED WITH AVERAGE

	Durham University Obsergatory			Crookfoot Reservoir		
	1966	1967	Av.	1966	1967	Av.
Temperature (°C)						
Mean daily maximum	11.7	12.4	11.9	-	-	-
Mean daily minimum	4.7	4.8	4.4	-	-	-
Mean	8.1	8.6	8.1	-	-	-
No. of ground frosts	128	95	-	-	-	-
Rainfall (inches)						
Annual total	30.04	28.26	25.60	31.85	29.69	24.90
No. of rain days	212	184	-	221	197	-
No. of days with snow lying at 0900hrs	33	9	-	-	-	-
Sunshine (hrs)						
Total for year	1124.3	1371.1	1318.0	-	-	-
Mean daily amount	3.08	3.76	3.61	-	-	-
No. of days with no recorded sunshine	93	61	-	-	-	-
Wind (m.p.h.)						
Mean wind speed	9.7	10.6	8.6	-	-	-

Figure 2.

Mean temperature, sunshine and rainfall at Durham, 1966.
(After DUO Daily Meteorological Observations)

Mean Temperature, Sunshine and Rainfall
Durham, 1966

mean temp. °C

— 1966
--- mean
· 1966 mean dly max
+ " " " min

15

0

mean daily sunshine (hours)

— 1966
--- mean

6
5
4
3
2
1

0

rainfall in inches

☐ 1966
— mean

6
5
4
3
2
1

j f m a m j j a s o n d
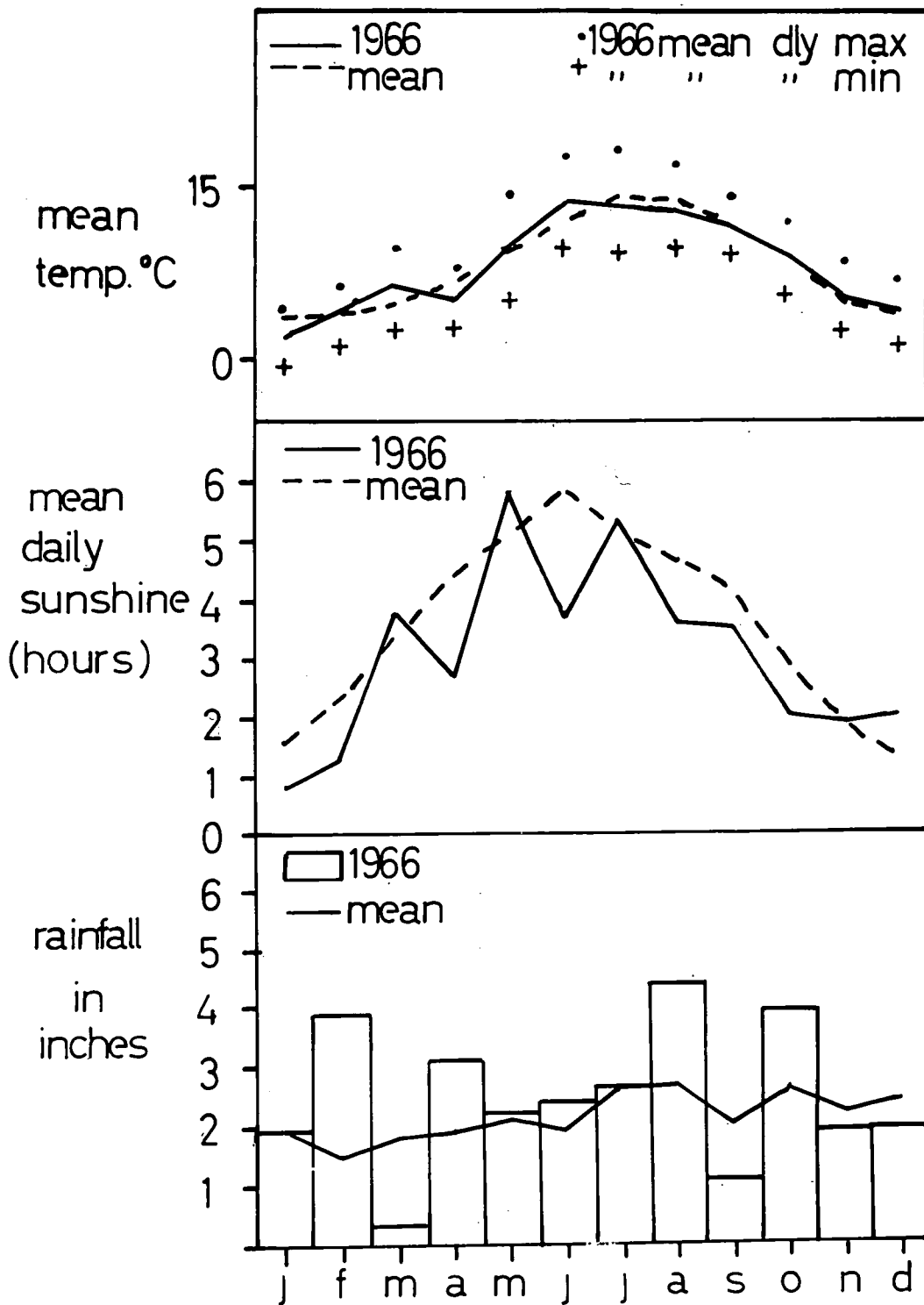
Figure 3.

Mean temperature, sunshine and rainfall at Durham, 1967.
(After DUO Daily Meteorological Observations)

Mean Temperature, Sunshine and Rainfall
Durham, 1967
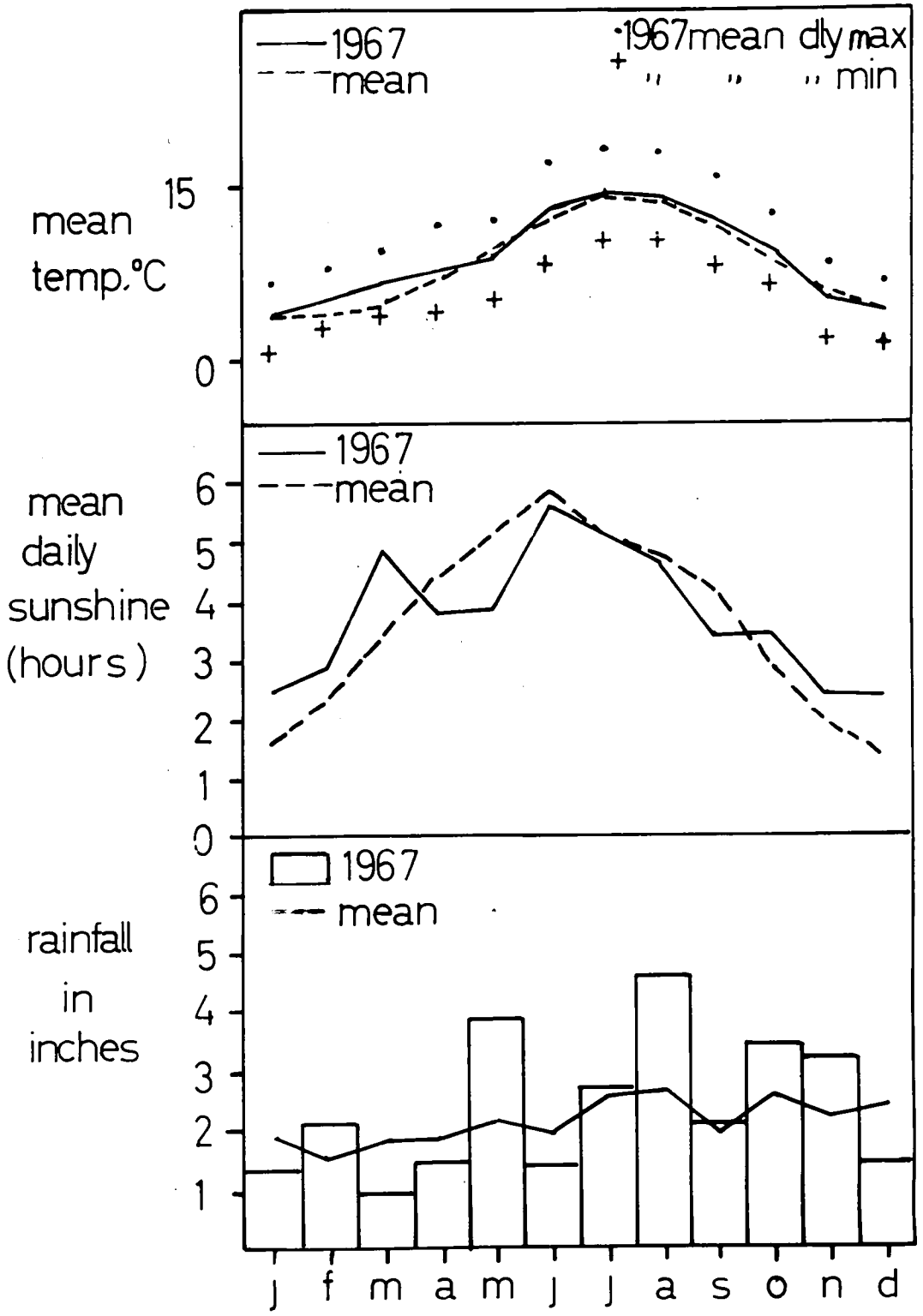
More detailed observations of the soil and forest floor temperatures were made by P.J. Bolton and S. Wignarajah respectively.

II.4 Vegetation

The vegetation in the Study Area could be called loosely an alder/birch wood. That is, the most numerous tree species were <u>Alnus glutinosa</u> (L) Gaetn. and <u>Betula pendula</u> Roth., <u>Acer pseudoplatanus</u> L. was present in small numbers. The Understorey consisted of widely dispersed young <u>B.pendula</u> Roth., <u>Crataegus monogyna</u> Jacq, <u>Sambucus nigra</u> L., <u>Rosa canina</u> agg. and <u>Quercus robur</u> L.. The field and ground layers, or Ground Vegetation as termed in this work, contained many more species than the upper strata. On inspection, the most important plants according to cover/abundance criteria were <u>Dryopteris filix-mas</u> (L) Scop. <u>Rubus fruticosus</u> L., sensu lato, <u>Chamaenerion angustifolium</u> (L) Scop. and several grass species. Also present were a variety of woodland herbs, including <u>Mercurialis perennis</u> L., <u>Viola riviniana</u> Rchb and <u>Ciraea lutetiana</u> L..

The Ground Vegetation was very well developed and constituted an important physiognomic characteristic of the woodland.

The detailed description of the vegetation of the Grid was carried out in two steps. Firstly, the tree species were enumerated and the diameter of the trunk at 1.3m above ground (d.b.h.) was measured for each tree where d.b.h. was greater than 2cm.

Secondly, cover/abundance estimates were made for the Understorey

and Ground Vegetation species in each of the eight 20 x 20 metres'

squares.   The species were listed according to their life-form.

Fig.4 shows the frequency distribution of the d.b.h.

of

a)   Non-coppiced stems

b)   Coppiced stems, for the 281 Alder stems on the Grid.   116

arose from 43 coppiced stools.   Fig.5 shows similar data for

Birch.   Of the 226 Birch stems on the grid, 77 arose from

32 coppiced stools.   The most striking feature of the Alder data

was the wide range of diameters in this woodland.   Alder normally

grows in even-aged stands;   therefore a narrow diameter distribution

could reasonably be expected.   In Section IV, data on the relation-

ship between tree diameter and age are presented;   these data cast

further light on the recent history of the tree populations.

From the relatively wide range of diameter data it may be deduced

that the coppicing of the population of alder led to regeneration

at several times in the life of the oldest trees.   The opening

up of the alder canopy in the Study Area by coppicing is considered

a necessary precondition of alder regeneration.   The wide diameter-

distribution for birch was not so noteworthy as it is already known

that :-

1)   even-aged birch trees may have widely different d.b.h's.

2)   birch regenerates well, within birch woods, which provide an

open canopy for this light-requiring species.

Figure 4.

Frequency distribution of alder diameter by 2 cm. classes.

Upper - coppiced shoots.
Lower - uncoppiced shoots.

DIAMETER DISTRIBUTION OF ALDER
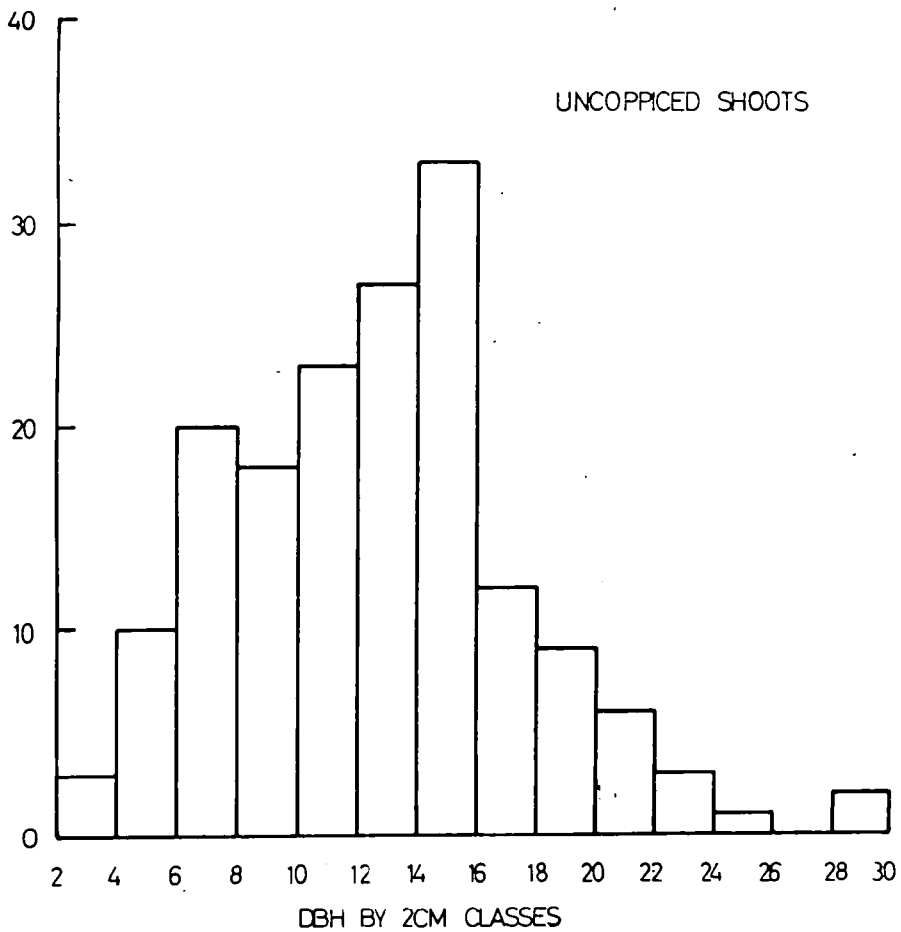
Figure 5.

Frequency distribution of birch diameter by 2 cm. classes.

Upper - coppiced shoots.
Lower - uncoppiced shoots.

DIAMETER DISTRIBUTION OF BIRCH

NO. TREES

COPPICED SHOOTS

UNCOPPICED SHOOTS

DBH BY 2CM CLASSES
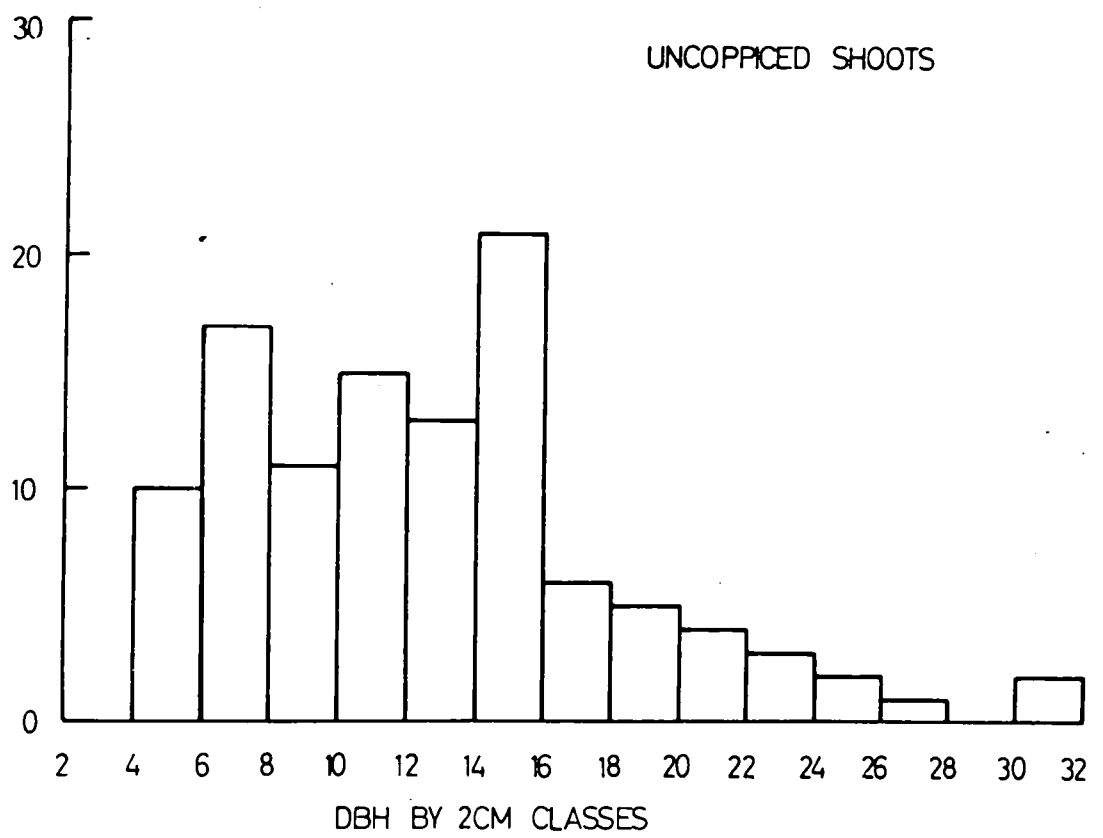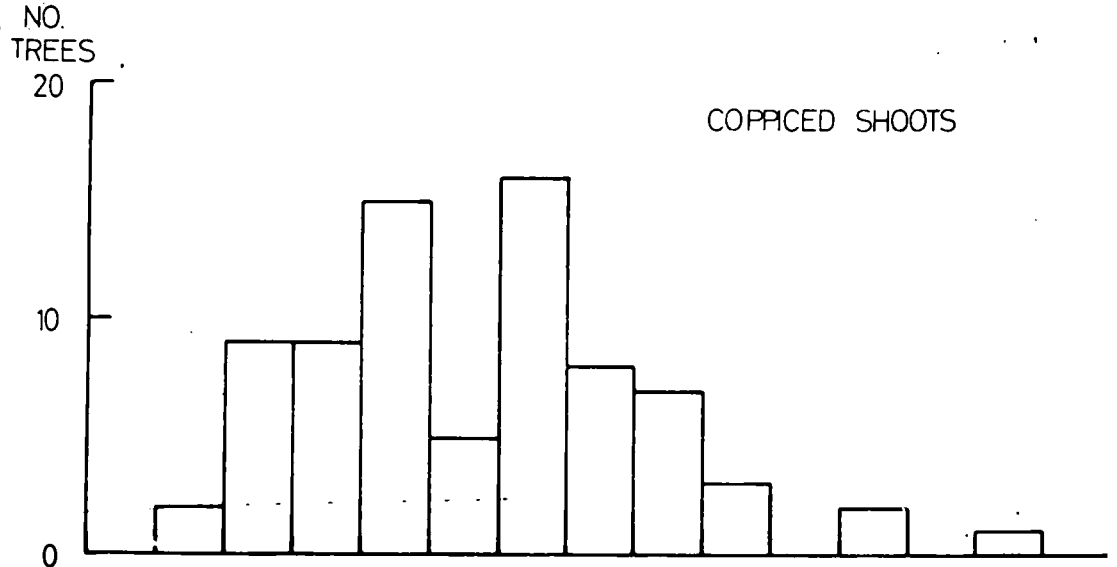
Figure 6.

Alder shoots per $10m^2$ on the Grid. In each square the
upper number is total shoots, the number in brackets
coppiced shoots.

Figure 7.

Birch shoots per $10m^2$ on the Grid. In each square the upper
number is total shoots, the number in brackets coppiced
shoots.

ALDER - SHOOTS /10M^2

–	–	–	10 (10)	–	4 (2)
13 (11)	10 (9)	10 (8)	–	–	–
18 (5)	29 (8)	7 (2)	2 (0)	3 (3)	–
18 (2)	26 (8)	17 (12)	21 (12)	8 (2)	–
10 (2)	20 (5)	13 (8)	8 (2)		
7 (2)	15 (4)	12 (2)	11 (4)		

BIRCH - SHOOTS/10M^2

7 (2)	11 (0)	8 (3)	14 (8)	4 (2)	20 (16)
6 (2)	7 (2)	6 (2)	9 (0)	21 (7)	17 (11)
1 (0)	1 (0)	11 (8)	13 (10)	5 (2)	4 (0)
—	1 (0)	2 (0)	2 (0)	4 (2)	4 (0)
—	2 (0)	5 (3)	4 (0)		
—	—	—	—		

Figure 8.

The division of the Grid into Alder and Birch Zones.

NEWTON HANZARD GRID
ZONE BOUNDARY

BIRCH

ALDER

B	D	F
A	C	E
G	H	
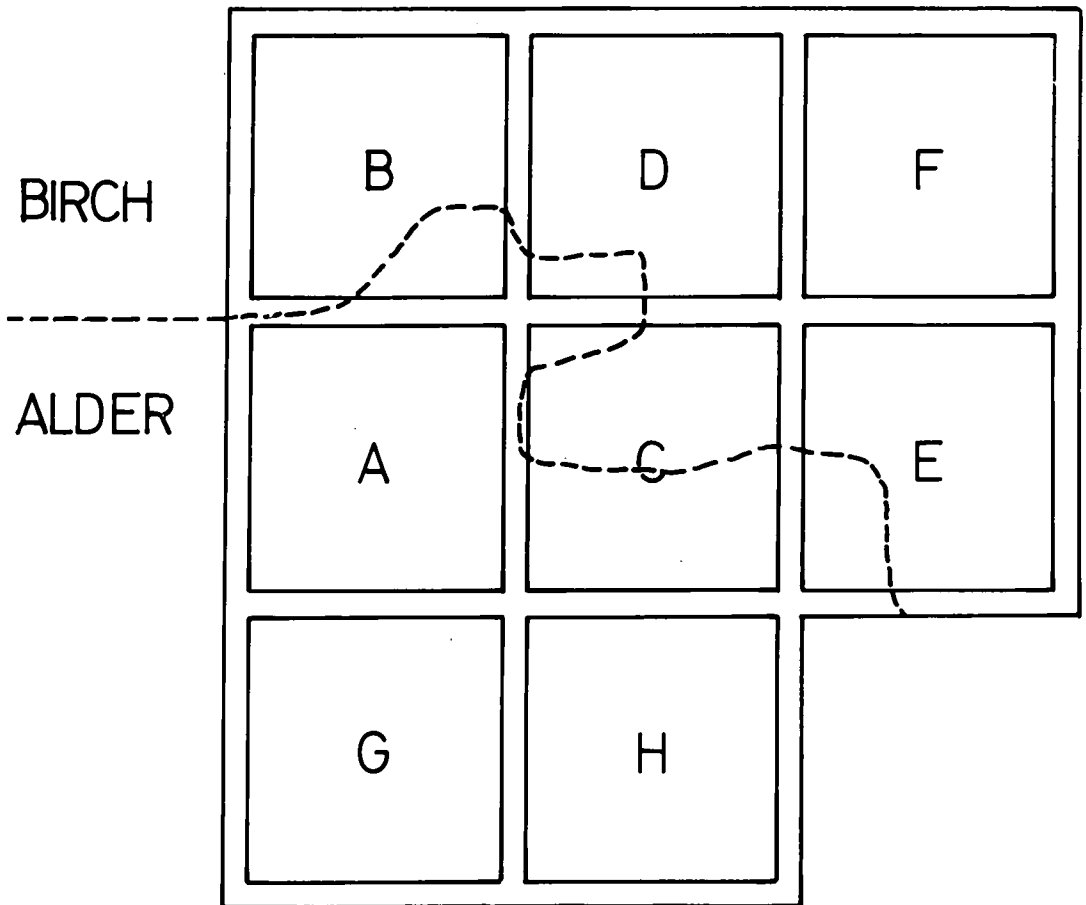
Figures 6 and 7 show the numbers of alder and birch stems respectively in the 32 10 x 10m squares which made up the Grid. In A, C, G and H, alder was most numerous, whereas in B,D,F, and E, birch was most numerous.   Throughout the Grid the canopy rose to about 12m.   In the predominantly alder areas it was almost completely closed.   In the predominantly birch areas it was much more open.   On the whole Grid there were 281 Alder stems, 226 Birch stems and 8 Sycamore stems.   Thus the tree density on the Grid was 1609 trees/ha.

Figs. 6 and 7 show that the Grid was divided into two areas, the Birch Zone and the Alder Zone.   Birch was generally more important to the northeast of the Grid, Alder to the south-east of the Grid.   Both species were present throughout the Study Area in almost equal numbers, but in the Grid a fairly clear pattern emerged.   The Grid was mapped into Alder and Birch Zones on the basis of tree distributions and physiognomic changes in the Ground Vegetation (Fig.8).   The winter and summer aspects of the birch and alder zones are shown in Fig.9 and 10.

Table IV shows Braun-Blanquet cover/abundance estimates for Understorey and Ground Vegetation Species in each of the 20 x 20m squares in each zone.   The species are listed according to Raunkaeir's (1934) life-form classification as given by Clapham, Tutin & Warburg (1962).   Leaving aside the mosses and leafy liverworts there were 21 Understorey and Ground Vegetation species in the Birch Zone, 20 in the Alder Zone;   whilst 14 occurred

Figure 9.

The Alder Zone.
Upper – winter aspect.
Lower – summer aspect.

Figure 10.

The Birch Zone.
Upper - winter aspect.
Lower - summer aspect.

TABLE IV.   BRAUN-BLANQUET COVER/ABUNDANCE ESTIMATES FOR UNDERSTOREY AND GROUND VEGETATION

SPECIES	Life-form	BIRCH COVER					ALDER COVER				
		B	C	D	E	F	A	C	G	H	E
Alnus glutinosa (L.) Gaertn.	MM	-	-	-	-	-	+	-	+	+	-
Betula pendula Roth.	MM	+	-	+	+	+	-	-	+	-	-
Acer pseudoplatanus L.	MM	+	-	-	+	-	+	-	+	-	-
Quercus robur L.	MM	+	-	-	+	-	-	-	-	-	-
Crataegus monogyna Jacq.	M	+	+	-	1	1	-	-	-	-	-
Sambucus nigra L.	M	+	+	-	+	-	+	-	-	-	-
Rosa canina agg.	M	1	-	1	+	+	+	-	-	-	-
Chamaephytes											
Poa trivialis L.	Chh or H$_s$	-	-	-	-	-	+	1	-	-	-
Hemicryptophytes											
Mercurialis perennis L.	H$_p$	-	-	-	-	-	-	1	-	+	1
Arrhenatherum elatius (L.) Beauv.ex J & C.Presl.	H$_p$	+	+	-	-	-	-	-	-	+	-
Holcus lanatus L.	H$_p$	-	-	-	-	-	+	+	+	1	+
Holcus mollis L.	H$_p$	-	-	+	+	+	1	1	1	+	+
Agrostis tenuis Sibth.	H$_p$	1	1	1	2	2	1	+	+	+	+
Ajuga reptans L.	H$_s$	-	-	-	-	-	+	-	-	+	+
Viola riviniana Rchb.	H$_s$	-	-	-	1	-	+	+	-	+	1
Potentilla sterilis (L.) Garke	H$_s$	+	+	+	-	+	+	+	-	+	+
Geum urbanum L.	H$_s$	-	-	-	-	+	+	+	+	-	+
Cirsium palustre	H$_s$	+	+	-	-	-	+	-	-	+	-
Deschampsia caespitosa (L.) Beauv.	H$_s$	+	1	+	1	+	-	+	-	-	-
Potentilla reptans L.	H$_r$	1	1	1	1	-	+	-	-	+	-
Chamaenerion angustifolium (L.) Scop.	H	1	1	1	1	+	+	+	-	+	+
Rubus fruticosus L. sensu lato	H	1	1	1	1	1	2	1	2	1	1
Dryopteris filix-mas (L.) Schott	H	1	1	1	1	1	2	1	2	2	1
Polystichum setiferum (Forsk.) Moynar	H	+	1	+	+	+	1	+	-	1	+
Geophytes											
Circaea lutetiana L.	Grh	-	+	+	-	-	+	+	+	+	+
Pteridium aquilinum (L.) Kuhn	Grh	1	1	-	-	1	-	-	-	-	-
Mosses											
Mnium hornum Hedw.		-	-	-	1	-	+	-	-	+	+
Polytrichum formosum Hedw.		-	+	-	+	-	+	-	+	-	-
Eurychium striatum (Hedw.) Schp.		-	-	-	+	-	+	-	+	-	-
Eurychium praelongum. (Hedw.) Hokk.		-	-	-	-	-	+	-	+	-	-
Dicranum scoparium Hedw.		-	-	-	-	-	-	-	-	+	-
Hypnum cupressiforme Hedw.		-	-	-	-	-	-	-	-	+	+
Dicranella heteromalla (Hedw.) Schp.		-	+	-	-	-	-	+	-	+	+
Thuidium tamariscinum (Hdw.) B & S		-	+	-	+	-	+	+	+	+	+
Fissidens bryoides Hedw.		-	-	-	-	-	-	-	-	+	-
Liverworts											
Pellia epiphylla (L.) Corda.		-	+	-	-	-	+	+	+	+	-
Lophocollea heterophylla (Schrad.) Dunn		-	-	-	-	-	-	-	-	+	-

<u>TABLE IV</u>   <u>KEY</u>

Life-form Classifications (From CTW, Flora of the British Isles,
after Raunkaeir)

Phanerophytes - woody plants with buds more than 25cm above soil level.

    MM - mega and mesophanerophytes - from 8m. upwards
     M -   microphanerophytes - 2 - 8m.
     N -   nannophanerophytes - 25cm - 2m

Chamaephytes (Ch) - woody or herbaceous plants with buds above the
soil surface but below 25cm.

    Chw - woody chamaephytes
    Chh - herbaceous "
    Chc - cushion plants

Hemicryptophytes (H) - herbs (very rarely woody plants) with buds
at soil level

    H_p - protohemicryptophytes - with uniformly leafy stems,
but the basal leaves usually smaller than the rest.
    H_s - semi-rosette hemicryptophytes - with leafy stems
but the lower leaves larger than the upper ones
and the basal internodes shortened.
    H_t - rosette hemicryptophytes, with leafless flowering
stems and a basal rosette of leaves

Geophytes (G) - herbs with buds below the soil surface

    Gb - with bulbs
    Gr - with buds on roots
    Grh - with rhizomes
    Grt - with root tubes
    Gt - with stem tubers and corms

Therophytes (Th) - annuals

CTW - Clapham, Tutin + Warburg (1962)

in both zones. Four moss and liverwort species were recorded in the Birch Zone and these and seven others occurred in the Alder Zone. There were more Phanerophyte individuals in the Understorey of the Birch Zone than of the Alder Zone. This was probably due in part to the open nature of the Birch canopy, but also to the falling out of Birch trees, making room for regeneration by other species.

Fig.11 shows the life-form spectrum of the flora of the Grid compared with those of a deciduous woodland in Germany and a Tropical Rain Forest in Guyana. The plants of the Rain Forest have their buds exposed, whereas those of the German and English Eorests more often have protected renewal organs. The differences between the Birch and Alder Zones are attributable to the canopy structure of the two species. What was remarkable was the relative lack of Geophytes at Wynyard, when compared with the deciduous woodland in Germany. This was probably due in large part to the high water table in the Study Area.

II.5 History of the Study Area

So far as can be discovered, no trees have been planted in the Study Area. Both alder and birch were common on the Wynyard Estate and probably 'drifted' into the Study Area without human interference. The presence of alder suggests that the area was open or clear-felled quite recently (within, say, 100 years). Alder does not usually regenerate itself, but coppicing and some

Figure 11.

Life-form spectra of the flora of the Grid compared with
a rainforest in Guyana and a deciduous forest in Germany
(Richards 1952).

Key: E - Epiphytes.
     P - Phanerophytes.
     C - Chamaephytes.
     H - Hemi-cryptophytes.
     G - Geophytes.
     T - Therophytes.

The figures against each life-form give the percentage of
the flora it represents.

LIFE-FORM SPECTRA

ALDER ZONE, WYNYARD   BIRCH ZONE, WYNYARD
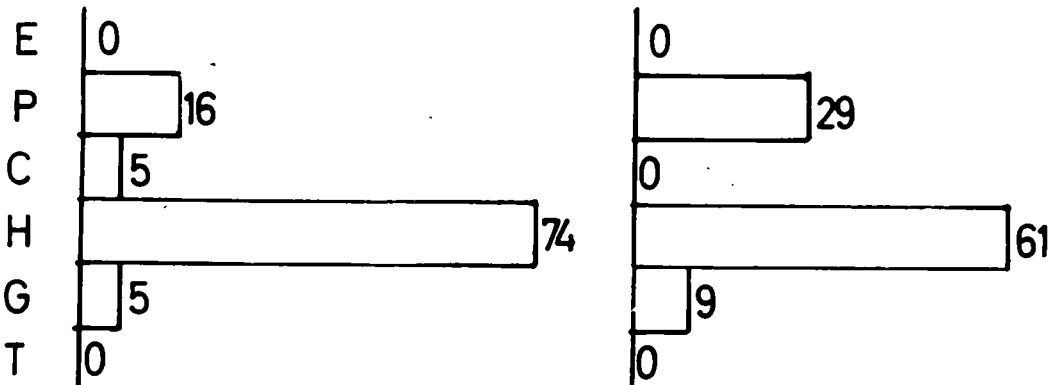
RAIN FOREST, GUYANA   GRID, WYNYARD
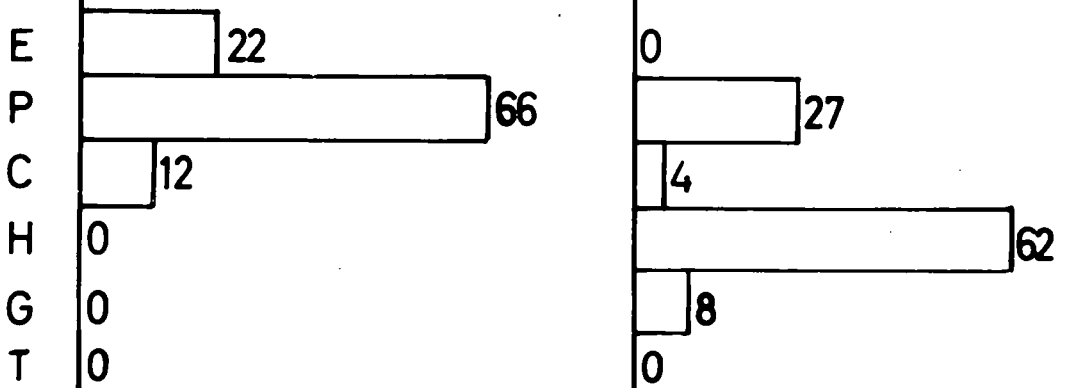
DECIDUOUS WOODLAND, GERMANY
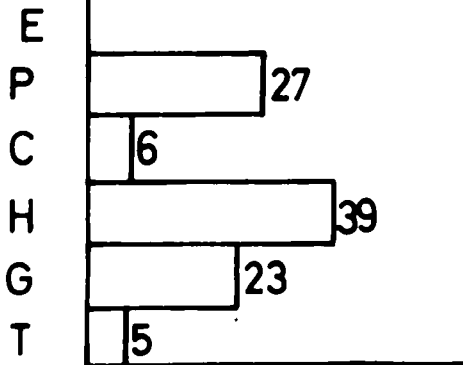
thinning has made this possible by opening up the canopy.

The ubiquitous birch probably drifted in at various times.

One very large birch (d.b.h. 32.5cm) was found in the southern

part of the Study Area and as it was dead, it was felled.   Ring

counts put its age at at least 110 years and it had probably been

dead for 10 years.   The birch was generally, though not exclusively,

found in the drier parts of the Study Area.

        The data on tree population age-structure are presented

and discussed in Section IV.

        Since 1952, when the Forestry Commission took over the

management of the Study Area, it has remained untouched.   Thus

the Ground Vegetation is an untampered with response to the

conditions existing in the alder/birch woodland.

Section III   Calorific Determinations

III.1 Introduction

Determination of the calorific values of ecological materials has received considerable attention (Cummins 1967; Golley 1961; Hadley & Kiekhefer 1963; Ivlev 1934; Kieckhefer 1962; Newbould 1967; Paine 1964; Phillipson 1964; Scott 1965; Slobodkin & Richman 1960; Teal 1957; Ovington 1961; Ovington & Lawrence 1967). Many authors determined calorific values in the course of ecological studies, but few made a critical assessment of the validity of using such values in ecological work. Scott (1965) pointed out that what is measured in these determinations is Heat of Combustion, the relevance of which to biology is that it represents the maximum energy which could be realised if the material were completely degraded by another organism. It gives a good estimate of the energy available in a non-conservative growth reaction. It is not a strictly accurate estimate, as it is derived under conditions of constant volume and temperature if an oxygen bomb calorimeter is used, whereas biological reactions take place at approximately constant pressures and temperatures.

In studies of the trophic energetics of ecosystems, or ecosystem components, the calorific content of materials, along with dry matter data, may be used to investigate the accumulation of energy at loci in the trophic matrix and the transfer of energy between such loci. This is the main use made of calorific values in this study.

Cummins (1967) pointed out the narrow range of calorific values possible for living material and within this range documented the variation in calorific values both within and between species dependent on season of collection, reproductive condition, and other factors. The errors involved in dry matter determinations of the kind outlined in I.2 are often large. It has been argued (Newbould 1967) that it may be most realistic to use a median calorific value, for example for plant material. In studies where an overall estimate of, for example, energy accumulation is required, this may be an adequate approach. However, if the study of energy transfer between 'Trophic levels' is envisaged, or if some indication of the phenology of energy transfer is required, it is clear that calorific determinations should be carried out on the relevant ecosystem components at all appropriate times.

In this study per gram dry weight calorific values (referred to below as Gross Calorific values) are used for the conversion of dry weight data to energy data; per gram ash-free dry weight data (referred to below as Ash-Free Calorific Values) are used for the comparison of materials from various ecological positions and taxa, and the tracing of the phenology of certain energy transfers, both within and between ecosystem components.

III.2 Collection and preparation of materials

The materials used in calorific determinations were collected in the course of the dry-weight determinations described

in later chapters. The principles applied in the choice of materials were as follows. Firstly, in the case of materials where there was a high standing crop and a good chance of seasonal changes in calorific value, samples were taken at intervals during the season (alder and birch canopy leaves, falling leaves, forest floor litter and the more important ground vegetation species). Those materials not important in terms of dry matter accumulation or transfer were dealt with only once (i.e. other trees, bryophytes, forbs and minor litter components). The most persistent materials were dealt with only once as no great seasonal change in calorific values was expected (i.e. bole and branch materials). Litter materials with a long residence time were analysed on only one or two occasions (fern, grass and bramble litter). As the Ground Vegetation litter of previous years comprised a large part of these latter materials no marked seasonal changes in calorific values were expected.

After collection the bryophyte material was dried for 24 hours at $85^{o}C$; the woody material was dried at $105^{o}C$ to constant weight; the other materials were dried for 24 hours at $105^{o}C$. The lower temperature was used for bryophytes so as to reduce the loss of, for example, lipids which form a greater part of their weight than for other plants. The dry material was milled to a fine powder in a Wiley mill and passed

through a 40 mesh-to-the-inch sieve. After thorough mixing

the plant powder was stored in a dessicator until required for

analysis. It was then dried for a further 24 hours at the

appropriate temperature and cooled in a dessicator. Three

pellets were made for each material, each weighing approximately

one gramme.

Each pellet was burned in a Gallenkamp Adiabatic

Bomb Calorimeter. The procedure followed was as detailed in

the manual for the Gallenkamp Adiabatic Bomb Calorimeter,

excepting that after combustion the crucible and its contents

were dried and weighed. Thus the proportion of the material

that was incombustible was calculated. This is presented below

as % ash and should be viewed with some caution, for this method

of ash determination does not have the accuracy of the muffle

furnace method. For any one material three replicates were

usually sufficient to give consistent gross and ash-free

calorific values.

III.3 Results

The results are listed according to the category of

plant material rather than according to the subsequent chapters

in which they are used.

Tree material - Alder

Table V shows the gross calorific value, % ash and

ash-free calorific value of the various alder materials according

to plant part, method of collection, and time of collection.

TABLE V. CALORIFIC VALUES FOR ALDER MATERIAL ($\pm$ 1 S.D.)

	Gross calorific value	% Ash	Ash-free calorific value
BOLE <u>TREE HARVEST</u> <u>SPRING 1968</u>	4540 $\pm$ 20	0.5	4565 $\pm$ 46
BRANCH <u>TREE HARVEST</u> <u>SPRING 1968</u>	5005 $\pm$ 22	1.1	5062 $\pm$ 34
LEAVES <u>DEFOL. STUDY</u>			
29. 5.67	5228 $\pm$ 23	4.2	5635 $\pm$ 45
29. 6.67	5179 $\pm$ 18	4.5	5423 $\pm$ 32
3. 8.67	4951 $\pm$ 19	3.7	5141 $\pm$ 27
17.10.66	4874 $\pm$ 18	4.7	5092 $\pm$ 22
<u>LEAVES, GREEN</u> <u>LITTER TRAPS</u>			
5. 8.66	4877 $\pm$ 18	4.2	5090 $\pm$ 37
17.10.66	4840 $\pm$ 17	4.8	5088 $\pm$ 33
7.11.66	4716 $\pm$ 14	3.6	5052 $\pm$ 24
<u>LEAVES, BROWN</u> <u>LITTER TRAPS</u>			
19. 9.66	4923 $\pm$ 19	4.3	5145 $\pm$ 32
17.10.66	5056 $\pm$ 21	0.5	5323 $\pm$ 25
7.11.66	5133 $\pm$ 23	3.7	5333 $\pm$ 40
17.11.66	5080 $\pm$ 19	3.4	5261 $\pm$ 19
LITTER <u>LEAVES</u> S/C			
Oct. 66	4874 $\pm$ 25	5.8	5174 $\pm$ 31
Dec. 66	4590 $\pm$ 18	8.0	4991 $\pm$ 27
Feb. 67	4900 $\pm$ 19	6.3	5229 $\pm$ 22
May 67	4676 $\pm$ 19	8.5	5111 $\pm$ 23
<u>SCALES</u> <u>LITTER TRAPS</u>	6096 $\pm$ 27	3.2	6296 $\pm$ 30
<u>CONES</u> <u>LITTER TRAPS</u>			
8.11.66	5479 $\pm$ 22	1.9	5585 $\pm$ 25

Figure 12.

Seasonal changes in ash-free calorific values of alder leaves.

Key: open circles - canopy leaves.
    closed circles - falling leaves - brown.
    plus signs - falling leaves - green.
    crosses - forest floor litter.

95% confidence limits are shown.

ASH-FREE CALORIFIC VALUES OF ALDER LEAVES
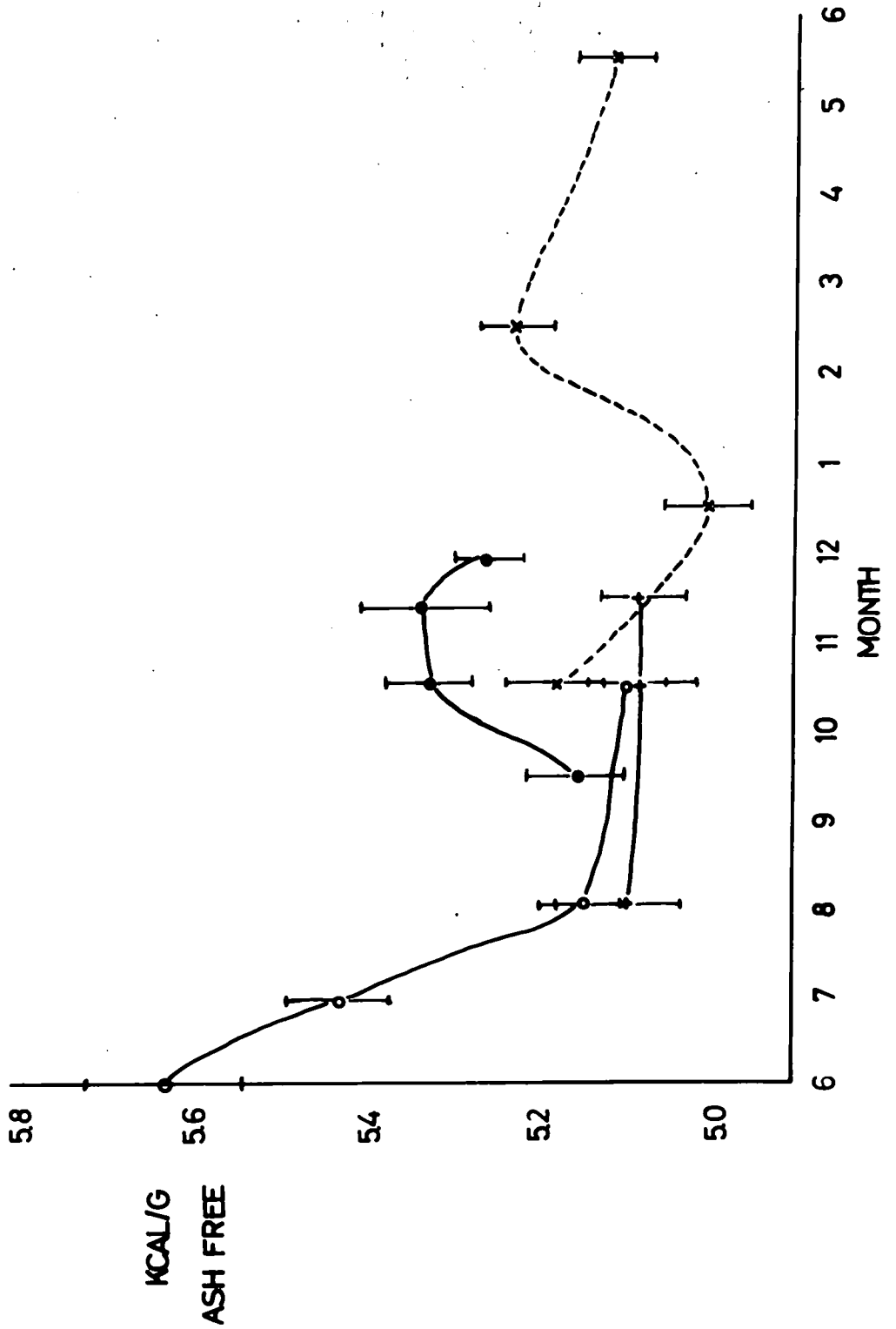
Each value is accompanied by one standard deviation. The branch wood had a markedly higher calorific value than the bole. This had the effect of increasing the relative importance of the branches as an energy store. The reproductive structures and scales also had high calorific values; this can be explained by their high lipid content. Fig.12 shows the seasonal changes in ash-free calorific value of alder leaves. The most dramatic change was the decrease in calorific value of the leaves on the canopy through the season. Morrison (1949) reported that in many plants the percentage of crude protein in the green foliage decreased, that of crude fibre (largely carbohydrate) and nitrogen-free extract increased, while that of ether extract (partly fat) remained constant throughout the growing season. Hence the calorific value of the foliage should be higher in the spring than in the autumn. This was clearly the case.

The ash-free calorific value of those leaves which fell green corresponded closely to that of those remaining in the canopy. However, at the time of maximum leaf-fall (October - November), the calorific value of brown leaves falling was considerably higher than that of leaves remaining in the canopy. That is, the processes associated with abcission brought with them an increase in the calorific value of leaf material.

Once on the ground (forest floor litter, collected during S/C determinations) the ash-free calorific value of the leaves at first decreased and then increased during January and

February. As the complex processes of leaching and decomposition are not well understood it would be rash to hazard any detailed explanation here. It may be suggested that the first decrease was due to the normal processes of microbial decomposition but that the low temperatures in December, January and February slowed these down. During this period the selective loss of low energy compounds by leaching became more important so that the ash-free calorific value increased. In the late spring the balance was reversed and the calorific value again fell.

Tree material - Birch

Values are presented in Table VI.

As in Alder the calorific value (both gross and ash-free) of the branch wood was higher than that of the bole wood. Both the scales and reproductive structures had lower calorific values than in the alder. Fig.13 shows the seasonal changes in ash-free calorific value of birch leaves. The pattern was similar to that for alder, although the general level of calorific values was lower. The most obvious difference from the alder was the higher ash-free calorific value of both brown and green falling leaves as compared with those remaining in the canopy. As will be shown in Section V, leaves falling green were much less important to litter fall in birch than in alder.

Tree material - Other

The other tree species were not important in dry matter accumulation in the Study Area and in general a value

TABLE VI. CALORIFIC VALUES FOR BIRCH MATERIAL ($\pm$ 1 S.D.)

|	Gross calorific value g.cals/g.	% Ash	Ash-free calorific value g.cals/g.
Bole, tree harvest, Nov.67	4723 $\pm$ 15	0.8	4810 $\pm$ 50
Branch, " "	5144 $\pm$ 19	1.2	5211 $\pm$ 30
Canopy leaves Defol.Study			
29. 5.67	5002 $\pm$ 19	4.2	5217 $\pm$ 59
5. 6.67	4715 $\pm$ 54	4.0	4906 $\pm$ 78
17. 8.66	4477 $\pm$ 25	3.3	4632 $\pm$ 21
27.10.66	4475 $\pm$ 25	3.9	4654 $\pm$ 15
Falling leaves – green – litter traps			
10. 7.67	4997 $\pm$ 4	3.5	5177 $\pm$ 5
5. 8.67	5168 $\pm$ 8	2.7	5312 $\pm$ 7
Falling leaves – brown – litter traps			
10. 7.67	5255 $\pm$ 2	2.5	5389 $\pm$ 5
18. 8.67	5231 $\pm$ 42	2.4	5369 $\pm$ 25
25. 9.67	5177 $\pm$ 45	3.4	5366 $\pm$ 30
17.10.67	5112 $\pm$ 20	3.2	5289 $\pm$ 11
17.11.67	5029 $\pm$ 4	3.2	5178 $\pm$ 4
Forest floor litter S/C.			
10.66	4693 $\pm$ 19	6.2	5010 $\pm$ 12
12.66	4531 $\pm$ 6	5.9	4814 $\pm$ 25
2.67	4809 $\pm$ 8	3.5	4986 $\pm$ 2
4.67	4793 $\pm$ 31	6.4	5137 $\pm$ 72
8.67	4776 $\pm$ 7	6.4	5097 $\pm$ 7
Scales – litter traps			
12/66 – 1.67	5247 $\pm$ 2	3.2	5426 $\pm$ 2
10. 6.67	4847 $\pm$ 2	5.4	5127 $\pm$ 21
Reproductive Structures 10. 6.67	5072 $\pm$ 11	3.2	5240 $\pm$ 6

Figure 13.

Seasonal changes in ash-free calorific values of birch
leaves.

Key: open circles - canopy leaves.
     closed circles - falling leaves - brown.
     plus signs - falling leaves - green.
     crosses - forest floor litter.

95% confidence limits are shown.

ASH-FREE CALORIFIC VALUES OF A
BIRCH LEAVES

KCAL/G
ASH FREE

MONTH
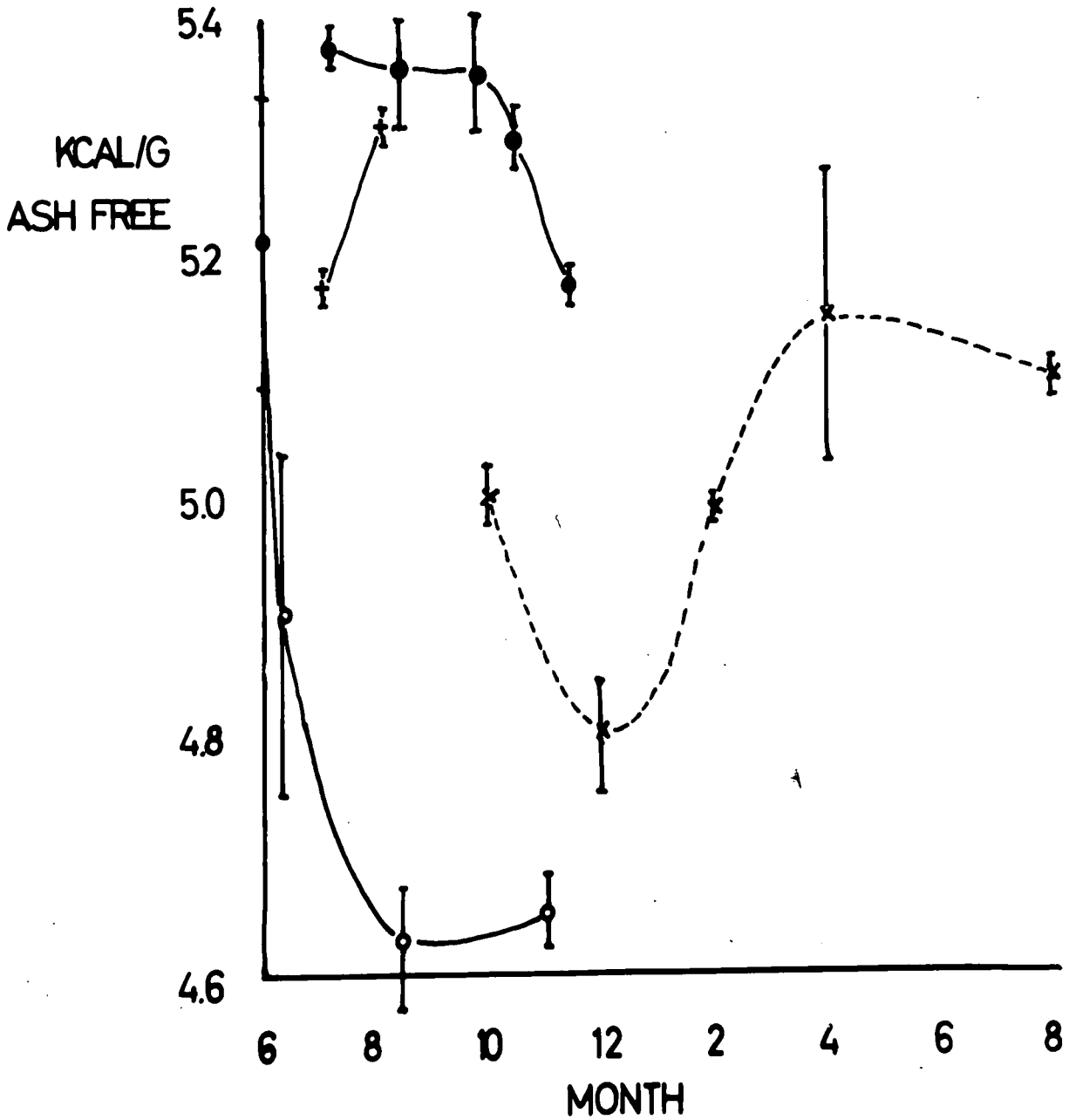
of 4.700Kcal/g dry weight was used (Newbould 1967). However, a calorific value for falling leaves was determined. This was 4.471Kcals/g dry weight, 3.8% ash, and therefore 4.649Kcals/g ash-free dry weight.

Ground Vegetation Material - Ferns

Table VII gives the calorific and ash data for fern materials. The gross calorific values of both live and dead fern material fell within the range 3.951 to 4.317Kcals/g. This range was lower than that for canopy leaves.

Fig.14 shows the seasonal changes in ash-free calorific value of live Dryopteris filix-mas and fern litter. The May sample consisted of young shoots, only partially extended. By June the fronds had opened out and the plant was probably growing by using the current year's photosynthate rather than drawing on the subterranean energy store. The highest ash-free calorific value was reached in August. Thereafter it decreased during die-back and the downward transfer of energy to the subterranean energy store. The summer and winter ash-free calorific values for fern litter were very similar and were considerably higher than the values for live fern material. This was thought to be the result of differential loss of low-energy compounds from the litter by leaching.

Ground Vegetation material - Rubus agg.

Table VIII gives the calorific and ash data for Rubus materials. The gross calorific values of both live and

TABLE VII   CALORIFIC VALUES FOR FERN MATERIAL ($\pm$ 1 S.D.)

		Gross CV gcals/g.	% Ash	Ash-free CV gcals/g.
Dryopteris filix-mas, live, S/C	5.67	3951 $\pm$ 12	4.8	4158 $\pm$ 12
	6.67	4001 $\pm$ 8	6.7	4344 $\pm$ 13
	8.67	4317 $\pm$ 1	4.6	4517 $\pm$ 20
	10.67	4036 $\pm$ 13	7.0	4342 $\pm$ 12
Fern Litter, S/C	1.67	3963 $\pm$ 42	16.6	4755 $\pm$ 49
	7.67	4130 $\pm$ 7	13.4	4772 $\pm$ 44

TABLE VIII   CALORIFIC VALUES FOR RUBUS AGG. MATERIAL ($\pm$ 1 S.D.)

		Gross CV gcals/g.	% Ash	Ash-free CV gcals/g.
Rubus Agg., live, S/C	2.67	4089 $\pm$ 10	3.7	4246 $\pm$ 11
	5.67	4050 $\pm$ 64	2.7	4170 $\pm$ 69
	8.67	4322 $\pm$ 82	1.3	4361 $\pm$ 72
	10.67	4128 $\pm$ 6	2.6	4245 $\pm$ 16
Rubus Litter, S/C	7.67	4158 $\pm$ 16	5.2	4387 $\pm$ 18
	12.67	4285 $\pm$ 6	4.8	4500 $\pm$ 4

TABLE IX   CALORIFIC VALUES FOR GRASS MATERIAL ($\pm$ 1 S.D.)

		Gross CV gcals/g.	% Ash	Ash-free CV gcals/g.
Agrostis Tenuis, live, S/C	4.67	4266 $\pm$ 6	4.6	4473 $\pm$ 7
	8.67	3913 $\pm$ 30	8.1	4260 $\pm$ 65
Deschampsia caespitosa, live, S/C	6.67	4059 $\pm$ 24	5.1	4278 $\pm$ 28
Holcus spp., live, S/C	5.67	3955 $\pm$ 9	7.8	4290 $\pm$ 10
Holcus mollis, live,"	7.67	3899 $\pm$ 8	8.6	4274 $\pm$ 8
Holcus lanatus, " "	7.67	3496 $\pm$ 6	20.0	4371 $\pm$ 23
Grass Litter, S/C	5.67	4029 $\pm$ 44	17.5	4555 $\pm$ 10
	10.67	3813 $\pm$ 3	14.4	4457 $\pm$ 24

Figure 14.

Seasonal changes in ash-free calorific values of fern materials.

Key: Open circles - live Dryopteris filix-mas.
     Crosses - fern litter.

ASH-FREE CALORIFIC VALUES OF FERN MATERIAL
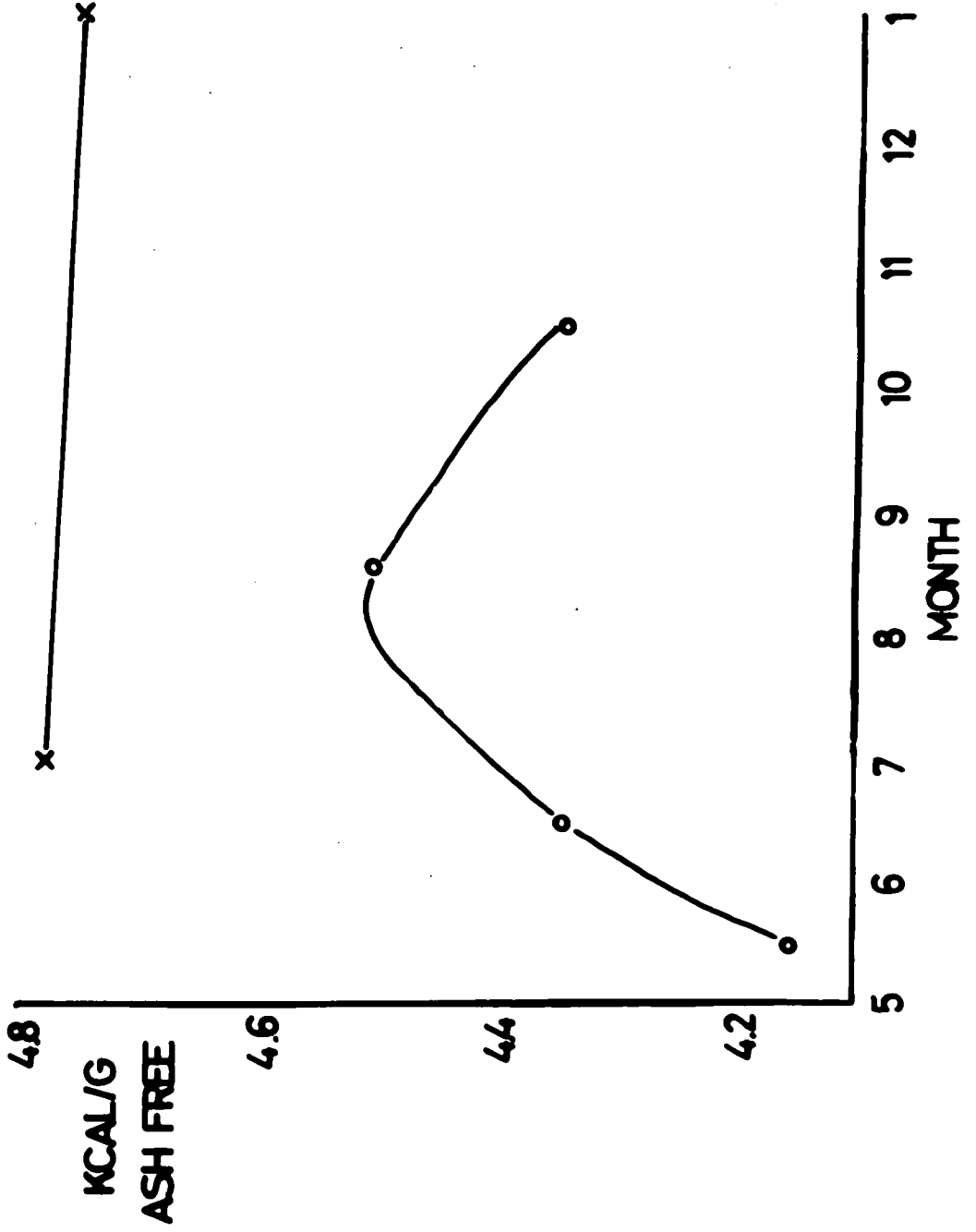
dead Rubus materials lay in the range 4.050 to 4.322Kcals/g

dry weight, a range similar to that for ferns.

Fig.15 shows the seasonal changes in ash-free calorific

values of live Rubus material and Rubus litter. The changes

here were not as great as those in canopy or fern materials.

The February and October values represent the overwintering

material. The May value represents the early part of the

growth season, and the August value shows a peak before die-back

and transfer of energy to the roots. The total change represents

less than 5% of the highest value.

The ash-free calorific values for Rubus litter were

higher than those for live material. The newly-fallen litter

in December had a slightly higher ash-free calorific value than

that sampled in July. As in other materials, the first major

loss was probably the leaching out of low-energy compounds,

giving the litter its high calorific value.

Ground Vegetation material - Grasses

Table IX gives the calorific and ash data for grass

materials. Apart from the high value for Agrostis tenuis

in April and the low value for Holcus lanatus in July, all

the gross calorific values live and dead fell within the range

3.813 to 4.059Kcal/g dry weight. This was lower than the

ranges for canopy leaves, ferns and Rubus agg. materials.

The ash-free calorific values for live grasses fell

between 4.260 and 4.473Kcal/g ash-free weight. In fact, only

Figure 15.

Seasonal changes in ash-free calorific values of Rubus
material.

Key: open circles - live Rubus material.
     crosses - Rubus litter.

ASH-FREE CALORIFIC VALUES OF RUBUS MATERIAL
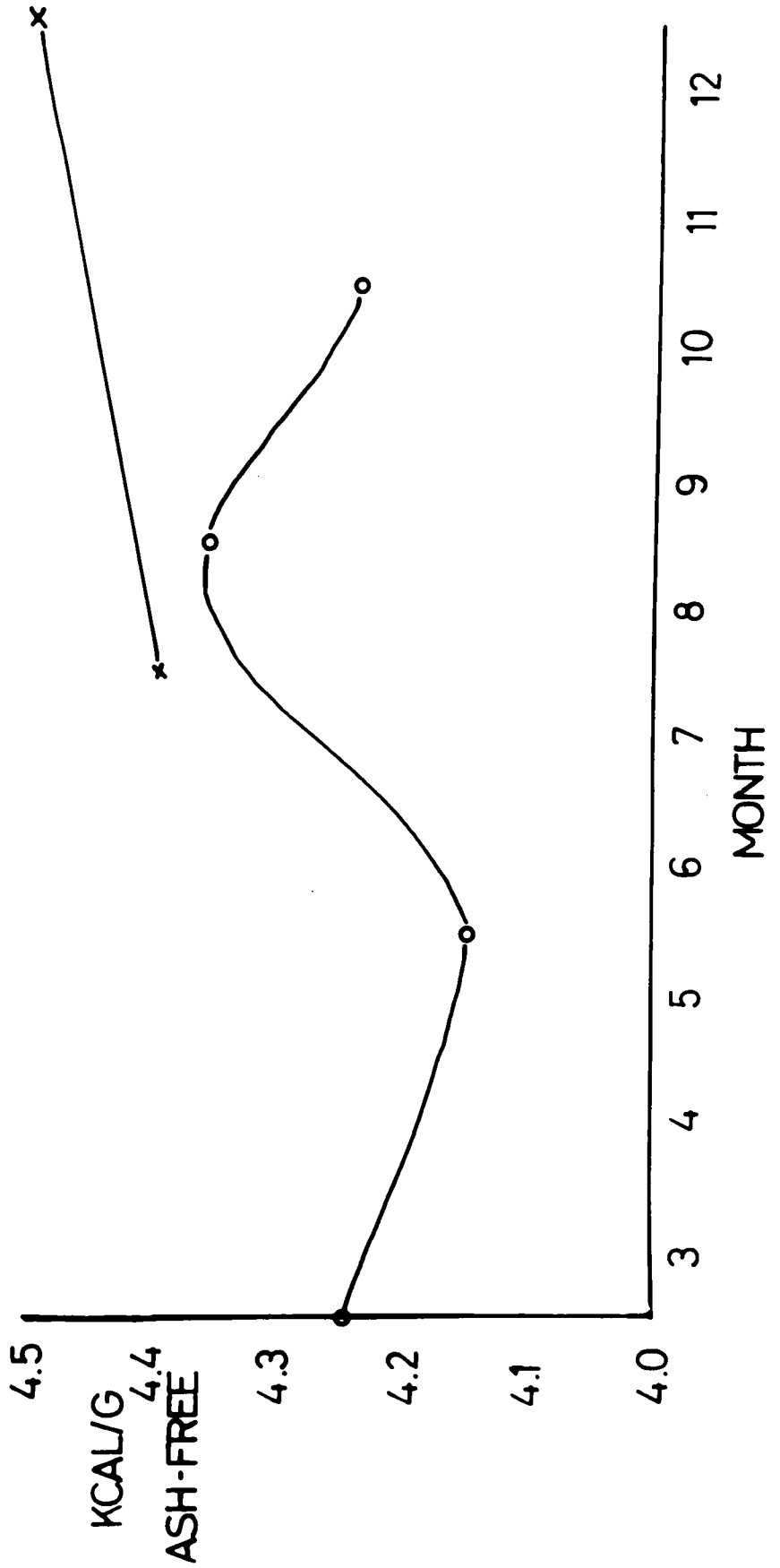
the April value for <u>Agrostis tenuis</u> and the July value for
<u>Agrostis tenuis</u> fell outside the range 4.260 to 4.290Kcal/g
ash-free dry weight.

The ash-free calorific values of grass litter,
4.457 and 4.555Kcal/g ash-free dry weight, were above the
general range for live materials.   The explanation of this
is probably similar to that for other persistent litters.

Ground Vegetation materials and Bryophytes

Table X gives the calorific and ash data for the
other Ground Vegetation Materials and the Bryophytes.   The
gross calorific values for <u>Chamaenerion angustifolium</u> and the
forbs fell within the range of the other live ground vegetation
materials.   The gross calorific value of the Bryophytes was
much lower.

This pattern was reversed in the case of the ash-free
calorific values, where the Bryophyte value was higher than any
given for live Ground Vegetation.   This reversal was caused by
the high ash-content of the Bryophyte powder and was probably
the result of soil particles adhering to the Bryophyte material.

III.4 Discussion

The different gross calorific values determined for
various species, plant parts and seasons suggest that it may
be important to use a calorific equivalent for each of these
categories rather than a single equivalent for them all, or
even for a major group of them.

TABLE X   CALORIFIC VALUES FOR OTHER GV CATEGORIES + BRYOPHYTES
(± 1 S.D.)

		Gross CV gcals/g.	% Ash	Ash-free CV gcals/g.
Chamaenerion angustifolium, live, S/C	1967	4245 ± 8	2.3	4346 ± 20
Forbs, live S/C	1967	3905 ± 62	8.4	4277 ± 22
Bryophytes	12.67	3507 ± 31	26.6	4774 ± 29

TABLE XI   GENERAL RANGES OF CALORIFIC VALUES

	Gross CV gcals/g.	Ash-free CV gcals/g.
Canopy leaves	4475 – 5228	4632 – 5635
Wood	4540 – 5144	4565 – 5211
Live Ground Vegetation	3899 – 4322	4158 – 4517
Ground Vegetation Litter	3813 – 4285	4387 – 4772
Forest Floor Tree Litter	4513 – 4900	4814 – 5229
Falling Leaves	4716 – 5255	5088 – 5389

Table XI gives the overall ranges of the calorific values of the major groups of materials. If ash-free calorific values are considered, then the range for live Ground Vegetation was lower than any other. None of the tree material ranges overlapped it. The ranges of the other live categories, tree wood and canopy leaves, were progressively higher and wider.

Of the litter categories, the Ground Vegetation Litter range was the lowest,ranging through canopy forest floor litter to falling canopy litter.

Whilst generally characteristic of position in the woodland stratification and ecological position, these ranges are broad. Only calorific values appropriate to a particular category of material provide adequate calorific equivalents for the conversion of dry weight data to energy data. This is particularly evident in the case of falling birch litter; the use of the wrong equivalent (that for canopy leaves) could decrease the estimate of this important category's energy contribution to the litter by 12%. There seems little reason to add to the errors of dry weight estimation by this amount. The differences observed between the calorific values of the various materials will have the effect of emphasising the role of the trees as against the ground vegetation in energy accumulation and transfer.

CHAPTER II – SECTION IV

Tree Wood Biomass and Biomass Change

IV. i. Introduction

As reported in Chapter I, Section II, the tree stratum
was physiognomically an important component of the vegetation of
the Study Area. Much has been written on the influence of tree
stratum on vegetation (Ovington 196$) but these general consid-
erations are not of direct relevance to this study. The aim
was to gain some understanding of the role of the trees in the
woodland as an energy-fixing, - storing and - dissipating system.
The approach that was adopted was to estimate biomass (and hence
biocontent) and dry matter transfers (and hence trophic energy
transfers) within the woodland ecosystem. No attempt was made
to estimate the biomass and growth of the below ground parts of
the vegetation.

For the tree stratum, the following estimates were made :-
   i. Biomass of the above-ground parts of the trees
  ii. Net annual above-ground primary production by trees.
With the calorific equivalents presented in Section III these
were converted to energy data. There were obvious mechanical
problems associated with sampling the tree stratum, both with
the size of trees and the scale of woodland pattern. These
problems have been discussed extensively in the forestry and
ecological literature summarized by Newbould (1967).

Estimation of tree stratum biomass is usually carried out in two stages. First, the individual trees in the study area are enumerated and various external dimensions, most commonly diameter at breast height (dbh), are noted. Second, a smaller destructive sample is taken so that the weight of trees or their separate components may be directly related to the external dimensions noted for the whole population, or to some function of them. It is in the choice of the small destructive sample and the method of relating the data thus obtained to the whole tree population that most variation between authors is found. Ratios between tree or component weight and external dimensions or functions of them may be determined for samples of dominant trees (Whittaker et al 1963), or selected 'mean' trees (Ovington & Pearsall 1956; Ovington 1957; Ovington & Madgwick 1959; Peterken & Newbould 1966). Ovington & Madgwick (1959b) and Baskerville (1965) pointed out inadequacies in these approaches, even when used for single-aged plantations. In the Study Area neither of these methods was possible. The wide diameter-distribution of the trees was indicative of the 'continuous variation' in size and form displayed. Clearly the selection of 'dominant' or 'mean' trees was neither practicable nor desirable in this many-aged stand. Instead, destructive samples were used to derive regression equations for the relation- ship between tree or component weight and external dimensions or

functions of them. Using these regression equations for the

relationship between tree or component weight and external

dimensions or functions of them, plus the census data, the dry

weight of the woody parts of each tree on the Grid was estimated.

Hence woody biomass was calculated. This approach, or the closely

related stand table approach, has been used successfully by other

workers (Whittaker & Woodwell 1968; Baskerville 1965).

In the estimation of net production of woodlands two

approaches have been widely used. These have been described in

detail by Kira & Shidei (1967) and Newbould (1967). The first

approach (Newbould's Method I) is to estimate the biomass of a

plant community at time t_1, biomass at a later date t_2, and to

estimate net production as :-

$$P_n = \triangle B + L + G,$$

where $\quad P_n =$ net production during $t_1 - t_2$

$\triangle B =$ Biomass change during $t_1 - t_2$

$\qquad L =$ Plant losses by death and shedding during $(t_1 - t_2)$

$\qquad G =$ Plant losses to consumer organisms during $(t_1 - t_2)$

The second approach (Newbould's Method II) is to

harvest the plants only once, at the end of the growing season (t_2)

and to separate the plant matter into current year organs and

older parts. Thus the amount of plant matter formed in the

latest one year period is estimated. Thus, net production,

$$P_n = B_{2N} + L_N + G_N$$

P_n = net production that year

where B_{2N} = apparent growth increment

   L_N = part of P_N which dies and is lost from the biomass

   G_N = part of P_N which is lost to consumer organisms.

Method I requires that biomass be estimated some years apart (Ovington & Madgwick 1959a; Ovington & Pearsall 1956; Ovington 1957; Muller & Nielsen 1965; Kira et al 1967). This was not practicable in this case where only two, consecutive, field seasons were available. Method II involves a complex sampling procedure requiring considerable resources of manpower at the time of sampling (Whittaker, Cohen & Olsen 1963; Whittaker & Woodwell 1968; Ovington, Heitkamp & Lawrence 1963). As extensive studies were simultaneously made of tree litter fall and ground vegetation biomass, net production and litter formation, and as the labour of more than one person was only available for very limited periods of time, this approach (Method II) was also ruled out. However, in the course of determining tree above-ground biomass, tree sections were used to investigate the relationship between the diameter (dbh) at the time of sampling (t) and that 5 years before (t - 5). Should this relationship prove suitable, the diameter 5 years before sampling was to be calculated for each tree on the Grid. Then biomass 5 years before sampling could be calculated using the regressions derived from the

destructive samples.   The assumption made was that the

relationship between external dimensions and tree or component

weights did not change during the five-year period.   Given this,

the two estimates of biomass should allow the calculation of tree

wood biomass change during the five-year period.   From this,

an annual value may be obtained.   To calculate wood net

production this value must be corrected for the loss, during

the period, of wood which has grown during the period and for

death of material included in the first biomass estimate.

This is essentially a modification of Newbould's Method I.

IV. ii. Methods for determining wood biomass and production

A. Non-destructive measurements

As described in Section II, a complete enumeration of

the tree stems on the Grid was carried out during the winter of

1967-8.   The diameter of each stem was measured at 1.3m above

ground on the uphill side of the tree.   Thus the stems have

been listed according to position on the grid, species, dbh

and whether or not they arose from coppiced stools.   A summary

of these data was presented in Section II.

B. Destructive measurements

Each individual tree stem and the branches and other

structures it carries above the soil surface is called a shoot

in this study.

(i) <u>Birch</u>. During the last two weeks of November 1967,
thirteen birch shoots were harvested.   They were chosen to
represent the range of diameters as completely as possible.
The sample shoots were taken from that part of the Study Area
immediately surrounding the Grid.   They included both coppiced
and uncoppiced shoots.   Separate analysis of coppiced and
uncoppiced shoots would have required a much more extensive
sampling programme than was possible.

The procedure used for each shoot was as follows :-
Using a power saw, the stem was cut off at the lowest possible
level; when fallen, a tape was stretched from the base of the
shoot to the top of the leading branch and the tree height was
recorded.   Then the stem was cut into sections at breast height
(1.3m above ground) and every 2m above this.   In addition a
2cm thick disc was cut from the stem at breast height and at
each 2m interval.   Care was taken to cut these discs at right
angles to the stem.   The tree sections and their appropriate
discs were then labelled and carefully carried to an open space
where a set of platform scales was set up.   These weighed up to
3cwt in 1oz intervals.   The weights were subsequently converted
to the metric scale.   First the discs were weighed and their
fresh weights recorded.   Then starting with the lowest section
the branches were cut off as near the stem as possible, put in
a bag for each section, and weighed.   Then the stem sections

were weighed.   Thus, for each shoot the fresh weights of the
branches and boles by height sections were obtained.   The inter-
section discs were transported to the laboratory along with five
branch subsamples of approximately 400g each for each shoot.   An
attempt was made to ensure that these subsamples were represent-
ative;   by chopping up branch material into small pieces, placing
in a large sack, shaking vigorously and then pouring out the
required amount of wood.

In the laboratory the following procedure was adopted.
The branch subsamples were cut into yet smaller fragments and
initially dried for one week in clothes driers.   Then they were
transferred to ovens and dried to constant weight at 105°C.   The
discs from all levels above 1.3m were cut into small segments,
the sawdust being carefully collected for each, and dried to
constant weight at 105°C.   The discs from the 1.3m or dbh discs,
as they will be called, were sanded on one side so that the annual
rings might be examined.   As far as possible, the dust produced
by sanding was collected for each disc.   Four radii were drawn
at 90° to one another on the sanded surface.   Using these,
outside diameter, diameter inside bark and bark thickness were
carefully measured.   A cross-checked ring count was carried
out using a binocular microscope.   Then the diameters every
5th ring were measured.   Thus the age and diameter of the tree
at the time of sanding was determined and estimates of its inside
bark diameter at 5 year intervals recorded.

(ii) <u>Alder</u>.   During the last two weeks of May 1968, twelve

alder shoots were harvested.   It was originally intended that

this sampling be carried out immediately after litter fall.

Unfortunately this was not possible and certain modifications

were made in the harvest and mensuration techniques.   The choice

of sample shoots was made on the same basis as for birch.   The

treatment of the materials was as for birch, except for the

branches.   Here the branches on each stem section were tallied

into basal girth classes (10cm and above this at 5cm girth

intervals) before being cut off.   For sample branches of each

major size group, all the leaves were stripped into bags and

taken to the laboratory where the number of leaves per bag (and

so per branch) was determined by weighing the fresh leaves and

then applying a weight/leaf number factor derived on the same day.

Thus it was possible to calculate the number of leaves carried by

each shoot sampled.

IV. iii. Results

A summary of the data obtained in the destructive

sampling is given in Appendix I.   Not all of these data were

used in the computation of wood biomass and biomass change.

They were incidentally obtained in the course of the sampling

procedure.   In addition, it is evident that the data presented

below could have been used in a number of other ways.   The sole

aim of this study was to investigate energy accumulation and

transfer within this woodland ecosystem. Therefore no attempt
was made to use the data obtained for any other purpose.

a. Birch

Diameter at breast height (dbh) was the external
dimension obtained for each tree shoot on the Grid and so the
weight data were related to this. For the twelve sample shoots,
the constants A and h in the allometric equation (Kira & Shidei 1967)

$$w \;=\; AD^h, \text{ where } w = \text{dry weight,}$$

$$D = \text{dbh}$$

were determined for w_b = branch dry weight

$$w_T = \text{bole dry weight}$$

$$w_S = \text{whole shoot dry weight}$$

In addition the correlation coefficient (r) and the relative
error of estimate (E or e) were determined. In a logarithmic
regression E is the antilogarithm of the standard error of
estimate. In a linear regression e is the ratio of standard
error of estimate to y, (Whittaker & Woodwell 1968).

These values are given in Table XII, and the data
shown in Figures 16a, b, and c. The form of the three expressions
is very similar, the only great difference between them being in
the proportional constant A, as would be expected. For all three
the correlation coefficient, r, is high, but as Whittaker &
Woodwell (op cit) have pointed out this is not a particularly
good indicator of the reliability of the equation for use in

Figure 16.

a. Birch branch dry weight (kg.), vs. diameter squared (cm^2).

b. Birch bole dry weight (kg.), vs. diameter squared (cm^2).

c. Birch shoot dry weight (kg.), vs. diameter squared (cm^2).

BIRCH BRANCH DRY WEIGHT VS DIAMETER SQUARED
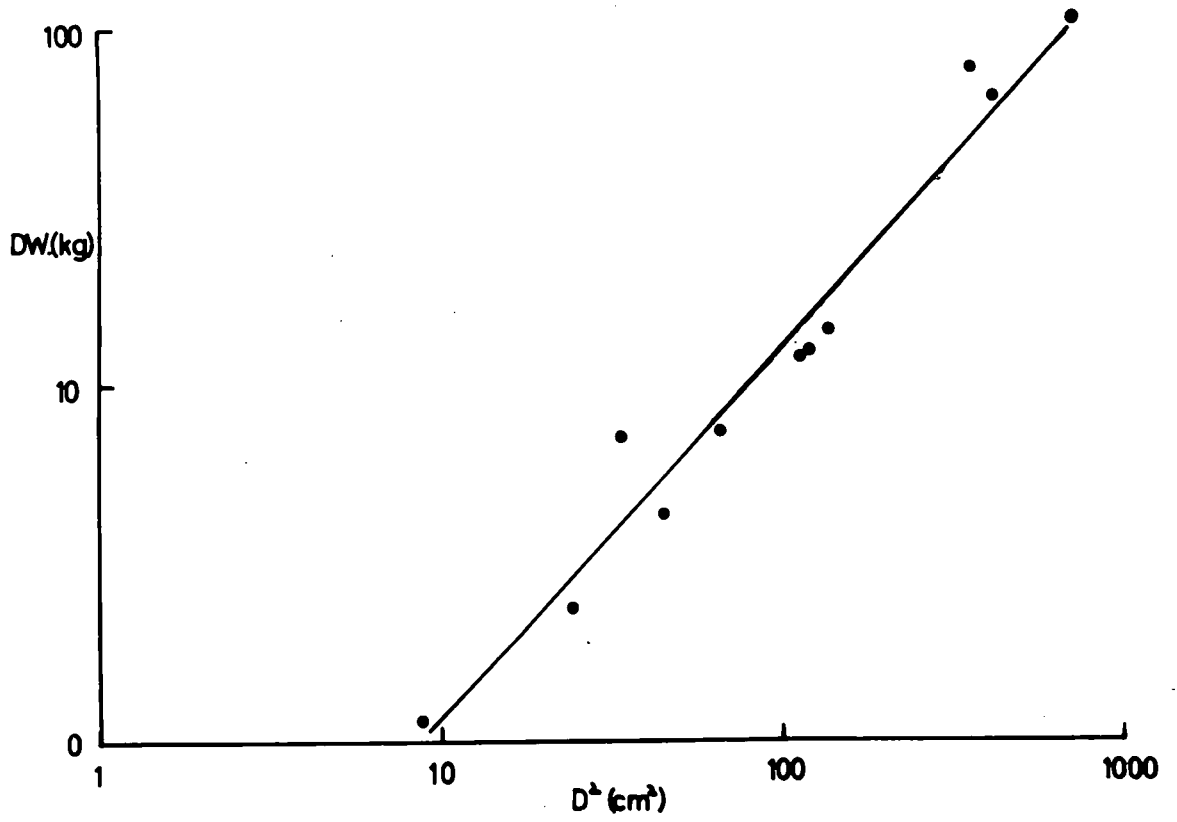
BIRCH BOLE DRY WEIGHT VS DIAMETER SQUARED
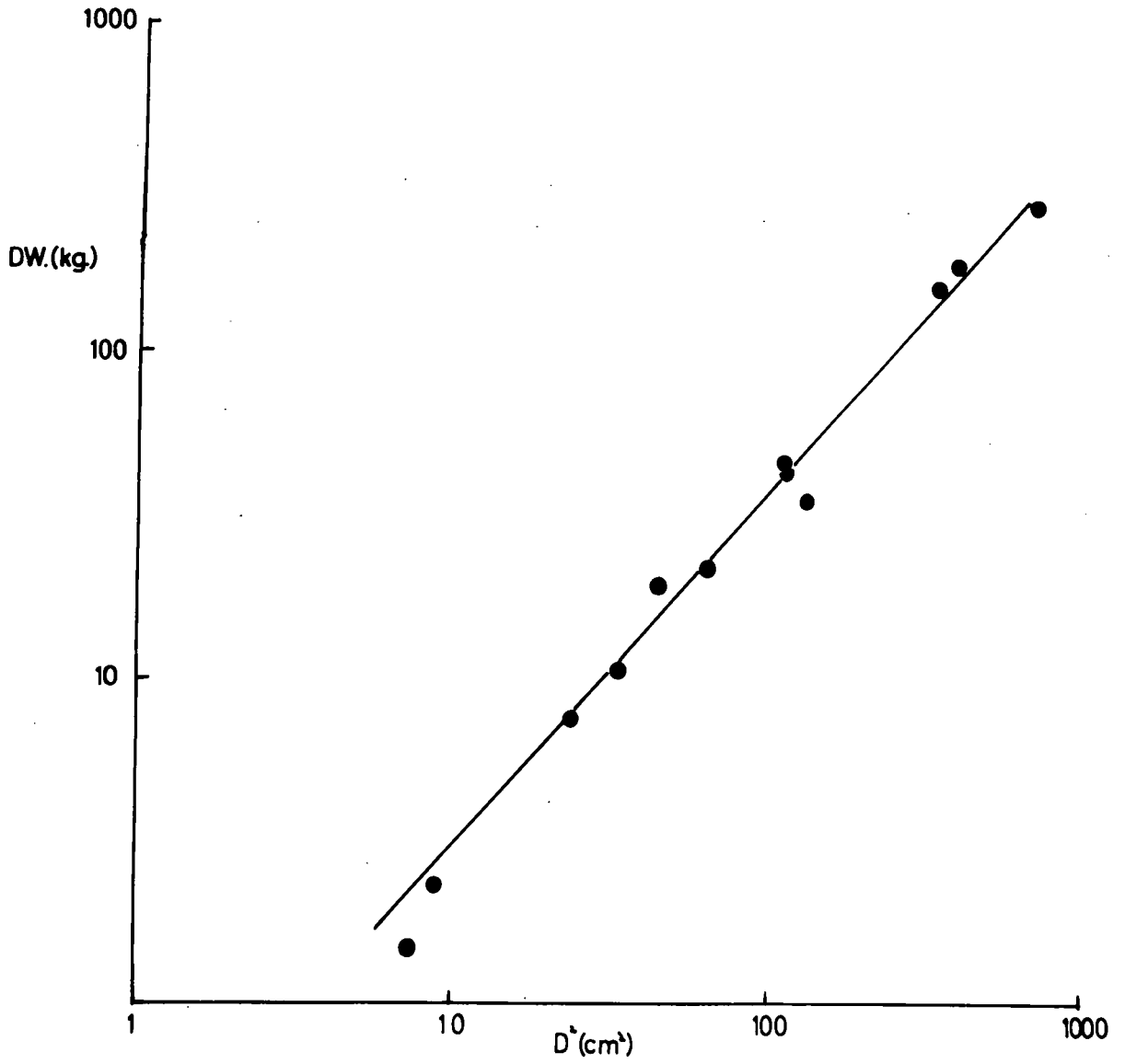
BIRCH SHOOT DRY WEIGHT VS DIAMETER SQUARED
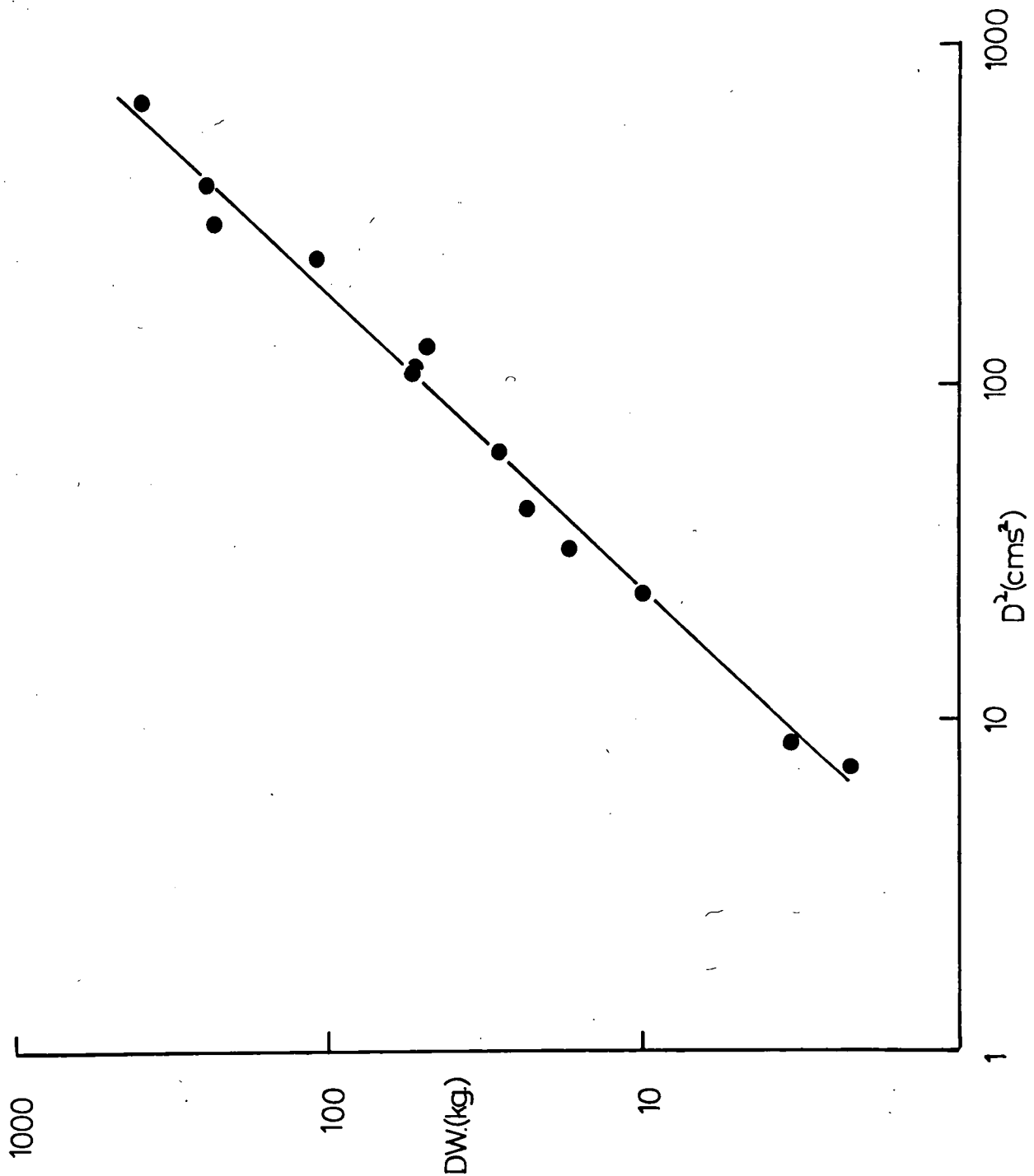
TABLE XII   Equations for Birch allometry

	A	h	r	E
w_B	0.07422	2.24079	0.9899	1.2226
w_S	0.19938	2.24910	0.9946	1.1765
w_t	0.25137	2.28654	0.99253	1.2151

where $w = AD^h$ x   or $\div$ E.

TABLE XIII   Biomass and Biocontent of Birch Boles and Branches

	Biomass	Biocontent
BIRCH ZONE	$11,883.4 g/m^2$	$57,623.2 Kcal/m^2$
	(9,779.8 - 14,439.5)	
ALDER ZONE	$1,212.7 g/m^2$	$5,880.3 Kcal/m^2$
	(998.0 - 1,473.6)	
GRID	$6,432.9 g/m^2$	$31,193 Kcal/m^2$
	$\left(5,467.8 - 7568.3 \right)$	

The figures in brackets are biomass x   or $\div$ E.

interpolation. E is lowest for w_T - bole weight vs dbh and highest for w_B - branch weight. That for w_S - whole shoot weight, is intermediate. All three values lie near the lower end of the range (E = 1.109 to 1.725) calculated for similar expressions for the Brookhaven Forest (Whittaker & Woodwell, op cit). Knowing E for each equation and the proportion of shoot weight attributable to the branches, it was possible to calculate the relative reliabilities of the two methods of calculating shoot dry weight. These methods are the direct method using $w_S = AD^h$, or the indirect method by adding w_B and w_T, determined by the relevant equations. For the extreme case of branch weight being 40% of shoot weight, the direct method gives a possible range of from 82.3 to 121.5% of the estimated shoot weight; the indirect method gives a range of 83.7 to 119.5%. For the other extreme case, where the branch weight is 18% of shoot weight, the indirect method gives a range of 84.4% to 118.5%. Thus the use of the indirect method is unlikely to improve the reliability of the estimate by more than 2 or 3% in any possible case. Therefore the biomass of woody birch shoots on the Grid was calculated from the Census data and the shorter, direct method using

$$w_S = AD^h \text{ for each shoot.}$$

Table XIII shows the biomass of birch boles and branches for the Grid, the Alder Zone and the Birch Zone as g/m^2. The range

of biomass x or $\dot{\div}$ E is given in brackets; the size of the

errors indicated here ($\overset{+}{-}$ 20% of the mean) should be viewed

with caution. E is a relative rather than an absolute estimate

of error. However, the most that can be said is that the

biomass estimates in Table XIII may be within 20% of the true

values. Table XIII also shows the biocontent estimates derived

from these biomasses.

From the measurements made on the dbh discs, the outside

diameter of the tree concerned 5 years before sampling (t - 5)

was estimated. A graph of bark thickness against inside dbh

was drawn. Total bark thickness rarely exceeded 10% of diameter

and so a 20% error here only gave rise to 2% error in the outside

diameter estimate. The outside diameter at (t - 5) was estimated

as inside diameter at (t - 5) plus calculated bark thickness.

Figure 17 shows the relationship between D - dbh at time of

sampling, and D (t - 5) - dbh five years before. The regression

equation takes the form :

$$D (t - 5) = 0.9401_{\mathbf{B}}^{\mathbf{B}}D - 0.5368$$
$$r = 0.9987, \quad e = 2.8\%.$$

This made it possible to calculate the dbh of a stem

at (t - 5) with some confidence. Dbh at (t - 5) was calculated

for each birch shoot on the Grid. Then, using the allometric

equation for w_S derived in the destructive sampling, the biomass

of wood in birch shoots at (t - 5) was calculated. These figures

Figure 17.

Diameter at time of sampling (D(t)) (cms) vs. diameter five
years before (D(t-5)) (cms.) for birch.

BIRCH
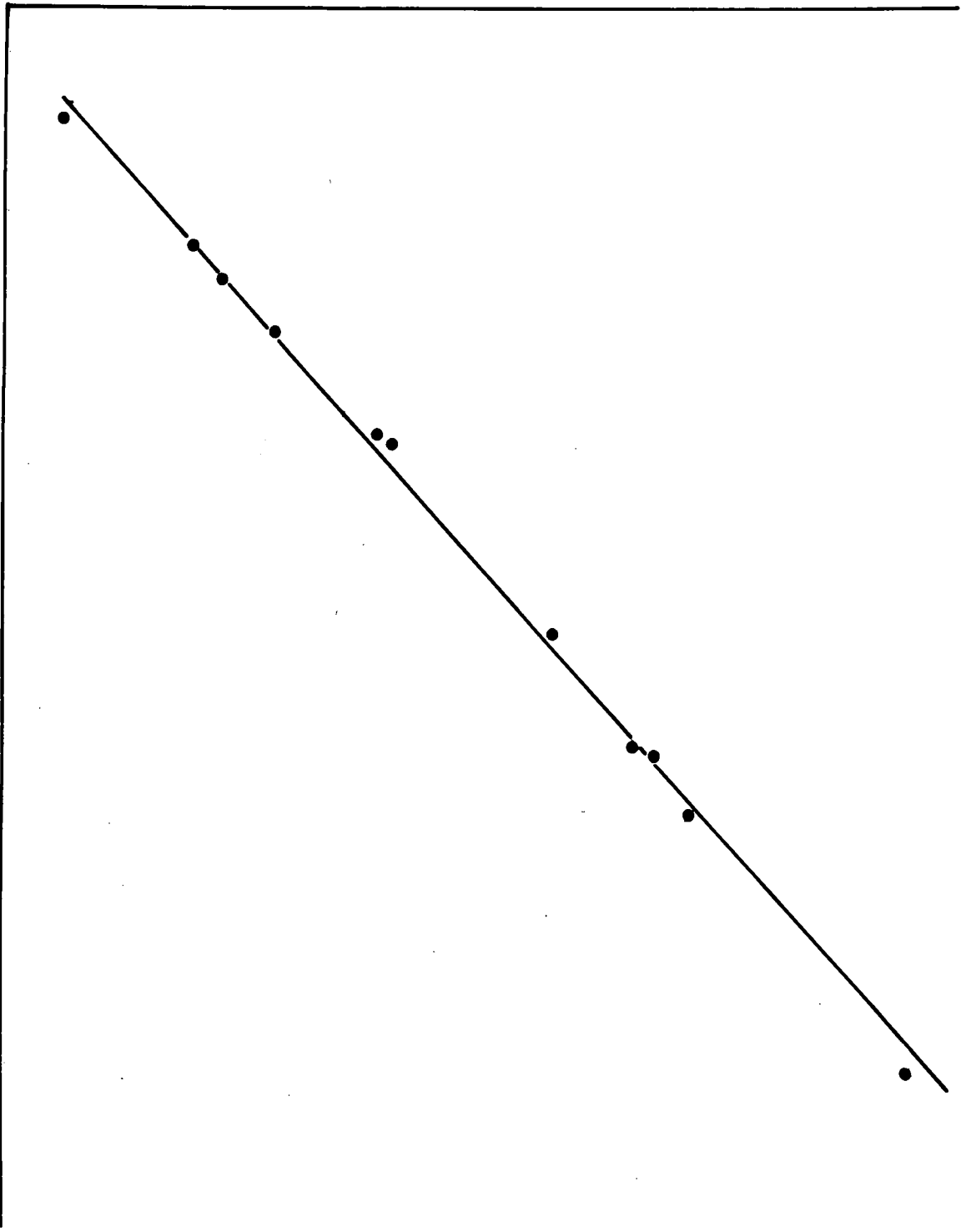
TABLE XIV   Biomass and Biocontent of Birch Boles and Branches
at (t - 5)

	BIOMASS (g/m^2)	BIOCONTENT ($Kcal/m^2$)
BIRCH ZONE	9,319.5	45,190
	(7,669.7 - 11,324.1)	
ALDER ZONE	1,048.2	5,083
	(8,626.4 - 1,273.7)	
GRID	5,094.5	24,703
	(4,192.6 - 6,190.3)	

The figures in brackets are biomass x or $\div$ E.

TABLE XV   Annual Change in Biomass and Biocontent of Birch Boles
and Branches

	Biomass Change ($g/m^2/yr$)	Biocontent Change ($Kcal/m^2/yr$)
BIRCH ZONE	512.8	2,486
ALDER ZONE	32.9	159
GRID	267.7	1,298

TABLE XVI   Equations for Alder allometry

	A	h	r	E
w_B	0.01465	2.51919	0.92451	1.3797
w_S	0.08598	2.35371	0.98509	1.2800
w_T	0.08419	2.45014	0.99166	1.2106

Where $w = AD^h$ x or $\div$ E.

are presented in Table XIV as biomass and biocontent. Thus
it was possible to calculate the change in biomass of birch
woody shoots from (t - 5) to (t), the time of sampling. This
five year figure may then be used to derive a figure of annual
change as in Table XV. This was taken as a simple annual
average. An assumption of linear rather than exponential
growth was implicit in this calculation. As the tree populations
on the Study Area were many-aged and only a few of the older trees
were likely to be in an exponential growth phase, it seemed wisest
to assume linear growth for the populations as a whole. No
reliable criterion was available for the division of shoots into
those in a linear growth phase and those in an exponential growth
phase. It was impractical to place realistic limits on the size
of the errors in this determination. It may be said that if the
two biomass estimates are in error, that error is probably not
due to any change in the equation for w_s on D during the short
period of 5 years. Hence, it seems reasonable to assume that
the errors in both cases will be of the same order and in the
same direction. Therefore the estimate of biomass change is
reasonably reliable.

The ratio of annual biomass change to biomass of
boles and branches at time of sampling was 0.043 for the Birch
Zone, 0.027 for the Alder Zone and 0.042 for the Grid as a whole.

The data on the relationship between birch shoot age dbh is presented in paragraph (c) along with that for Alder.

(b) Alder

The alder woody shoot data are presented in the same form as those for birch. Table XVI and Fig.18a, b, c, show the relationship between w_B (branch dry weight) w_T (bole dry weight), w_S (shoot dry weight) and dbh. The equations are basically similar in form to those for birch, h generally being a little higher, and A considerably lower. This means that for most of the diameter range an alder tree will be lighter than a birch with the same dbh. The correlation coefficient r is a little lower than for the corresponding birch equations. The values for E fall into the same range as Whittaker & Woodwell's (op cit), that for w_B being considerably higher than those for w_S and w_T. The relative reliabilities of estimates of shoot dry weight either directly or indirectly were estimated as for birch. For the extreme case of branch weight being 38% of shoot weight, the indirect method gives a possible range of from 75.9% to 132.0%. If branch weight is 8% of shoot weight, the range is from 77.7% to 128.8%. The direct method gives a range of from 82.3% to 121.5%. Thus the direct method is the more reliable and therefore the biomass of woody alder shoots on the Grid has been calculated from the Census data by the direct method using :-

Figure 18.

a. Alder branch dry weight (kg.) vs diameter (cms).
b. Alder bole dry weight (kg.) vs diameter (cms).
c. Alder shoot dry weight (kg.) vs diameter (cms).

ALDER ALLOMETRIES

BRANCH WEIGHT VS. DBH

BOLE WEIGHT VS. DBH

SHOOT WEIGHT VS. DBH

DW (kg)

D (cm.)
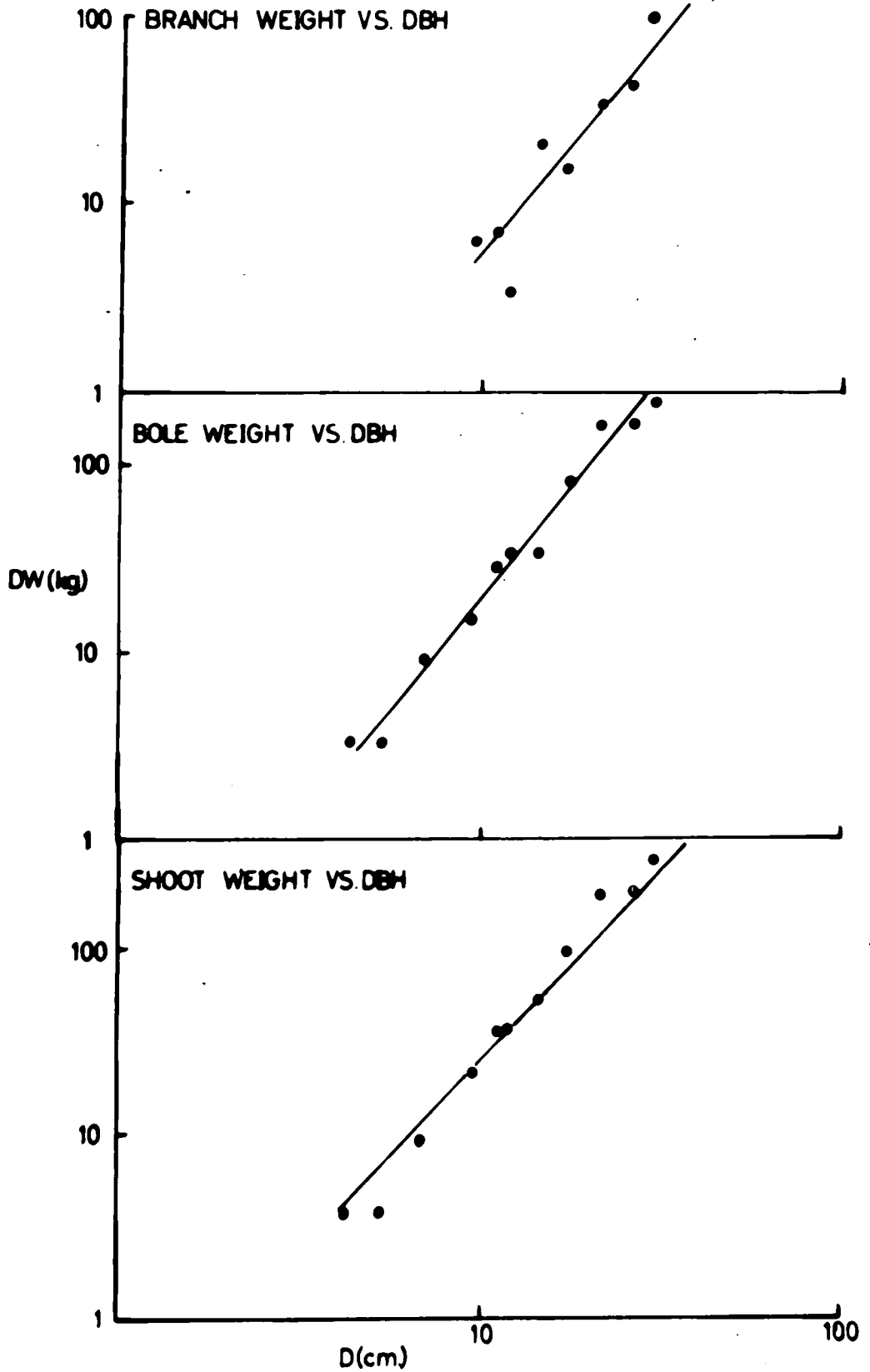
$$w_S = \text{0.08419} \quad \text{45014} \quad 0.08598 \ D^{235371}$$

Table XVII shows the biomass and biocontent of the alder boles and branches for the Grid, Alder Zone and Birch Zone. The range of biomass x or $\pm$ E is given in brackets. As with birch, the ranges shown (about 20%) may not represent a realistic estimate of errors. The biomass and biocontent of alder boles and branches represented 66% and 63% respectively of those for birch.

The relationship between $D_{(t)}$ and $D_{(t-5)}$ was derived in the same way as for birch. Figure 19 shows the relationship between $D_{(t)}$ and $D_{(t-5)}$. The regression equation takes the form

$$D \ (t-5) = 0.9799D(t) - 1.1675$$

$$r = 0.9939 \text{ and } e = 4.3\%$$

Using this equation, $D(t-5)$ was calculated for each alder shoot on the Grid. The error was probably of the order 5%. Then w_S at $(t-5)$ was calculated for each stem by the direct method. These figures are presented in Table XVIII. The figures for annual bole and branch biomass and biocontent change are given in Table XIX. The same comments apply to the reliability of these estimates as to those for birch.

The ratio of annual bole and branch biomass change to biomass at the time of sampling in alder was 0.0372 for the Alder Zone, 0.0772 for the Birch Zone and 0.0371 for the Grid.

Figure 19.

Diameter at time of sampling (D(t)) (cms.) vs. diameter
five years before (D(t-5)) (cms.) for alder.

ALDER   D(t-5) VS. D(t)
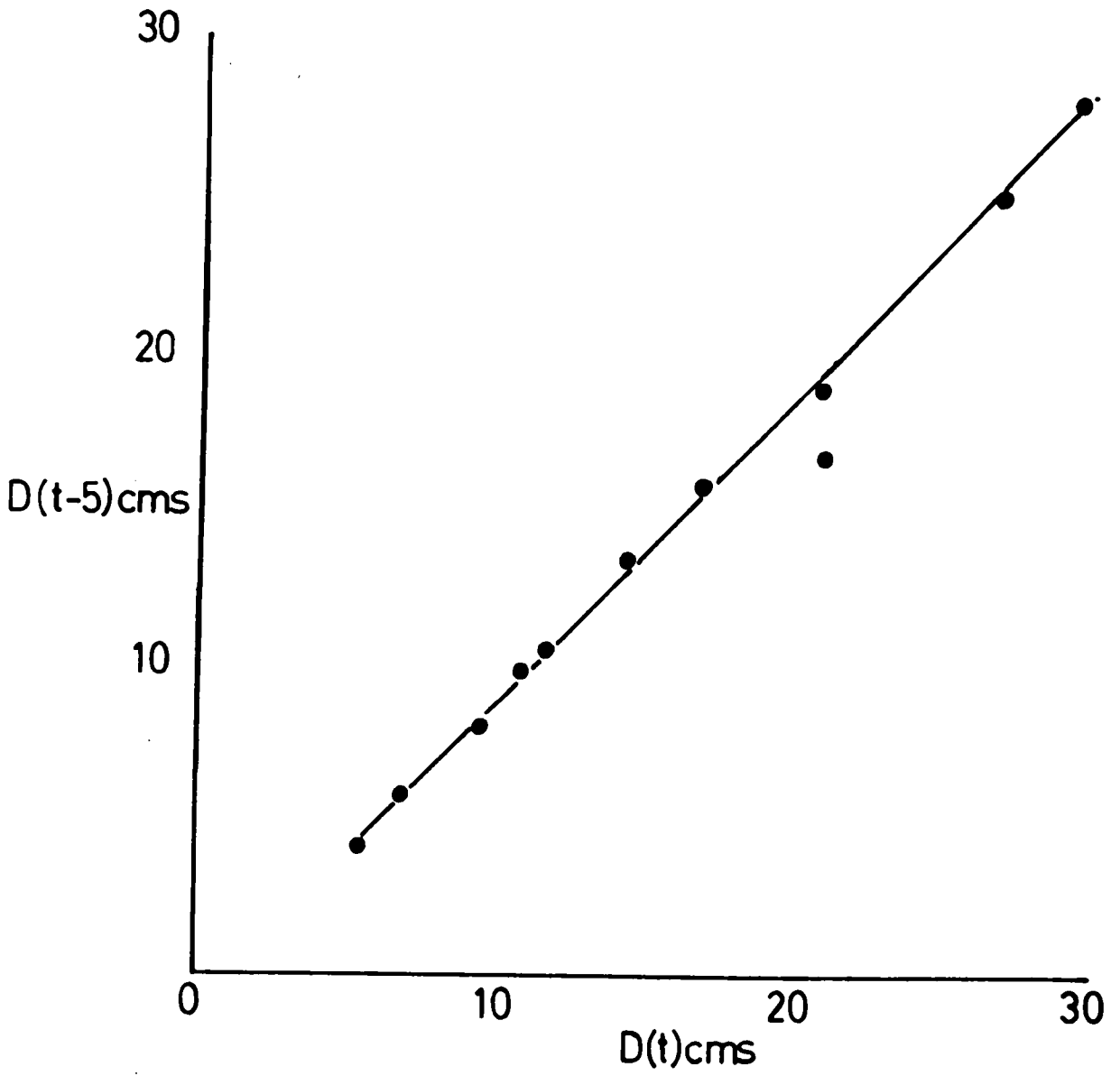
TABLE XVII   Biomass and Biocontent of Alder Boles and Branches
1967-8

	BIOMASS (g/m^2)	BIOCONTENT ($Kcal/m^2$)
ALDER ZONE	7,418.1	34,363.4
	(6,126.8 - 8,980.3)	
BIRCH ZONE	956.1	4,429.6
	(789.8 - 1,157.4)	
GRID	4,256.3	19,719.4
	(3,515.8 - 5,152.7)	

The figures in brackets are biomass x or $\div$ E.

TABLE XVIII   Biomass and Biocontent of Alder Boles and Branches

	BIOMASS (g/m^2)	BIOCONTENT ($Kcal/m^2$)
ALDER ZONE	6,038.0	27,974.0
	(4,987.6 - 7,309.6)	
BIRCH ZONE	777.9	3,604.0
	(642.6 - 941.7)	
GRID	3,261.0	15,108.2
	(2,693.7 - 3,947.8)	

The figures in brackets are biomass x or $\div$ E.

TABLE XIX   Annual change in Biomass and Biocontent of Alder
Boles and Branches

	BIOMASS ($g/m^2/yr$)	BIOCONTENT ($Kcal/m^2/yr$)
ALDER ZONE	275.8	1,277.8
BIRCH ZONE	35.6	164.9
GRID	158.3	733.4

(c) The tree Age-distributions and the History of the Study Area

A detailed history of the Study Area is not available. However, using data obtained in the course of destructive sampling for woody biomass, it was possible to make a partial reconstruction of the history of the Study Area. This information was of value in understanding the current situation, even though it was not possible to calculate a production history of the Study Area.

From the sample birch shoots a regression equation for shoot age on dbh was derived -

$$\text{Shoot Age} = 4.529D^{0.80309}$$

$$r = 0.9530; \quad E = x \text{ or } \overset{+}{\underset{.}{-}} 1.1970$$

Ovington & Madgwick (1959) noted wide variation in dbh for birch trees of one age. Using the above equation, the ages of shoots at the limits of individual dbh classes in Fig. Section II, were calculated. Graphs of cumulative frequency by age for coppiced and uncoppiced birch shoots were drawn (Fig.20a, and b, and from these the frequency distribution by age of the birch shoots was constructed (Fig.21a and b). Despite the possible errors involved in each stage of this construction, it gives some indication of the history of this population of trees. The most striking characteristic of the age distribution was the wide age-range of the shoots. An individual shoot 120 or more years old was found in the Study Area. This was dead when found indicating that birch has been

Figure 20.

Cumulative frequency by age - birch.
a. coppiced.
b. uncoppiced.

CUMULATIVE FREQUENCY BY AGE - BIRCH
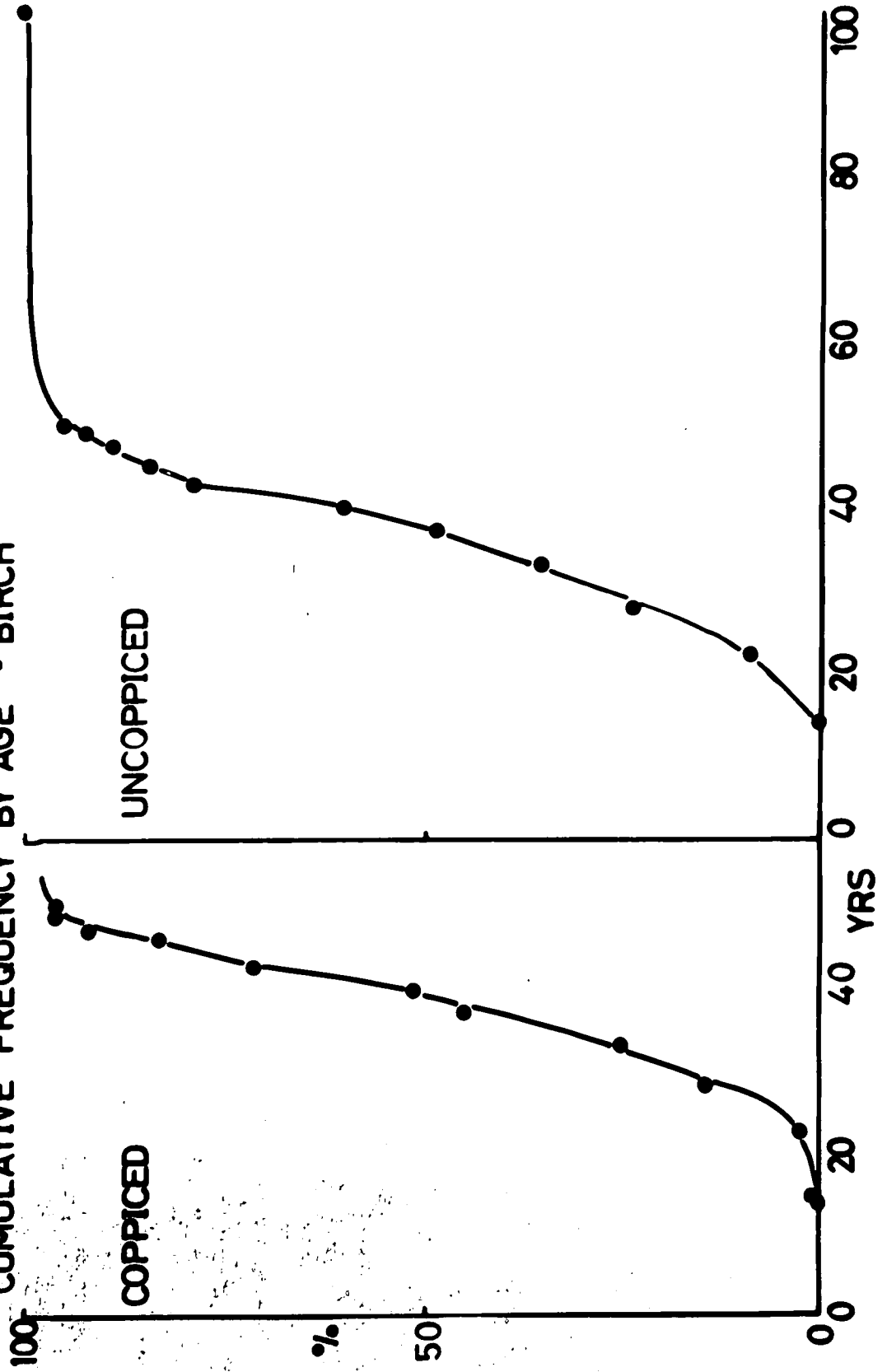
Figure 21.

Frequency distribution by age - birch.
a. coppiced.
b. uncoppiced.

FREQUENCY DISTRIBUTION BY AGE - BIRCH
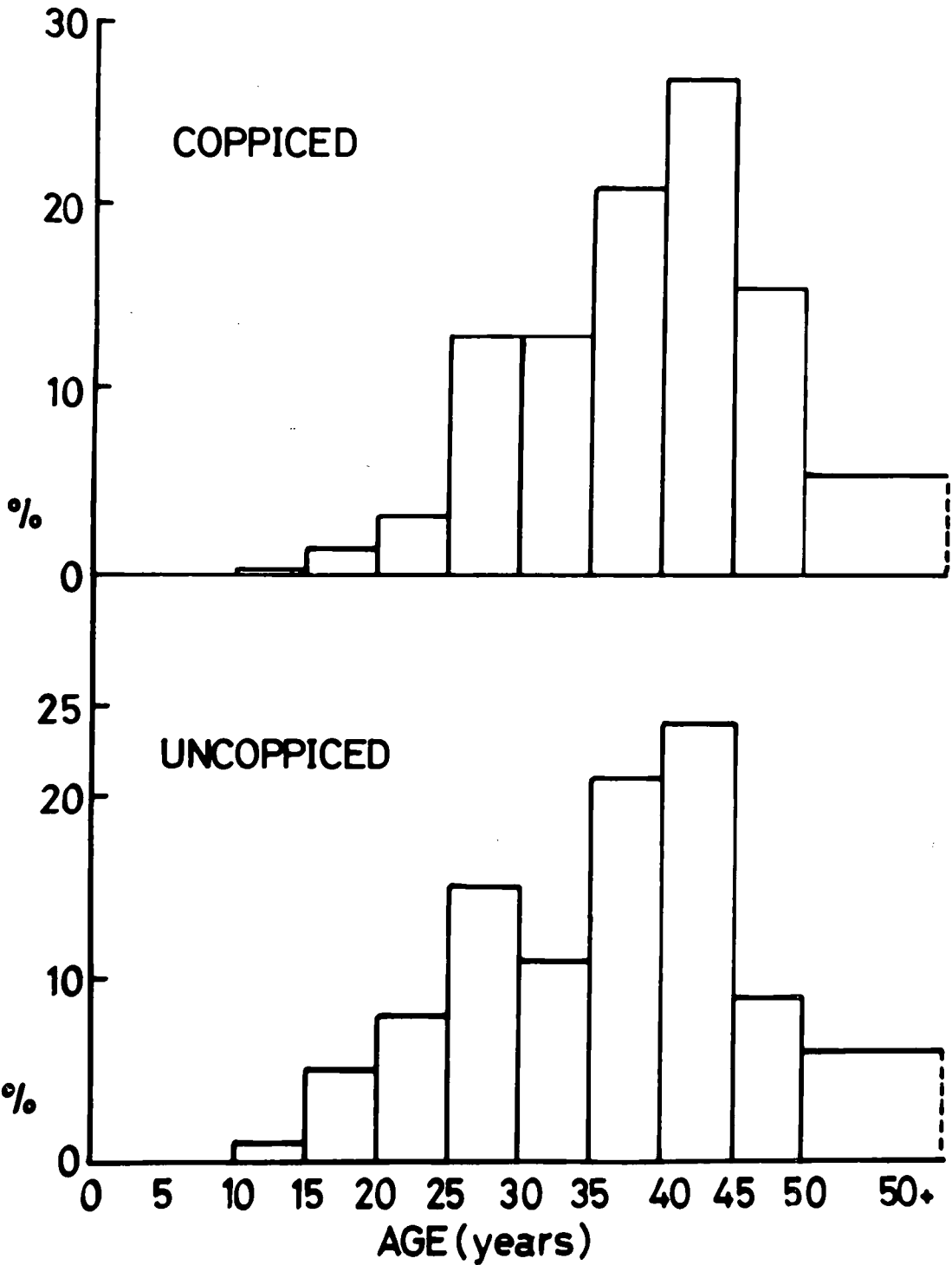
present for at least that period of time. In fact half or
more of the birch shoots were between 35 and 45 years of age.
If the age-distribution of coppiced shoots is compared with
that of uncoppiced shoots, some light may be thrown on the
development of the stand. The two distributions were quite
similar, suggesting that birch stools were already available
for coppicing at about the same time as the oldest extant trees
began growth. Coppicing has the initial effect of opening up
the canopy and most probably leads to increased regeneration
by sexual means. Very little coppicing, if any, of birch has
taken place in the last 25 years.

In the case of alder, age may be derived from diameter
by a simple graphical method (Fig.22). Thereafter the construction
of age-distribution for alder follows that for birch (Fig.23a and b,
and Fig.24a and b). Alder is often seen as even-aged stands
(McVean 1953). Thereafter the wide age-range here is at first
sight surprising. The explanation is that the canopy in the
Study Area has been opened periodically by coppicing, for example,
65 - 60 years ago, and 30 - 20 years ago. In the first case the
coppicing was followed in the subsequent 5 - 10 years by an
increase in sexual reproduction. Sporadic coppicing possibly
took place from 80 to 16 years ago. Figure 25 summarizes the
history of the Study Area as indicated by the tree age-distributions.
The successional condition has been maintained by management

Figure 22.

Diameter squared (cm^2) vs. age - alder.

D² VS. AGE - ALDER
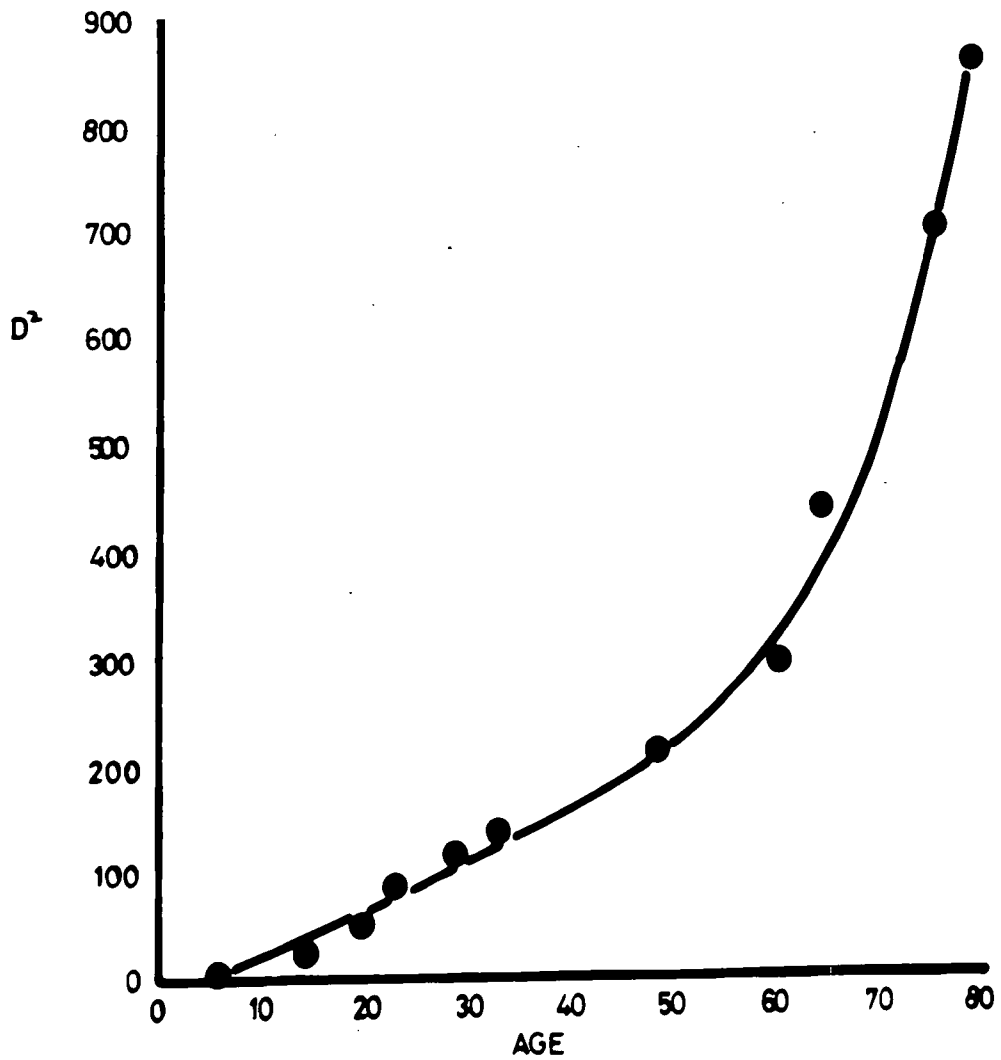
Figure 23.

Cumulative frequency by age - alder.
a. coppiced.
b. uncoppiced.

CUMULATIVE FREQUENCY BY AGE - ALDER
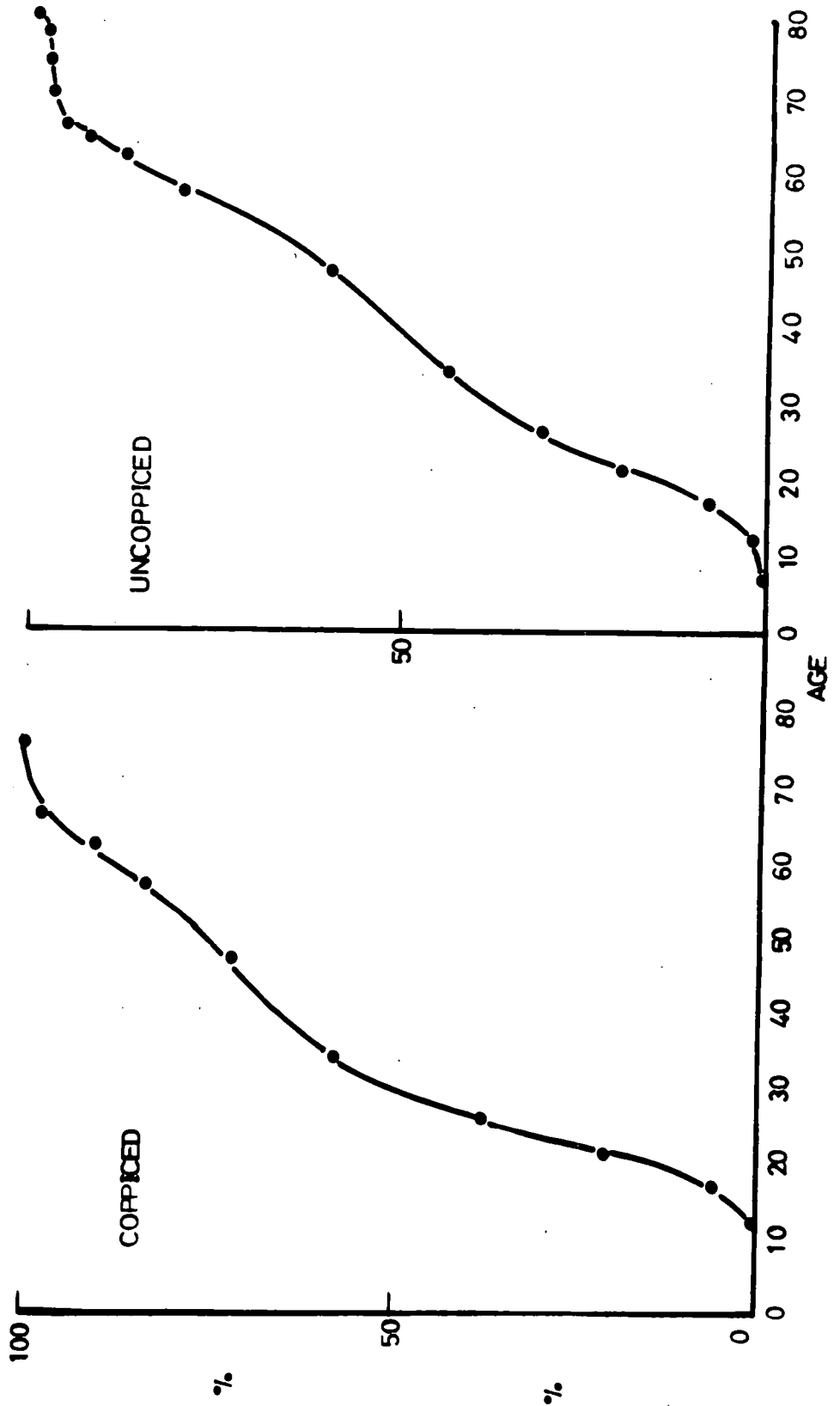
Figure 24.

Frequency distribution by age - alder.
a. coppiced.
b. uncoppiced.

FREQUENCY DISTRIBUTION BY AGE · ALDER

COPPICED

UNCOPPICED

AGE
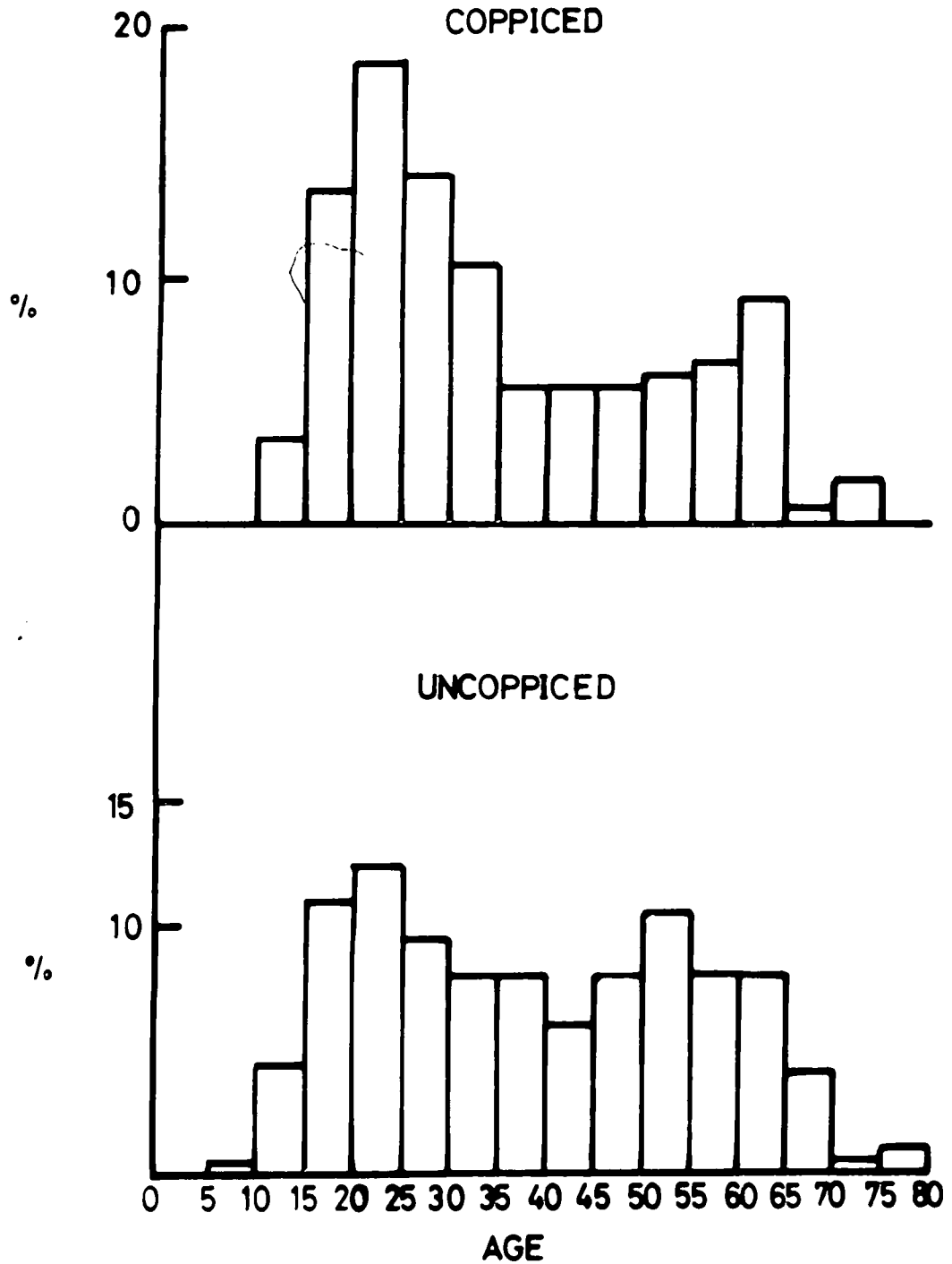
Figure 25.

The history of the Study Area as indicated by tree age-distribution.

STUDY AREA HISTORY

DATE	ALDER	BIRCH
1865		PRESENT
1875	? PRESENT	
1885		
1895		
1905	EXTENSIVE COPPICING – REGENERATION	
1915		EXTENSIVE COPPICING – REGENERATION
1925		↓
1935	EXTENSIVE COPPICING – REGENERATION	
1945		REGENERATION
1955	FORESTRY COMMISION MANAGEMENT	
1965	STUDY PERIOD	

practices.   Since 1952 these practices have ceased and already other tree species are gaining ground in the understorey of the Birch Zone.

Unfortunately, there are no records of material removed from the Study Area, and the calculation of the production history of the extant trees would tell little about the development of the vegetation.

CHAPTER II - SECTION V

Tree Litter and Canopy Biomass

V. i. <u>Introduction</u>

Without doubt, the most striking and fascinating series of changes taking place in a deciduous woodland is the annual appearance, growth, colour change and eventual fall of tree leaves. These events have an aesthetic appeal which is only outstripped for the ecologist by their <u>a priori</u> importance in forest processes. The opening of buds and the subsequent increase in leaf area and biocontent represent the sum of many complex chains of events that end in leaf browning, abcission, and the fall of newly-fixed carbon to the soil, returning with it other materials originally derived from the soil. It is here that the interdependence of the two main ecosystem processes, that is, energy flow and mineral cycling, may be seen most clearly. In order to demonstrate the connection it is sufficient to trace the life-history of a single leaf. Its primordia come from the tree's stored energy and material; it acts as a part of the forest's photosynthetic machinery, a role which demands very specific nutrient supplies; it changes its role to become a transfer agent, its chemistry changing for the part; and then falls to the ground so that the return of the nutrients to the soil and eventually back into the plants may begin. That is, the trees sacrifice a major portion of the energy they have fixed during the summer so as to support

those organisms essential to the release and recirculation of
the nutrients on which they, the trees, depend.   These organisms
are not only concerned directly with nutrient recirculation but
also with the whole complex of tasks resulting in the maintenance
of soil conditions suitable for a massive ecosystem.

In short, the circulation of minerals in an ecosystem
is, in large part, work-requiring.   All free energy in the
ecosystem has been fixed by the trees and other autotrophs.
All free energy available to a major part of the biota,
essential to mineral cycling, is in the form of tree litter
biocontent.   Tree litter does not consist only of leaves,
but contains dead and fallen materials from other tree organs,
e.g. twigs, bark, fruits and indeed whole stems.   Any study of
litter fall must include these components.

The importance of litter fall in forests has been
recognized by many workers in diverse fields.   A review of
this work was produced by Bray & Gorham (1964).   The field
is a wide one and the review cited comprehensive;   therefore
no attempt is made to review it here.   It is, however, possible
to summarize certain methodological conclusions from the literature.
First, the obvious means by which to estimate litter fall is to
catch the falling litter on, or in, a series of trapping devices
presenting a known horizontal area.   What is seldom stated
explicitly in the literature is whether litter falling from

the trees is to be measured, or material arriving on a given ground area in known time.   Whilst in many cases these two quantities are probably identical, under certain conditions, for example where a substantial wind-blow of fallen material takes place, it is possible that they could differ (Ovington 1963). Therefore care must be taken in trap design and placement to achieve one or other measurement, and the aim should be explicitly stated.

Second, a number of types of trapping devices have been used to measure falling litter including a cleared soil surface;   a metal or plastic screen just above soil surface; metal, wood or plastic boxes or buckets with free drainage, often containing a cloth lining;   deep cloth bags suspended from a hoop 1m or so above ground;   large plastic funnels and so on.   Newbould (1967) has listed eight requirements a trap for falling litter should meet.   With one modification (No.vi) these may be stated thus :-

    i.   that litter should drop into the trap without any aero-dynamic effects preventing this.

    ii.   that the trap opening should be well above soil surface.

    iii.   that the trap be large enough both for (i) and for sampling purposes.

    iv.   that the rim be level.

    v.   that the rim be well-defined.

vi. that material from the ground should not get in (including tree litter blowing across the ground, M.K.H.).

vii. that litter should not drop or blow out of the trap again.

viii. that litter in the trap should not decompose before being collected.

It should be added to requirement (ii), where applicable, that the trap opening should be well above the ground vegetation. Requirements (i) to (v) are concerned with the trap actually catching the litter that would normally fall through the horizontal area presented by the trap if the trap were absent. Requirements (iii) to (v) are also concerned with the precision of the estimate made by sampling a small proportion of the litter falling through the horizontal plane at the level of the trap tops. Requirements (vi) to (viii) are concerned with the addition to or loss from the trap of material other than by litter fall and clearance by the observer. Requirement (viii) may be met as much by frequent clearance as by trap design.

The third main methodological conclusion may be drawn from the literature on the measurement of litter fall in forests concerns the size and number of traps used. Medwecka-Kornas (in press) has pointed out that the size and number of traps used must be related to the scale of pattern in the woodland

studied and the degree of precision required for the litter

fall estimate. It being impossible to collect all the litter

falling in a large area, it is necessary to depend on a sample

consisting of a smaller area. This could either comprise one

or few large sample units, or a larger number of more widely

distributed small sample units. Because of the lateral

heterogeneity of most woodland systems, most workers have taken

the latter course (e.g. Ovington 1963; Bray & Gorham 1964;

Carlisle, Brown & White 1966; Scott 1955; Lindquist 1938).

It is of course necessary to reconcile the need for a large

number of small traps and the need for large traps discussed

above (requirement (iii) in the discussion of trap design).

The fourth methodological conclusion on litter fall

studies concerns the period and frequency of litter fall sampling.

Ovington (1963) has clearly demonstrated that litter fall should

be measured all the year round if a serious underestimate is to

be avoided. This is because several litter components fall at

times other than in the autumn. Such components, for example,

flowers and seeds or branches and twigs, may form a large part

of the litter fall. In order to prevent the accumulation of

large amounts of material in a litter trap at any time of year,

frequent emptying of the traps is important. If this is not

done it is possible that humidity in the trap may rise and

decomposition of the trapped materials accelerate.

Fifthly, Bray & Gorham (1964) have clearly established that the size of litter fall may change quite markedly from year to year. Therefore, in order to characterize litter fall at a given stage in the development of a woodland, it should be measured over several years.

In addition to the study of litter fall, the biomass, biocontent, number and area of the canopy leaves were studied. This work is described in this Section. The basic technique uses the numbers of leaves per unit area derived from the litter trap data and periodic sampling of canopy leaves for the relevant attributes. This method assumes that the total number of leaves falling corresponds to the number of leaves actually present in the canopy from bud-burst to leaf-fall. Whether or not this was actually the case is discussed along with the presentation of the data.

V. ii. <u>Methods</u>

The methods described here are for :-

a) the estimation of litter fall other than large branches and tree stems

b) the estimation of the fall of large branches and tree stems

c) the estimation of canopy biomass, biocontent and Leaf Area Index. This is dealt with third because it depends on certain litter fall data being available.

These will be described in turn.

a) the estimation of litter fall other than large branches and tree stems. It is with this estimation that most of the studies cited in the Introduction (V.i) to this section have been concerned. As falling litter was measured, a trap design meeting the eight requirements listed above was needed. The type used is shown in Figure 26. It consisted of a calico bag suspended from a galvanized iron hoop of ~~diameter~~ radius 28.2cms and depth 8cms. The bag, which was 1.28m deep, hung 1.10m from the hoop, presenting a horizontal opening of 0.25m^2. The bag was sewn in such a way that there were no corners inside it where material might stick. The bag was tied, by sewn-on tapes, to the hoop so that the rim presented to falling litter was well-defined. The hoop was supported as shown in Figure 26 at 1.3m above the ground by a 5 x 5cm stake, driven a further 30cm into the ground. The bottom of the bag was tied firmly to the stake by tapes. Such a trap, with a well-defined rim and steep, deep sides, allowed litter to drop in without hindrance from aero-dynamic effects. It was well above the soil and ground vegetation and appeared to be large enough for aerodynamic purposes. The stout hoop and fixing kept the rim well-defined. With such a deep bag there was little likelihood of material from the ground getting in. Neither could material blow or drop out. The material was freely water-permeable and so, providing that the trap was cleared frequently enough, too much decomposition did not take place in the trap. Thus this type of trap met all the conditions suggested by Newbould (1967).

Figure 26.

Litter trap. An explanation is given on page 49.

LITTER TRAP

METAL SLEEVE FIXING HOOP TO STAKE

5x5 CM WOODEN STAKE

GALVANIZED HOOP RIVETED TO SLEEVE

BAG TIED TO HOOP

20 CM.

SOIL SURFACE
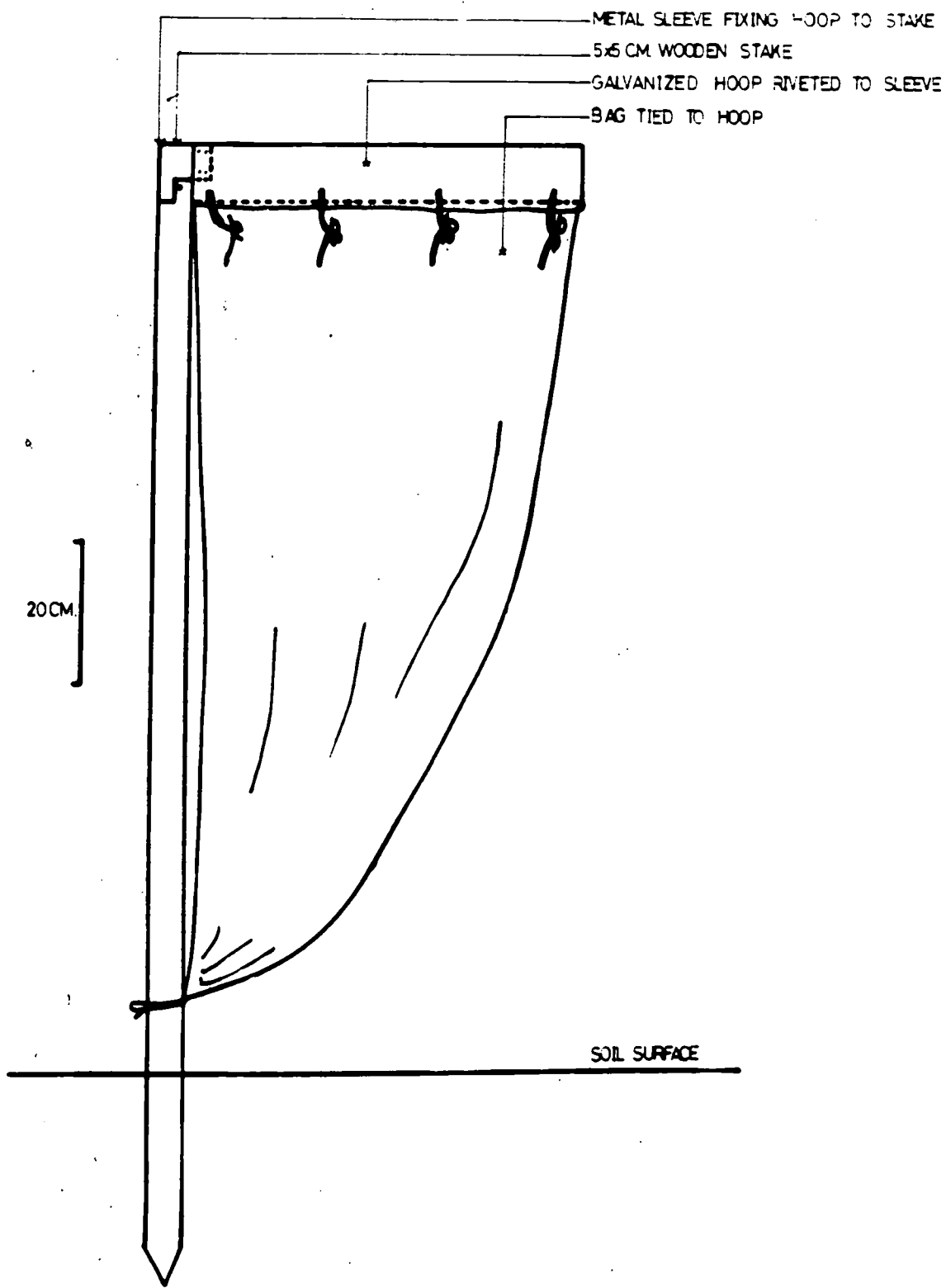
In May 1966 three such traps were erected at random in each of the eight 20 x 20m squares making up the Grid (Fig.27). Thus the 24 traps each presenting an area of $0.25m^2$ made up a total sample area of $6m^2$ on the $3,200m^2$ Grid, these traps being placed in a stratified random manner. As little information on woodland pattern was available at this time, a stratified random distribution of the traps was chosen as being the most likely to yield reasonable data for the area studied. The number of traps was determined in part by the time available to deal with collected material and by the need to keep down the number of regularly visited points in the Grid area.

From May 30 1966 until May 25 1968 the traps were visited and cleared as frequently as pssible. Due to transport difficulties traps could not be visited with absolute regularity. Excepting in winter, the traps were rarely left more than three weeks and were usually cleared fortnightly. On each occasion the contents of each trap were emptied into a separate labelled polythene bag. The calico bag was turned inside out and its bottom end shaken inside the polythene bag to remove any material sticking to the trap. All woody material of diameter greater than 2.5cms was discarded. That part of any branch or twig found lying across the trap which had a smaller diameter than this was cut at the rim of the trap and placed in the polythene bag. All the traps were inspected on each clearance occasion and faulty parts repaired or replaced.

Figure 27.

Litter trap positions on the Grid.

NEWTON HANZARD GRID
LITTER TRAP POSITIONS
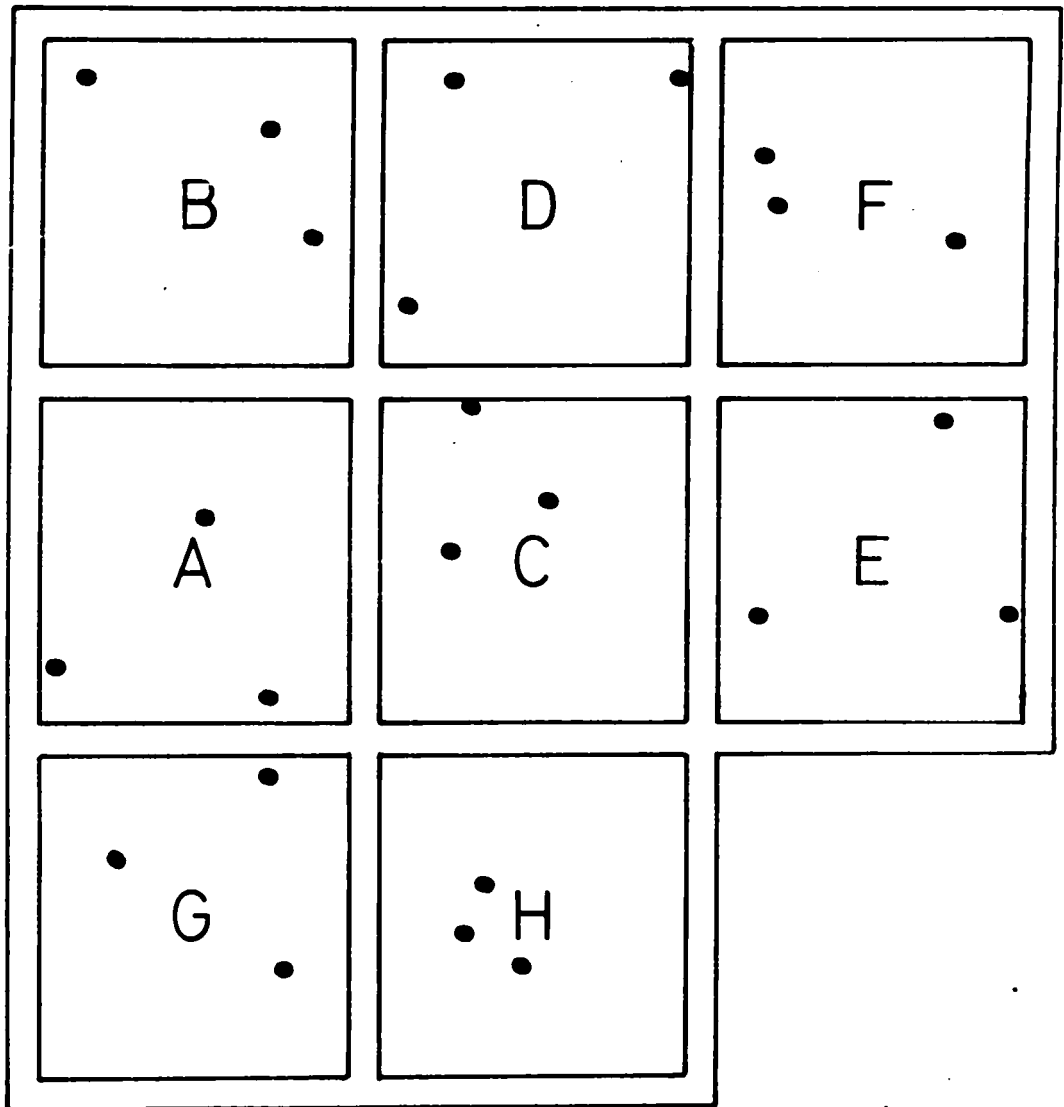
LITTER TRAP - •

In the laboratory the material collected from each trap was sorted as soon as possible. If any delay arose, the material was stored in a deep-freeze cabinet. The material was sorted into the following categories :-

completely green alder leaves

mottled or brown alder leaves

completely green birch leaves

mottled or brown birch leaves

litter of other tree species

Alder female reproductive structures

Alder male reproductive structures

Birch female reproductive structures

Birch male reproductive structures

Woody material smaller than 2.5cm diam.

Bud scales and detritus larger than 1mm dia.

Detritus smaller than 1mm diam.

In fact, the contents of each polythene bag were emptied onto a 1mm sieve and the various types of material lifted off. The alder and birch leaves were counted in 1966-7, but not 1967-8. After sorting, each category of material from each trap was placed in an unglazed paper bag and dried at 105°C for 24 hours. Then the materials were weighed to 1mg on a Mettler balance. Thus the mean weight of each category of litter cleared from the 24 traps on each occasion and through the whole

year could be calculated.   After drying, a subsample of each

category of material was milled and pelleted for calorific

analysis (cf. Section III).

b) The estimation of the fall of large branches and tree stems.

The 20 x 20m square marked 'C' in the diagram of the Grid

(Fig.1, Section II) was used for this estimation.   All the

branches and stems of diameter greater than 2.5cm lying on the

Forest Floor were marked with two circles of red paint at their

thickest end in April 1967.   In April 1968 all unmarked fallen

branches of this size in that area were picked up and weighed

fresh, using a spring balance.   Subsamples were taken and dried

at 105°C to constant weight.   Thus an estimate of the total dry

weight of branch material of diameter greater than 2.5cms falling

onto this 400m area was obtained.

Throughout the period April 1966 - April 1968 the fall

of any trees on the Grid was noted and their diameter at breast

height so that, using the allometries described in Section Iv,

the dry weight of the fallen tree might be calculated.

c) The estimation of canopy biomass, biocontent and Leaf Area

Index.   In the summer of 1966, leaves were collected from the

tree canopy on several occasions by climbing trees and picking

all the leaves from a branch.   Thus, on each occasion, 100

leaves of birch and 100 of alder were picked.   Of each hundred,

25 were taken from a branch 9 - 12m above ground, 25 from 6 - 9m,

25 from 3 - 6m, and 25 from 0 - 3m. Each branch was on a
different tree. The trees from which the sample branches were
taken lay on the periphery of the Grid. Four numbers of outer
corner posts were chosen at random and a branch taken from the
nearest alder and birch tree to each, outside the Grid. The
lowest sample was taken from the first position to come up for
birch, the highest for alder. Then higher samples for birch and
lower for alder were taken from each successive position. For
each branch all the leaves were placed in opaque polythene bags,
which were shaken thoroughly before the sample of 25 was pulled out.
The remaining leaves from all the branches were bulked, shaken up
and used for calorific analysis (see Section III). The sample
leaves were taken to the laboratory and contact prints made of
them. The area of each leaf was determined from its print by
counting using a transparent 1mm grid placed over the print.
All 1mm squares half or more white were counted in the leaf area.
Then the sample leaves were dried at 105°C for 24 hours in un-
glazed paper bags. The dried leaves were weighed in tens to
1mg on a Mettler balance. Hence the mean dry weight, biocontent
and area per leaf was determined. The lower leaves may have
been over-represented because a simple bulking of leaves from
the four height zones was used. However, these 'per leaf'
data were combined with the leaf number data from the litter trap
studies so that canopy biomass, biocontent, and Leaf Area Index
could be calculated.

In the summer of 1967 the same procedure was adopted, using the weight /litter leaf data from the previous year, excepting that the branches from which the sample leaves were obtained were cut down using a 10m aluminium extension pruner.

V. iii. Results of Tree Litter Fall Studies

(a) Biomass

First the litter fall data by clearing date and trap are given for 1966-7 and then for 1967-8. The data for large litter fall are then presented.

Table XX shows the mean dry weight of each category of material cleared from the 24 traps on each occasion from 20 May 1966 to 20 May 1967. The seasonal pattern of litter fall will be discussed with the biocontent results. Table XXI shows the mean and standard error of the total dry weight of each category of litter falling into the 24 traps during the whole period 20 May 1966 to 20 May 1967. Of the total of 263.288 $\pm$ 11.687g/m^2, the alder and birch leaf fall (185.353 $\pm$ 7.889g/m^2) contributed 70.78%. Of the remaining 29.22%, almost exactly half fell as wood litter, the other 15% or so of the total fell as flowers and fruits, scales and detritus smaller than 1mm, along with the litter of the other tree species.

Table XXII shows the mean dry weight of each category of material cleared from the 24 traps on each occasion from

TABLE XX   Litter trap data by occasion of clearing 1966-7 mg/m^2 (1 S.E.)

CATEGORY	DATE									
	20/5	15/6	6/7	5/8	17/8	10/9	19/9	4/10	17/10	25/10
Alder leaves, green	-	151.8 (44.9)	22007.6 (376.0)	3865.8 (839.6)	6505.3 (2586.6)	6251.2 (1231.6)	897.8 (97.9)	-	179.2	674.4 (245.5)
Alder leaves, brown	-	-	-	-	-	-	3165.6 (678.3)	10000 (1820.0)	25392.0 (4303.6)	16160 (2460)
Birch leaves, green	-	448.4 (85.2)	2326.0 (443.6)	2519.5 (422.4)	2742.0 (428.0)	7318.0 (1453.6)	343.3 (110.9)	-	34.5	-
Birch leaves, brown	-	-	-	-	-	-	4732.6 (1003.6)	14840.0 (29200.0)	18028.0 (3379.0)	10026.0 (1804.0)
Other Tree Litter	-	16.9 (5.96)	167.0 (106.0)	9.7	38.0 (15.0)	37.2 (17.2)	53.2 (21.2)	3.1	4.9	44.4 (22.1)
Alder rep ♀	-	-	-	15.4 (54.0)	-	298.0 (70.0)	73.3 (25.0)	39.9 (10.5)	73.5 (19.2)	7.8 (5.2)
Alder rep ♂	-	-	372.0 (135.0)	-	1021.7 (370.4)	-	39.7 (15.2)	93.7 (32.1)	-	98.0 (25.2)
Birch rep ♀	-	-	-	-	-	-	25.6 (19.2)	-	90.1 (29.2)	52.8 (21.1)
Birch rep ♂	-	19.3 (9.5)	-	25.4 (8.7)	102.0 (36.0)	66.8 (28.5)	91.2 (32.1)	69.8 (22.1)	-	42.2 (21.1)
Scales	-	776.5 (75.9)	1158.0 (123.0)	905.0 (71.8)	797.0 (69.0)	1026.4 (93.2)	432.2 (51.2)	171.6 (34.7)	42.2 (8.6)	56.7 (8.3)
Micro	-	148.5 (65.9)	236.5 (43.0)	44.9 (7.8)	36.0 (10.0)	154.8 (25.6)	66.0 (8.96)	23.7 (5.1)	1.51 (-)	9.30 (2.66)
Wood	-	529.0 (202.4)	2314.0 (578.8)	1265.2 (425.7)	16804.0 (5712)	992.4 (88.0)	902.8 (437.4)	35.9 (11.0)	2.6	124.5 (42.6)

TABLE XX (Contd.)   Litter trap data by occasion of clearing 1966/7 mg/m^2 (1 S.E.)

CATEGORY	DATE									
	7/11	17/11	5/12	13/12	11/1	10/2	22/3	10/4	8/5	20/5
Alder leaves, green	3107.8 (504.0)	420.8 (121.1)	866.7	5.4	-	-	-	-	29.7	39.6
Alder leaves, brown	13720.0 (2580.0)	16864.4 (3356.4)	-	-	18.1	21.8	-	110.5	2.6	19.7
Birch leaves, green	-	-	-	-	-	-	-	-	314.9	235.3
Birch leaves, brown	8952.0 (1306.0)	2812.0 (574.2)	165.5	-	0.5	5.3	-	1.6	-	-
Other tree litter	2319.2 (432.1)	3172.7 (223.1)	559.9 (210.1)	43.8 (21.1)	39.7 (15.3)	-	-	2.4	6.4	-
Alder rep ♀	216.0 (97.2)	1083.8 (210.1)	643.3 (221.1)	7.8	296.8 (31.1)	37.6 (11.1)	1330.0 (311.1)	29.1 (20.0)	-	26.6 (21.2)
Alder rep ♂	173.9 (81.2)	204.6 (71.1)	407.7 (110.7)	85.2 (11.1)	50.4 (42.2)	61.3 (11.5)	1675.0 (210.1)	1671.7 (192.5)	710.4 (151.8)	92.1 (42.5)
Birch rep ♀	37.2 (16.3)	-	7.7	-	53.6 (9.3)	-	80.0 (26.7)	81.9 (50.0)	-	128.3 (26.6)
Birch rep ♂	33.2 (11.1)	87.7 (17.7)	71.9 (31.2)	-	135.1 (21.1)	22.5 (8.5)	458.3 (123.7)	213.1 (10.1)	903.8 (172.2)	320.2 (100.1)
Scales	52.9 (12.6)	101.1 (25.3)	767.7 (62.0)	85.6 (15.2)	95.3 (20.1)	192.0 (32.2)	936.7 (111.5)	336.7 (71.1)	3461.9 (710.1)	3914.8 (159.9)
Micro	2.8 (0.9)	8.0 (1.1)	198.5 (36.0)	27.0 (3.0)	9.8 (1.4)	216.8 (42.2)	310.0 (52.5)	107.5 (8.8)	35.7 (10.0)	363.2 (61.1)
Wood	1367.7 (675.2)	2024.0 (610.2)	5500.2 (1017.2)	50.7 (15.0)	2297.6 (811.8)	461.0 (235.5)	16595.0 (16101.1)	1135.4 (511.1)	776.5 (113.3)	1205.3 (511.1)

TABLE XXI   Composition of Tree Litter 1966-7 (mg/m^2 $\pm$ 1 S.E.)

Alder	leaves	Green	25,103.3	$\pm$	4,792.2
"	"	Brown	85,504.7	$\pm$	4,263.6
Birch	"	Green	16,171.9	$\pm$	2,514.0
"	"	Brown	59,572.7	$\pm$	9,483.2
Other	Tree leaves		6,519.9	$\pm$	1,793.6
Alder	rep.	♀	5,047.0	$\pm$	1,239.6
"	"	♂	5,363.7	$\pm$	1,229.2
Birch	"	♀	770.7	$\pm$	260.0
"	"	♂	3,449.0	$\pm$	572.4
Scales			15,305.0	$\pm$	460.4
Micro			2,000.5	$\pm$	95.6
Wood			38,479.6	$\pm$	7,127.2
	TOTAL		263,288.0	$\pm$	11,687.3

20 May 1967 to 30 May 1968. Table XXIII shows the mean and standard error of the total dry weight of each category of litter falling into the 24 traps during the whole period 20 May 1967 to 30 May 1968. The total ($272.497 \pm 9.546 g/m^2$) was not significantly different from the 1966-7 total. The alder and birch leaves contributed a smaller proportion of the total (63.05%) than in the first year. The wood litter again came to about half of the remaining 36.95%.

The standard error of the total dry weight of litter falling into the traps was 4.43% and 3.50% of the mean in 1966-7 and 1967-8 respectively. Thus the 95% confidence limits of the total litter trapped as dry weight fell well within the $\pm$ 10% range which Newbould (1967) suggests as desirable. The corresponding figures for total alder and birch leaf fall were 4.23% and 5.13% respectively. The standard errors of the individual components were larger, and whilst sampling intensity was great enough to obtain reliable totals, it was not great enough to give 95% confidence limits of less than $\pm$ 10% for most of the components.

If the map of litter trap positions (Fig.27, this Section) is compared with the map of the two vegetation zones (Fig.8, Section II 13 of the litter traps may be seen to lie in the Alder Zone and 11 in the Birch Zone. Thus it was possible to calculate litter fall for each of the zones separately although the validity of these estimates must be limited because the positions of the traps were

TABLE XXIII   Composition of Tree Litter, Grid 1967-8

$(mg/m^2 \pm 1 \text{ S.E.})$

Alder leaves	Green	7,822.6	±	1,717.2
" "	Brown	80,968.2	±	14,782.4
Birch leaves	Green	10,790.2	±	2,092.8
" "	Brown	72,234.1	±	9,905.7
Other Tree leaves		5,779.8	±	2,780.8
Alder rep. ♀		4,903.1	±	1,198.4
" " ♂		8,749.6	±	1,592.3
Birch " ♀		741.9	±	284.9
" " ♂		3,314.6	±	687.6
Scales		21,846.8	±	1,489.8
Micro		3,807.9	±	412.9
Wood		51,538.8	±	4,606.4
	TOTAL	272,497.6	±	9,546.4

TABLE XXIV   Composition of Tree Litter, Alder Zone 1967-8

$(mg/m^2 \pm 1 \text{ S.E.})$

Alder leaves	Green	7,025.6	±	1,033.2
" "	Brown	136,912.8	±	13,891.6
Birch leaves	Green	444.0	±	93.6
" "	Brown	29,400.6	±	7,333.6
Other Tree leaves		3,056.9	±	1,962.8
Alder rep ♀		9,189.3	±	1,514.0
" " ♂		14,489.7	±	1,737.2
Birch rep ♀		153.5	±	146.4
" " ♂		1,367.8	±	233.2
Scales		18,601.0	±	716.8
Micro		3,189.2	±	313.6
Wood		46,315.3	±	6,579.2
	TOTAL	269,945.7	mg/m^2	

not decided with reference to the vegetation zones. However,
the data may be instructive. Tables XXIV and XXV show the
means of trap totals for Alder and Birch Zones respectively.
The two calculated totals are within $5g/m^2$ of one another.
The total alder and birch leaf fall in the Alder Zone was
$173.784g/m^2$, and in the Birch Zone $169.923g/m^2$. However, in
the Alder Zone about 80% of this was as alder leaves and in
the Birch Zone a slightly smaller proportion than this was
birch leaves. The litter of other tree leaves was more than
twice as important in the Birch Zone as in the Alder Zone.
The fall of scales, micro-litter and wood were greater in the
Birch Zone, but that of fruits and other reproductive parts
was much greater in the Alder Zone. This was largely due to
Alder 'catkins'.

When these estimates were combined to give an estimate
for the Grid where the between-zones sum of squares is excluded
from the calculation of standard error (Table XXVI), much smaller
standard errors than in Table XXIII resulted. It would not be
valid to use these estimates because the positioning of the traps
was not appropriate, but they do indicate that particular care
should be taken in the positioning of litter traps relative to
woodland pattern.

The total fall of new branch material on square 'C' in
1967-8 was 4,075.32 grams, or $10.188g/m^2$. This material did

TABLE XXV   Tree Litter, Birch Zone 1967-8 (mg/m^2 ± 1 S.E.)

Alder	Leaves	Green		8,588.5	± 3,547.4
"	"	Brown		27,217.4	± 9,060.8
Birch	Leaves	Green		20,730.5	± 610.4
"	"	Brown		113,387.9	± 3,688.8
Other	Tree Leaves			8,395.9	± 5,480.8
Alder	rep	♀		785.2	± 396.0
"	"	♂		3,234.7	± 831.6
Birch	rep	♀		1,307.2	± 502.8
"	"	♂		5,195.1	± 826.4
Scales				24,965.3	± 2,414.4
Micro				4,402.4	± 683.4
Wood				56,557.4	± 5,951.6

TOTAL   274,757.5 mg/m^2

TABLE XXVI   Composition of Tree Litter, Grid 1967-8

Calculated from alder and birch zone data

mg/m^2 ± 1 S.E.)

Alder	Leaves	Green		7,791.4	± 1,815.2
"	"	Brown		83,162.0	± 8,360.0
Birch	Leaves	Green		10,384.3	± 302.8
"	"	Brown		70,554.4	± 1,313.2
Other	Tree Leaves			5,779.8	± 226.6
Alder	rep	♀		5,071.2	± 796.0
"	"	♂		8,974.7	± 974.8
Birch	"	♀		718.8	± 257.6
"	"	♂		3,238.3	± 118.8
Scales				21,719.4	± 1,238.0
Micro				3,783.7	± 370.8
Wood				51,333.9	± 4,443.6

TOTAL   272,511.9

not appear to have undergone any substantial decomposition
before collection.   Square 'C' contained parts of both
vegetation zones.   One tree fell on the Grid during the period
April 1966 to April 1968.   This was a birch of dbh 10.5cms
blown over by strong winds in April 1967.   The root system
was not completely severed, and an apparently full complement
of leaves was formed in 1967 and 1968;   this tree could not be
included in the estimate of litter fall.   Thus almost 85% of
the wood litter in the period April 1967 - April 1968 fell as
branches or twigs of diameter less than 2.5cms.

(b)   Biocontent

First the litter fall biocontent data by clearing date
and cumulatively is given for 1966-7 and then for 1967-8.

Table XXVII shows the mean biocontent as $Kcals/m^2$
of each category cleared from the 24 traps on each occasion
from 20 May 1966 to 20 May 1967.   The seasonal pattern of
biocontent fall is best seen by an examination of Table XXVIII
which shows cumulative litter biocontent fall.   The total fall
of 1,422.906 $Kcal/m^2$ came at all times of year (Fig.28), but the
major part of it (75%) fell in the months of August to November
inclusive.   Most (65%) of the total fall was made up of Alder
(553.697 $Kcal/m^2$) and Birch (388.002$Kcal/m^2$) leaves.   These
leaves fell (Fig.29) largely in October (almost 50% of the
totals of each) and September in Birch, November in Alder.
The 35% other than Alder and Birch leaves fell a little more

TABLE XXII

Litter Trap Data by occasion of clearing 1967-8   (mg/m² ± 1 S.E.)

D A T E

CATEGORY	2∅/5	10/6	10/7	31/7	18/8	6/9	25/9	11/10	26/10	14/11	27/11	18/1	20/2	20/3	10/4	8/5	25/5
Alder leaves, green	-	122.8	180.8	180.8	38.3	1461.8	1745.0	709.1	1614.9	145.0	1489.1	-	-	-	-	24.4	30.1
Alder leaves, brown	-	58.5	1229.5	4310.1	3074.1	3606.0	7733.6	4525.0	22227.6	30562.7	9265.6	-	-	-	46.2	-	-
Birch leaves, green	-	369.2	97.5	81.6	11.5	292.7	-	41.2	-	-	-	-	-	-	-	-	-
Birch leaves, brown	-	-	7133.4	1850.5	1606.3	5752.5	7298.0	7299.7	8206.9	14166.2	1293.1	-	-	-	68.2	282.7	-
Other tree litter	-	-	37.0	23.3	8.0	24.0	-	449.7	611.6	342.6	928.1	15.0	-	-	-	-	-
Alder rep ♀	-	86.8	56.7	-	5.3	341.8	-	786.2	590.0	821.6	5.0	1298.4	353.3	866.9	33.7	-	-
Alder rep ♂	-	53.8	-	46.5	-	117.8	61.7	-	228.3	406.7	43.3	516.7	4503.1	1177.2	869.4	657.8	646.3
Birch rep ♀	-	417.5	9.3	18.2	49.1	106.4	-	-	-	-	-	-	-	-	-	-	-
Birch rep ♂	-	57.8	3.8	14.3	134.5	400.3	37.3	61.5	-	60.0	20.3	-	80.0	358.2	170.2	798.7	996.0
Scales	-	2729.1	2436.4	413.5	368.3	3805.6	327.6	957.8	1278.3	938.3	16.8	-	1243.9	643.1	288.3	3115.4	2960.1
Micro	-	610.2	735.8	43.0	16.4	705.1	13.0	119.4	-	-	-	-	701.5	324.3	119.4	26.6	327.9
Wood	-	1762.8	861.8	2693.7	1977.0	4924.8	15.0	2590.0	3185.0	5193.5	70.9	10554.8	4833.0	10179.3	1729.8	300.5	137.9

TABLE XXII Litter Trap Data by occasion of clearing 1967-8   (mg/m² ± 1 S.E.)

DATE

CATEGORY	20/5	10/6	10/7	31/7	18/8	6/9	25/9	11/10	26/10
Alder leaves, green	-	122.8	180.8	180.8	38.3	1461.8	1745.0	709.1	1614.9
Alder leaves, brown	-	58.5	1229.5	4310.1	3074.1	3606.0	7733.6	4525.0	22227.6
Birch leaves, green	-	369.2	97.5	81.6	11.5	292.7	-	41.2	-
Birch leaves, brown	-	-	7133.4	1850.5	1606.3	5752.5	7298.0	7299.7	8206.9
Other tree litter	-	-	37.0	23.3	8.0	24.0	-	449.7	611.6
Alder rep ♀	-	86.8	56.7	-	5.3	341.8	-	786.2	590.0
Alder rep ♂	-	53.8	-	46.5	-	117.8	61.7	-	228.3
Birch rep ♀	-	417.5	9.3	18.2	49.1	106.4	-	61.5	-
Birch rep ♂	-	57.8	3.8	14.3	134.5	400.3	37.3	-	-
Scales	-	2729.1	2436.4	413.5	368.3	3805.6	327.6	957.8	1278.3
Micro	-	610.2	735.8	43.0	16.4	705.1	13.0	119.4	-
Wood	-	1762.8	861.8	2693.7	1977.0	4924.8	15.0	2590.0	3185.0

CATEGORY	14/11	27/11	18/1	20/2	20/3	10/4	8/5	25/5
Alder leaves, green	145.0	1489.1	-	-	-	-	24.4	30.1
Alder leaves, brown	30562.7	9265.6	-	-	-	46.2	-	-
Birch leaves, green	-	-	-	-	-	-	282.7	-
Birch leaves, brown	14166.2	1293.1	-	-	-	68.2	-	-
Other tree litter	3421.6	928.1	15.0	-	-	-	-	-
Alder rep ♀	821.6	5.0	1298.4	353.3	866.9	33.7	-	-
Alder rep ♂	406.7	43.3	516.7	4503.1	1177.2	869.4	657.8	646.3
Birch rep ♀	-	20.3	-	-	-	-	-	-
Birch rep ♂	60.0	-	-	80.0	358.2	170.2	798.7	996.0
Scales	938.3	16.8	-	1243.9	643.1	288.3	3115.4	2960.1
Micro	-	-	-	701.5	324.3	119.4	26.6	327.9
Wood	5193.5	70.9	10554.8	4833.0	10179.3	1729.8	300.5	137.9

TABLE XXVII   Litter Trap Data by occasion of clearing 1966-7   (Kcal/m^2)

CATEGORY	20/5	15/6	6/7	5/8	17/8	10/9	19/9	4/10	17/10	7/11
Alder leaves, green	-	0.7404	9.791	19.3412	31.7264	30.4876	4.3786	-	0.8673	14.6564
Alder leaves, brown	-	-	-	-	-	-	15.338	49.624	128.382	70.425
Birch leaves, green	-	2.241	11.623	13.021	14.171	37.251	1.774	-	0.178	-
Birch leaves, brown	-	-	-	-	-	-	24.499	76.827	92.210	45.040
Other tree litter	-	0.076	0.747	0.043	0.169	0.175	0.238	0.014	0.022	10.369
Alder rep ♀	-	+	2.038	0.829	5.598	1.633	0.402	0.219	0.403	1.183
Alder rep ♂	-	-	-	-	-	-	0.217	0.513	-	0.953
Birch rep ♀	-	0.099	+	0.129	0.517	0.339	0.130	-	0.457	0.189
Birch rep ♂	-	-	-	-	-	-	0.462	0.354	-	0.168
Scales	-	4.248	6.335	4.951	4.360	5.821	2.451	0.973	0.239	0.300
Micro	-	0.742	1.182	0.224	0.180	0.774	0.330	0.118	0.008	0.014
Wood	-	2.684	11.741	6.420	85.263	5.035	4.581	0.182	0.013	6.940

CATEGORY	17/11	5/12	13/12	11/1	10/2	23/3	10/4	8/5	20/5
Alder leaves, green	1.9845	4.0873	0.0255	-	-	-	-	0.1401	0.1867
Alder leaves, brown	85.671	-	-	0.092	0.111	-	0.561	0.013	0.100
Birch leaves, green	-	-	-	-	-	-	-	1.752	1.176
Birch leaves, brown	14.141	0.832	-	0.002	0.027	-	0.004	-	-
Other tree litter	14.183	2.503	0.196	0.177	-	-	0.011	0.029	-
Alder rep ♀	5.938	3.525	0.043	1.626	0.206	7.287	0.159	-	0.201
Alder rep ♂	1.121	2.234	0.467	0.276	0.336	9.177	9.159	3.892	0.505
Birch rep ♀	-	0.039	-	0.272	-	0.406	0.415	-	0.651
Birch rep ♂	0.445	0.365	-	0.685	0.114	2.324	1.081	4.584	6.696
Scales	0.573	4.354	0.400	0.445	0.897	5.125	1.842	18.940	21.418
Micro	0.040	0.992	0.135	0.049	1.084	1.550	0.537	0.178	1.816
Wood	10.270	27.908	0.257	11.657	2.339	84.203	5.761	3.940	6.116

TABLE XXVIII

Cumulative Litter Trap biocontent data 1966-7 (Kcals/m^2)

CATEGORY	15/6	6/7	5/8	17/8	10/9	19/9	4/10	17/10	25/10	7/11
Alder leaves green	0.740	10.531	29.872	61.598	92.085	96.464	96.464	97.331	100.595	115.251
Alder leaves brown	-	-	-	-	-	15.338	64.962	193.344	275.049	345.474
Birch leaves green	2.241	13.864	26.885	41.056	78.307	80.081	80.081	80.259	80.259	80.259
Birch leaves brown	-	-	-	-	-	24.499	101.326	193.536	244.789	289.809
Other Tree Litter	0.076	0.823	0.866	1.035	1.210	1.448	1.462	1.484	1.682	12.051
Alder rep ♀	+	2.038	2.867	8.465	10.098	10.500	10.719	11.122	11.165	12.348
Alder rep ♂	-	-	-	-	-	0.217	0.730	0.730	1.267	2.220
Birch rep ♀	0.099	0.099	0.228	0.745	1.084	1.214	1.214	1.671	1.939	2.128
Birch rep ♂	-	-	-	-	-	0.462	0.816	0.816	1.036	1.198
Scales	4.248	10.583	15.534	19.894	25.715	28.166	29.139	29.378	29.699	29.999
Micro	0.742	1.924	2.148	2.328	3.102	3.432	3.550	3.558	3.604	3.618
Wood	2.684	14.425	20.845	106.108	111.143	15.724	115.906	115.919	116.551	123.491
Total canopy leaves	2.981	24.395	56.757	102.654	170.392	216.382	342.833	564.470	700.692	830.793
Total other litter	5.165	15.467	21.643	32.467	41.209	45.439	47.630	48.759	50.392	63.562
Grand Total	10.930	54.287	99.245	241.429	322.774	377.545	506.369	729.148	867.335	1017.846

CATEGORY	17/11	5/12	13/12	11/1	10/2	22/3	10/4	8/5	20/5
Alder leaves green	117.235	121.322	121.348	121.348	121.348	121.348	121.348	121.488	121.675
Alder leaves brown	431.145	431.145	431.145	431.237	431.348	431.348	431.909	431.922	432.022
Birch leaves green	No change							82.011	83.187
Birch leaves brown	303.950	304.782	304.782	304.784	304.811	304.811	304.815	304.815	304.815
Other Tree Litter	26.234	28.737	28.933	29.110	29.110	29.110	29.121	29.150	29.150
Alder rep ♀	18.286	21.811	21.854	23.480	23.686	30.973	31.132	31.132	31.333
Alder rep ♂	3.341	5.575	6.042	6.318	6.654	15.831	24.990	28.882	29.387
Birch rep ♀	2.128	2.167	2.167	2.439	2.439	2.845	3.260	3.260	3.911
Birch rep ♂	1.643	2.008	2.008	2.693	2.807	5.131	6.212	10.796	17.492
Scales	30.572	34.926	35.324	35.771	36.668	41.793	43.635	62.575	83.993
Micro	3.658	4.650	4.785	4.834	5.918	7.468	8.005	8.183	9.999
Wood	133.761	161.669	161.926	173.583	175.922	260.125	265.886	269.826	275.942
Total canopy leaves	932.589	937.508	937.534	937.628	937.766	937.766	938.331	940.236	941.699
Total other litter	85.862	99.874	101.108	104.645	107.282	133.151	146.355	173.978	205.265
Grand Total	1152.212	1199.051	1200.568	1215.856	1220.970	1331.042	1350.542	1384.040	1422.906

Figure 28.

Monthly % of total litter fall biocontent, 1966-7.

Figure 29.

Monthly % of alder and birch leaf fall biocontent.
Key: open circles - birch.
     plus signs - alder.

MONTHLY % OF TOTAL LITTER FALL BIOCONTENT 1966-7
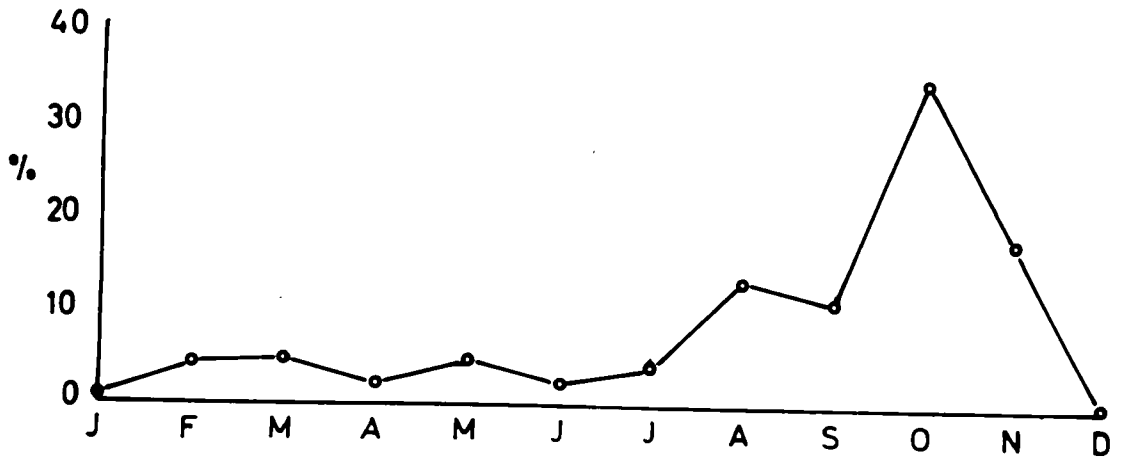
MONTHLY% OF ALDER AND BIRCH LEAF FALL BIOCONTENT
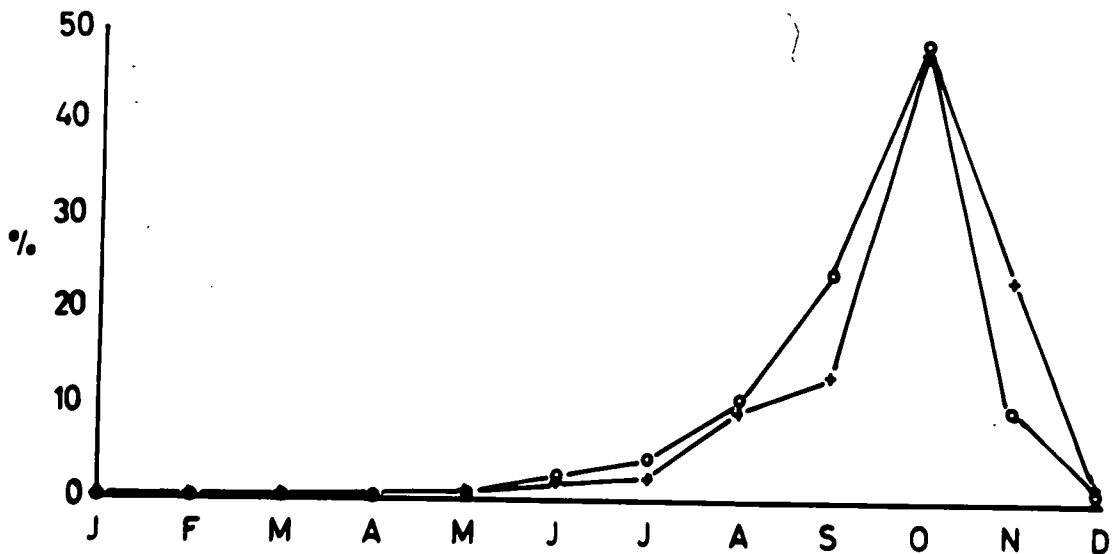
evenly through the year. The litter of other tree species (mainly leaves) fell almost entirely in November. The reproductive categories fell fairly constantly after the end of July, except for a December-January lull in Alder. The most marked exception to this were the Birch male reproductive parts which fell largely in late winter and spring. The fall of scales was greatest in April and May, but continued through the summer till September. The micro-material fell evenly excepting from September to January. Wood fall was by far the most sporadic, over 60% of the fallen wood biocontent being collected on two occasions (17 August 1966 and 22 March 1967).

The contribution of Alder and Birch leaves to biocontent was slightly less important (66%) than their contribution to biomass (71%). The contribution of wood (smaller than 2.5cm diameter) litter fall to biocontent was 19.2% whereas that to biomass was 14.5%. Similarly the contribution of the other categories to biocontent was 14.3%, almost the same (14.5%) as to biomass. Thus the use of biocontent rather than biomass emphasizes the importance of woody litter as against leaf litter, although the latter remains the dominant category of material.

Table XXIX shows the mean biocontent as Kcals/m^2 of each category cleared from the 24 traps on each occasion from 20 May 1967 to 25 May 1968. As for 1966-7 the data have been shown as cumulative litter fall biocontent in Table XXX.

TABLE XXIX

Litter Trap Data by occasion of clearing 1967-8 (Kcal/m^2)

CATEGORY	20/5	10/6	10/7	31/7	18/8	6/9	25/9	11/10	26/10
Alder leaves green	-	0.598	0.887	0.881	0.186	7.140	8.500	3.420	7.830
Alder leaves brown	-	0.288	6.070	21.300	15.200	17.801	38.110	22.998	112.753
Birch leaves green	-	1.840	0.486	0.407	0.053	1.460	-	0.213	-
Birch leaves brown	-	-	37.510	9.720	8.430	27.537	37.501	37.305	142.303
Other Tree Litter	-	-	0.164	0.104	0.036	0.107	-	2.020	2.721
Alder rep ♀	-	0.474	0.310	-	0.029	0.188	-	4.310	3.233
Alder rep ♂	-	0.295	-	0.255	-	0.640	0.337	-	1.231
Birch rep ♀	-	2.120	0.047	0.092	0.249	0.539	-	0.312	-
Birch rep ♂	-	0.292	0.019	0.072	0.682	2.080	0.289	-	-
Scales	-	14.870	13.250	2.255	2.010	20.850	1.791	5.320	7.000
Micro	-	3.050	3.680	0.215	0.082	3.502	0.065	0.598	-
Wood	-	8.900	4.351	13.650	10.001	24.999	0.076	13.110	16.171

CATEGORY	14/11	20/11	18/1	30/2	20/3	10/4	8/5	25/5
Alder leaves green	0.685	7.020	-	-	-	-	0.119	0.146
Alder leaves brown	157.292	46.935	-	-	-	0.235	-	-
Birch leaves green	-	-	-	-	-	-	1.453	-
Birch leaves brown	71.223	6.520	-	-	-	0.345	-	-
Other Tree Litter	15.310	4.140	0.067	-	-	-	-	-
Alder rep ♀	4.500	0.027	7.110	1.933	4.749	0.185	-	0.505
Alder rep ♂	2.230	0.149	2.830	24.701	6.400	4.761	3.650	3.536
Birch rep ♀	-	0.106	-	-	-	-	-	-
Birch rep ♂	0.304	-	-	0.405	1.850	0.867	4.041	5.055
Scales	5.135	0.091	-	6.811	3.521	1.576	17.000	16.210
Micro	-	-	-	3.520	1.620	0.597	0.134	1.641
Wood	26.250	0.359	53.401	24.499	52.410	8.790	1.539	7.000

TABLE XXX

Cumulative Litter Trap biocontent data 1967-8 (Kcal/m^2)

CATEGORY	20/5	10/6	10/7	31/7	18/8	6/9	20/9	11/10	26/10
Alder leaves green	—	0.598	1.479	2.350	2.536	9.676	18.176	21.596	29.426
Alder leaves brown	—	0.288	6.358	27.658	42.858	60.659	98.769	121.767	234.520
Birch leaves green	—	1.840	2.326	2.733	2.786	4.246	4.246	4.459	4.459
Birch leaves brown	—	—	37.510	47.230	55.660	83.197	120.698	158.003	300.306
Other Tree Litter	—	—	0.164	0.268	0.304	0.411	0.411	2.431	5.152
Alder rep ♀	—	0.474	0.784	0.784	0.813	1.001	1.001	5.311	8.544
Alder rep ♂	—	0.295	0.295	0.550	0.550	1.190	1.527	1.527	2.758
Birch rep ♀	—	2.120	2.167	2.259	2.508	3.047	3.047	3.359	3.359
Birch rep ♂	—	0.292	0.311	0.383	1.065	3.145	3.434	3.434	3.434
Scales	—	14.870	28.120	30.375	32.385	53.035	54.826	60.146	67.146
Micro	—	3.050	6.730	6.945	7.027	10.529	10.594	11.192	11.192
Wood	—	8.900	12.251	25.901	35.902	60.901	60.977	74.087	90.259
Total canopy leaves	—	2.726	47.663	79.971	103.840	157.778	241.889	305.825	568.71
Total other Litter	—	20.901	36.481	41.564	43.662	72.358	74.840	87.400	101.585
Ground Total	—	32.527	96.395	147.436	183.404	291.037	377.706	467.312	760.555

CATEGORY	14/11	27/11	18/1	20/2	20/3	10/4	8/5	28/5
Alder leaves green	29.711	36.731	36.731	36.731	36.731	36.731	36.850	36.996
Alder leaves brown	391.812	438.747	438.747	438.747	438.747	438.982	438.982	438.982
Birch leaves green	4.459	4.459	4.459	4.459	4.459	4.459	5.912	5.912
Birch leaves brown	371.529	378.049	378.049	378.049	378.049	378.394	378.394	378.394
Other Tree Litter	20.462	24.602	24.669	24.669	24.669	24.669	24.669	24.669
Alder rep ♀	13.044	13.071	20.181	22.114	26.863	27.048	27.048	27.553
Alder rep ♂	4.988	5.137	7.967	32.668	39.068	43.829	47.479	51.015
Birch rep ♀	3.359	3.465	3.465	3.465	3.465	3.465	3.465	3.465
Birch rep ♂	3.738	3.738	3.738	4.143	5.993	6.860	10.901	15.956
Scales	72.281	72.372	72.372	79.183	82.704	84.280	101.280	117.490
Micro	11.192	11.192	11.192	14.712	16.332	16.929	17.063	18.704
Wood	116.509	116.868	170.269	194.768	247.178	255.968	257.507	264.507
Total canopy leaves	797.511	857.986	857.986	857.986	857.986	858.566	860.138	860.284
Total other Litter	129.064	132.977	143.584	180.954	199.094	206.880	231.905	258.192
Ground Total	1043.084	1107.831	1171.839	1233.708	1304.258	1319.414	1349.550	1382.983

The total litter fall biocontent for 1967-8 (1,382.983Kcal/m^2) was within 40Kcal/m^2 of the 1966-7 value, as would be expected from the biomass data.   There was no important difference in the seasonal pattern, providing that green and brown alder and birch leaves were not considered separately.   In 1966-7 almost all the leaves which fell before the beginning of September were green, whereas in 1967-8 a high proportion of the leaves falling before September were sorted as brown.   It is not possible to say whether this was a real effect or an artefact of technique.

The 1967-8 litter fall biocontent measured by litter traps was made up as follows :- alder and birch leaves, 62.2%, wood smaller than 2.5cms, 19.1%, other litter 18.7%.   Thus whilst the importance of the canopy leaves had decreased slightly, that of material other than small twigs had increased.   This increase was largely as Alder male reproductive structures, scales and micro-litter.

In addition to the litter trap data, the large litter fall must be included in the estimate of biocontent of litter fall.   This was only measured once, and must be included in the estimate for both years.   Table XXXI shows the summary of bio-content of litter fall for the two study years.

V. iv. Results of Canopy Studies

The Leaf Area Index, biomass and biocontent of the Alder and Birch canopy components are given in Table XXXII

TABLE XXXI   Summary of Litter Fall (Kcals/m^2)

	1966-7	1967-8
Alder and Birch Leaves	941.699	860.284
Twigs smaller than 2.5cm diam.	275.942	264.507
Larger wood	57.000	57.000
Other litter	205.265	258.192
TOTAL	1,479.906	1,439.983

(a) and (b) for 1966-7 and Table XXXIII (a) and (b) for 1967-8.

The sources of these data were as follows. The number of

leaves in the canopy on any sampling occasion was calculated

by assuming that all leaves were derived from buds opening more

or less simultaneously at the end of April. It was assumed that

no significant number of leaves was derived from buds opening

later in the season. This was consistent with field observations.

Thus the number of leaves remaining in the canopy at a given time

was calculated as the total number of leaves that fell during the

whole season less the number that had fallen up to the date in

question. The data for area per leaf, dry-weight per leaf and

biocontent per leaf were obtained as described in the Methods

section. For each sampling occasion each of these three values

was multiplied by the estimated number of leaves per square metre

so that Leaf Area, biomass and biocontent might be expressed on

a per square metre basis.

The Leaf Area Index (LAI) may be seen in Figures

30 (a) and (b). In both years the total LAI rose sharply from

late April to a peak in early July, that in 1966-7 being rather

higher ($3.635m^2/m^2$) than that in 1967 ($3.053m^2/m^2$). This early

summer increase was due to the expansion and growth of individual

leaves. After early July the total LAI fell steadily until early

December. This decline was largely due to leaf fall, although

some of it was accounted for by a decrease in the area per leaf

TABLE XXXII

Canopy Area, biomass and biocontent, 1966-7

ALDER

Date	No. of leaves /m²	Area /LF (cm²)	LAI m²/m²	mg/ LF	G/ m²	Kcal/LF	Kcal/m²
1. 5.66	1,778.4	1.16±0.17	0.207	?	?	?	?
25. 5.66	1,776.0	6.97±0.31	1.240	31.2±1.5	55.4	0.164	292.0
22. 6.66	1,776.0	9.82±0.62	1.745	47.5±2.7	84.2	0.245	437.0
6. 7.66	1,743.8	11.87±0.84	2.080	53.7±3.8	93.8	0.275	480.0
17. 8.66	1,576.1	9.17±0.52	1.442	53.1±3.0	83.9	0.264	416.0
17.10.66	988.3	9.01±0.67	0.847	50.1±4.1	47.0	0.244	228.0

BIRCH

Date	No. of leaves /m²	Area /LF (cm²)	LAI m²/m²	mg/ LF	G/ m²	Kcal/LF	Kcal/m²
1. 5.66	3,284.6	1.16±0.08	0.379	?	?	?	?
25. 5.66	3,466.9	3.62±0.36	1.183	18.2±1.0	59.5	0.091	295.0
22. 6.66	3,266.9	3.76±0.34	1.227	19.7±0.9	64.3	0.093	304.5
6. 7.66	3,174.9	4.88±0.31	1.555	21.3±1.4	67.8	0.100	317.5
17. 8.66	2,966.7	4.67±0.25	1.363	25.8±1.4	76.6	0.116	344.0
17.10.66	942.6	4.65±0.27	0.439	23.5±2.1	22.1	0.096	90.3
27.10.66	552.8	4.67±0.30	0.258	21.9±4.0	12.1	0.098	54.2

LF = leaf

G/m² = grammes/sq-metre

Figure 30.

Canopy Leaf Area Index (m^2/m^2).
a. 1966-7.
b. 1967-8.

Key: open circles - total LAI.
     closed circles - alder LAI.
     plus signs - birch LAI.

CANOPY LEAF AREA INDEX (m^2/m^2)
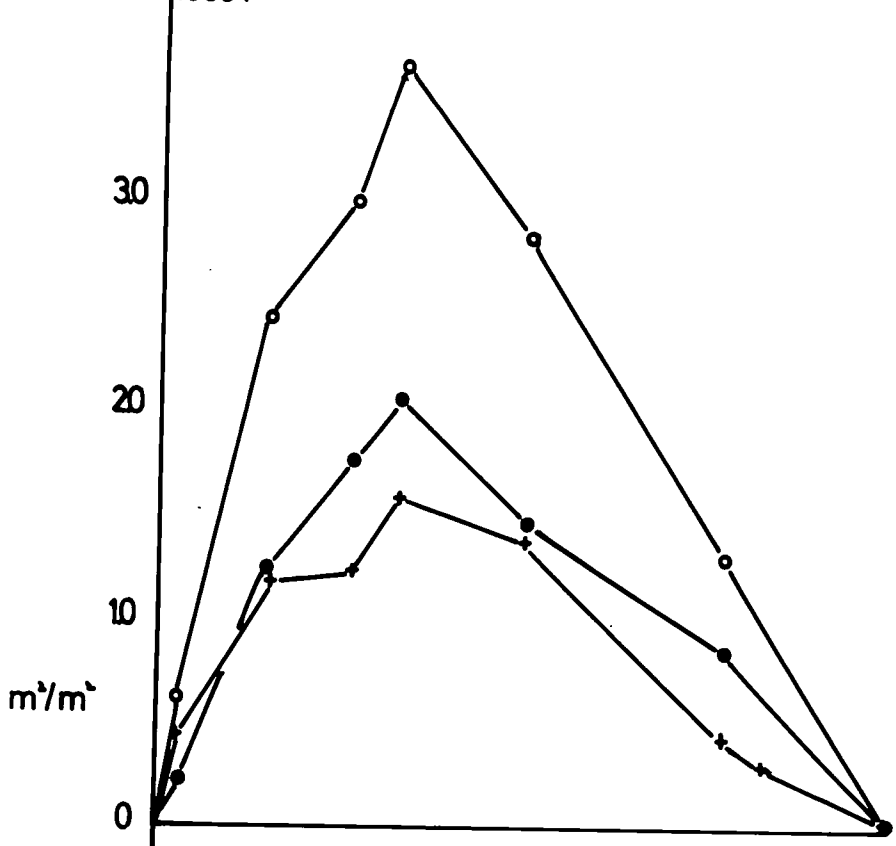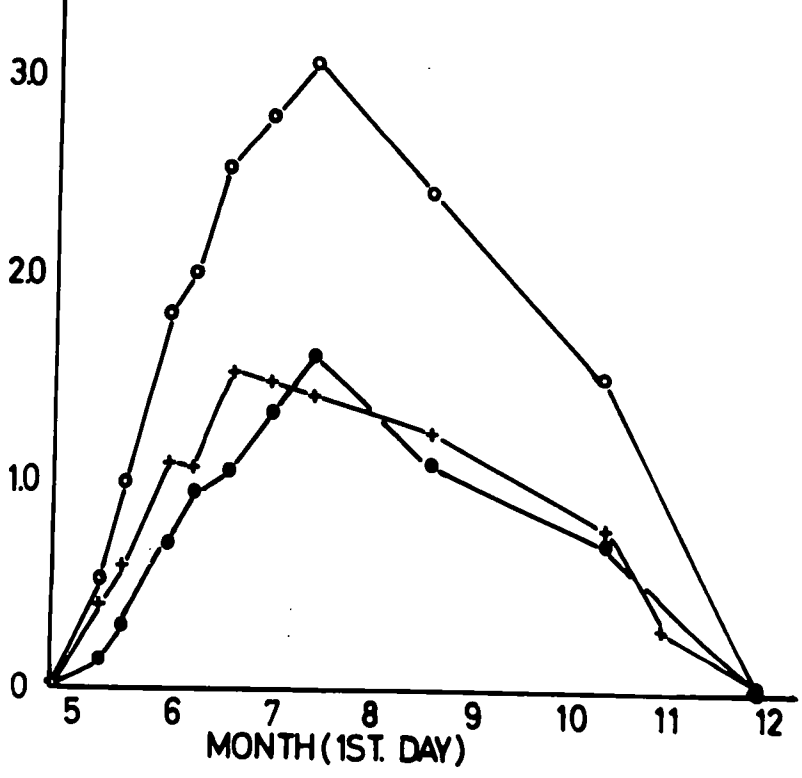
of both species after high summer. Defoliation and differential
leaf fall may have been factors here. Alder taken individually
peaked in early July both years, the 1966 peak being the highest
($2.080m^2/m^2$ as against $1.650m^2/m^2$ in 1967-8). Birch had a
maximum LAI of $1.555m^2/m^2$ in early July 1966 and $1.519m^2/m^2$ in
mid-June 1967. In both years the birch LAI remained close to
its maximum, at least until mid-August although the alder LAI
had fallen away markedly by this time. These data are referred
to below, particularly in Chapter IV.

The biomass data will not be examined in detail,
those for biocontent being more relevant to the purpose of this
investigation. For both species, canopy biomass showed a
seasonal pattern generally similar to that for LAI. The peak
alder canopy biomass was $93.8g/m^2$ in early July 1966 and $74.8g/m^2$
in early July 1967. For birch, the 1966 peak was $76.6g/m^2$ in
mid-August and in 1967 $69.8g/m^2$ in mid-August. The birch canopy
biomass in both years was above $60g/m^2$ from late May until the
peak. In both years the alder canopy peak biomass was about
$15g/m^2$ less than the alder litter fall. The peak Birch canopy
biomass was almost the same as the birch leaf litter fall in 1966,
but $13g/m^2$ less than in 1967. In the case of alder, it was not
possible to explain the discrepancy by litter fall before peak
canopy biomass, this being negligible. In birch, there was a
considerable litter fall before peak canopy biomass in both years,

this being $7.79g/m^2$ in 1966 and $11.15g/m^2$ in 1967. This clearly
does not explain the difference between the two years' data.
It is possible that we are working within the range of observ-
ational errors and the variability of the data here.

The biocontent data will be examined in rather greater
detail. It is clear from Tables XXXII and XXXIII that canopy
biocontent showed seasonal patterns basically similar to biomass,
although certain modifications due to calorific value changes
may be noted. Thus a slightly higher birch canopy biocontent
was calculated for early July 1967 than for mid-August when the
biomass peak occurred. In every case except birch 1967, litter
fall biocontent was greater than peak canopy biocontent. For
alder the difference was 70.5 and $86.5Kcal/m^2$ in 1966 and 1967
respectively. In birch the difference was 15.0 and $-17.5Kcal/m^2$
in 1966 and 1967 respectively. This effect might have been
explained by litter fall prior to peak canopy biocontent, but
as the alder figures for this were only 10.5 and $7.8Kcal/m^2$ in
1966 and 1967 respectively, this possibility was rejected for
alder. In the case of birch in 1966 when litter fall was
greater than peak canopy biomass, there was no litter fall
before peak canopy biomass. This peak was not a sharp one,
rather a plateau, and $28.5Kcal/m^2$ litter had fallen by its end
on 29 June 1966. This would overcompensate for the difference
between a peak canopy biocontent and litter fall. In 1967, when

birch peak canopy biomass exceeded litter fall, 41.0Kcal/m^2 litter fell before the peak.   Even bearing the inherent uncertainty of the data in mind, the differences between peak canopy biocontent and litter fall are not explicable in terms of early litter fall, particularly in the case of Alder.

Figures 31 and 32 show, first, canopy biocontent calculated assuming no litter fall (A);   second, canopy biocontent assuming litter fall (B) as in Tables XXXII and XXXIII;   and third, the first line (canopy biocontent calculated assuming no litter fall) less the litter fall biocontent (C) actually recorded (i.e. A - C).   It is clear that in every case actual litter fall biocontent was greater than the product of total leaf number and biocontent per canopy leaf during the period of fall, i.e. C > A - B.   This was because the calorific value of almost all falling leaf materials was greater than the calorific value of corresponding canopy leaf materials (cf. Section III, Tables V and VI) during the period of fall.

Summation shows that

$$\Sigma C - [A(\text{terminal}) - B(\text{terminal})] = \begin{array}{ccc} \text{ALDER} & \text{BIRCH} & \\ 127.5 & 63.0 & 1966 \\ 130.5 & 38.5 & 1967 \end{array}$$

in Kcal/m^2

These were all greater than litter fall minus peak canopy biocontent (B max) excepting for Birch 1967.

Figure 31.

Canopy biocontent (Kcal/m^2) 1966-7.

Key: open circles - A,canopy biocontent assuming no litter
                    fall.
     plus signs - B, canopy biocontent assuming litter fall.
     closed circles A- C = A minus recorded litter fall.

CANOPY BIOCONTENT (kcal/m²) 1966-7

ALDER

kcal/m²

BIRCH

MONTH (1ST. DAY)
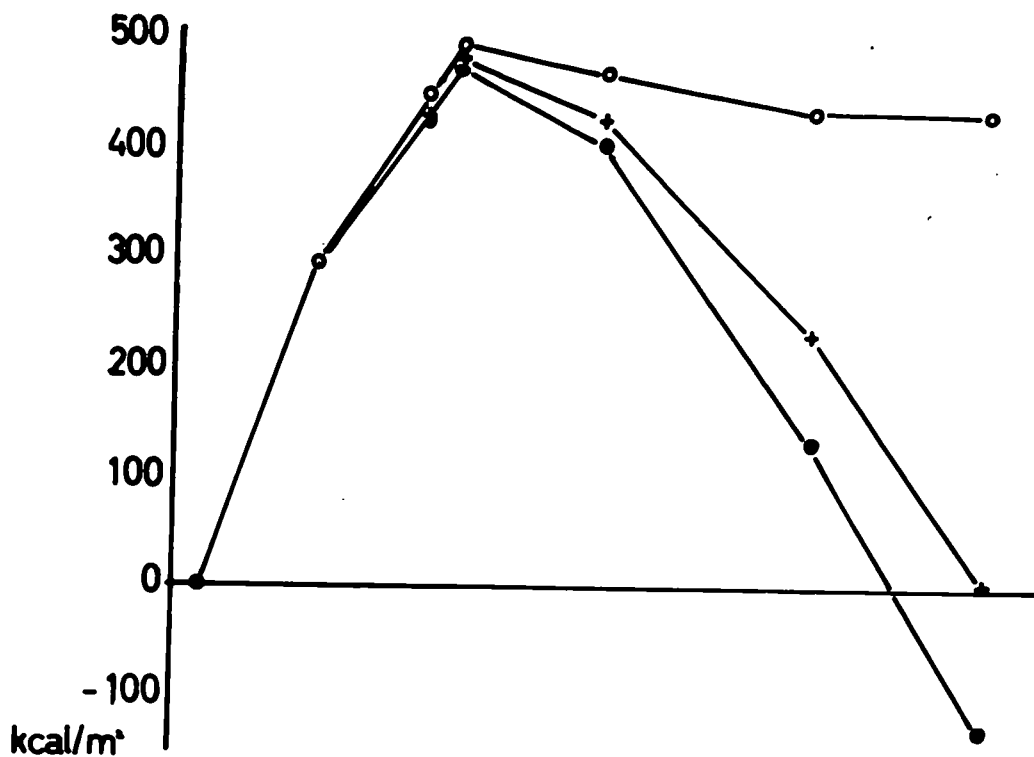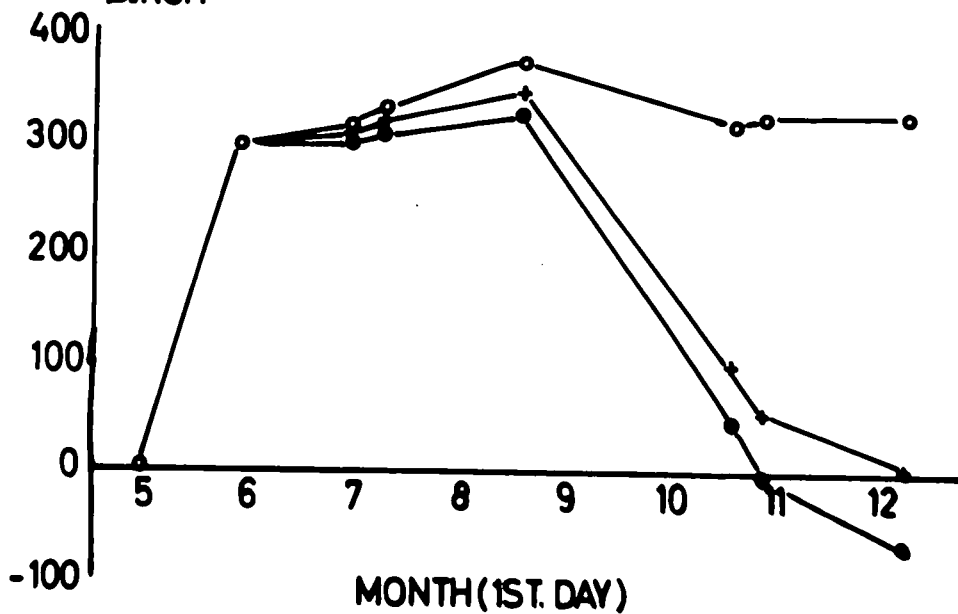
Figure 32.

Canopy biocontent (Kcal/m^2) 1967-8.

Key: open circles - A, canopy biocontent assuming no litter
     fall.
     plus signs - B, canopy biocontent assuming litter fall.
     closed circlesA- C, = A minus recorded litter fall.

CANOPY BIOCONTENT (kcal/m²) 1967-8
ALDER

BIRCH

kcal/m²

MONTH (1ST. DAY)
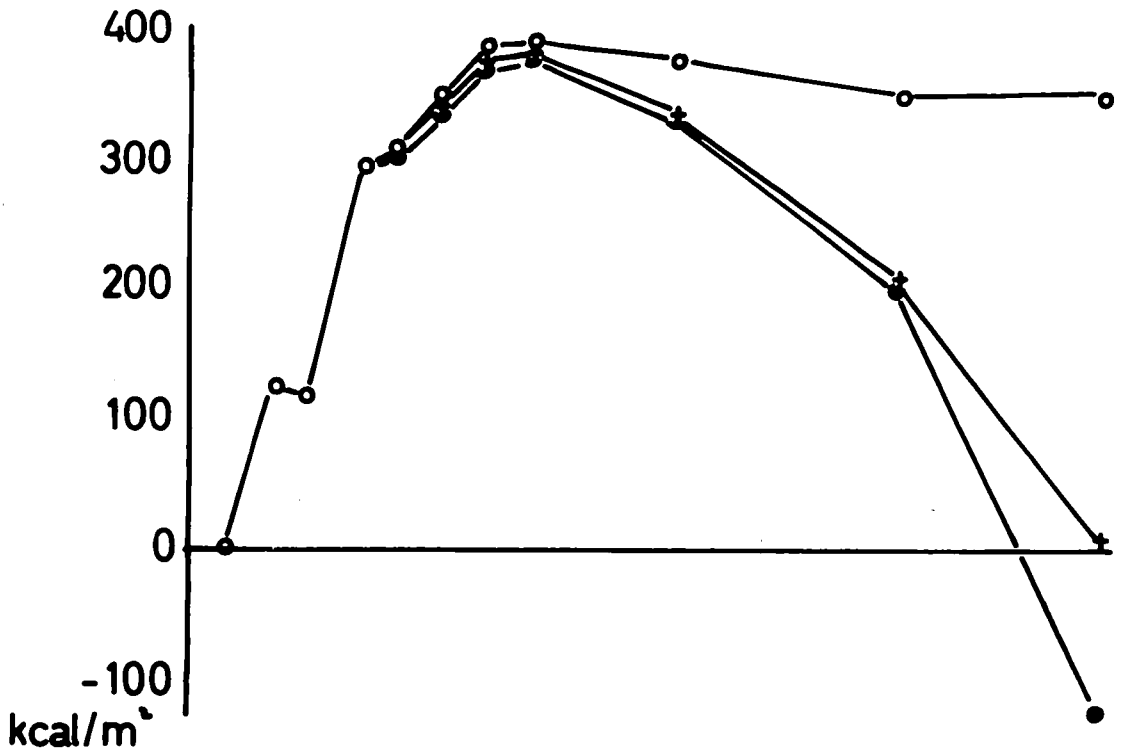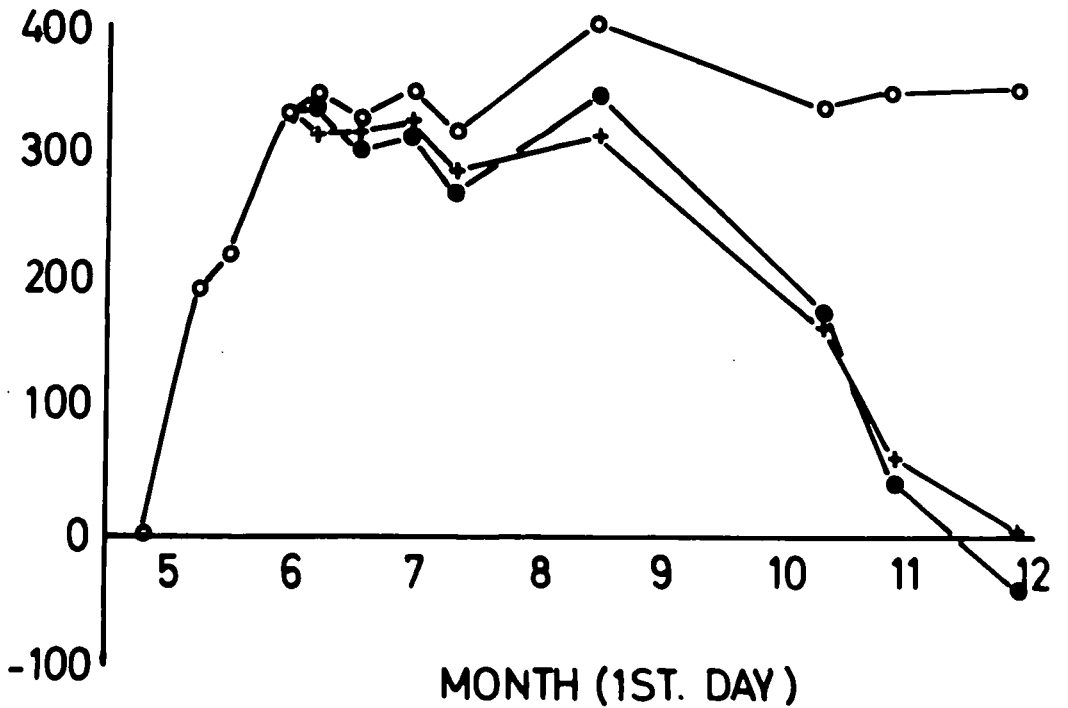
The difference between C - B max and C - (A - B) is given by the post-peak decline of A (i.e. A max - A Terminal). This corresponds to the decrease in the value of Kcals/leaf for canopy leaves.

Thus it is possible to say that the difference between peak canopy biocontent (B max) and litter fall (C) is given by the excess of the biocontent of leaves that actually fall over the biocontent loss from the canopy by leaf fall, less the decrease of canopy biocontent due to the post-peak decline in Kcals/leaf on the canopy.

It is possible to present three simple models of canopy biocontent change. All three assume that products of photosynthesis not destined for storage or degradation in the canopy leaves are instantaneously translocated out of the leaves on production, instantaneously here meaning in an interval much shorter than that between samples. In all three the changes in biocontent may be explained by the following inputs :- upward transfer from the wood store.

- net photosynthesis whose products are not transported out of the leaf.

and outputs :- downward transfer to the wood store.

- litter fall.

Model I has leaf growth commenced by a small upward energy transfer in late April (bud-opening) followed by period of no

losses, in which leaf biocontent climbs rapidly to its peak.
Thereafter energy is lost by downward transfer to the wood
store and by litter fall. Just prior to abcission there is
a marked increase in leaf weight and biocontent as a result of
a major upward transfer from the wood store. Thus litter fall
can be greater than peak canopy biocontent. This model assumes
a homogeneous canopy leaf population.

Model II is essentially similar, excepting that the
difference between calorific values for canopy leaves and falling
leaves is explained by canopy heterogeneity, i.e. heavy leaves
fall first. This model demands that peak canopy biocontent
equals litter fall biocontent.

Model III is an extension of either of these by which
a difference between litter fall and peak canopy biocontent is
explained by a pre-peak fall of leaves.

It is possible to reject Model III immediately for
alder. It may apply in the case of birch. Similarly with
Model II. The very simple Model I would seem to be an adequate
representation of reality for the purpose of this study so far as
alder canopy biocontent is concerned, with the modification that
some of the post-peak decline of canopy biocontent is probably
due to defoliators.

These conclusions are supported by an examination of
Tables XXXIV and XXXV. These show canopy and falling leaf dry
weight and biocontent for alder and birch respectively. The data

TABLE XXXIV Alder leaf data 1967

| | CANOPY LEAVES | | FALLING LEAVES | | | |
| | mg/LF | Kcals/LF | mg/LF | | Kcals/LF | |
			Green	Brown	Green	Brown
8. 5.67	17.0	0.089	-	-	-	-
15. 5.67	15.5	0.081	-	-	-	-
29. 5.67	39.7	0.207	-	-	-	-
5. 6.67	41.0	0.214	-	-	-	-
17. 6.67	46.9	0.243	-	-	-	-
29. 6.67	52.8	0.272	-	-	-	-
10. 7.67	53.7	0.275	-	-	-	-
18. 8.67	53.1	0.264	62.4	-	0.298	-
6. 9.67	-	-	48.0	-	0.229	-
25. 9.67	-	-	42.1	45.3	0.201	0.223
11.10.67	50.1	0.244	35.2	62.7	0.168	0.317
26.10.67	-	-	50.3	76.4	0.238	0.394
14.11.67	-	-	56.4	83.6	0.266	0.424

TABLE XXXV Birch leaf data 1967

| | CANOPY LEAVES | | FALLING LEAVES | | | |
| | mg/LF | Kcals/LF | mg/LF | | Kcals/LF | |
			Green	Brown	Green	Brown
8. 5.67	12.0	0.060	-	-	-	-
15. 5.67	13.6	0.068	-	-	-	-
29. 5.67	21.0	0.106	-	-	-	-
5. 6.67	21.1	0.099	-	-	-	-
17. 6.67	21.5	0.101	-	-	-	-
29. 6.67	21.6	0.110	-	-	-	-
10. 7.67	21.3	0.100	-	-	-	-
31. 7.67	-	-	-	-	-	-
18. 8.67	25.8	0.116	25.3	-	0.130	-
6. 9.67	-	-	22.2	-	0.114	-
25. 9.67	-	-	24.5	19.7	0.126	0.102
11.10.67	23.5	0.096	28.7	23.2	0.147	0.119
26.10.67	21.9	0.098	-	25.7	-	0.132

LF = leaf

for 1967 are shown. It is clear that although leaf weight
may be the same or even less in falling leaves, the calorific
content per leaf of the important category of falling leaves,
green or brown, depending on time of fall, is always markedly
greater than the calorific content per leaf of leaves
remaining attached. At the time of greatest fall in both
species, the Kcals/leaf were much greater in falling leaves
than they ever were in attached canopy leaves. In alder this
was effected largely by an increase in leaf weight as well as
calorific equivalent; in birch largely by an increase in
calorific equivalent. The vast bulk of alder leaves fell in
this heavier, more calorie-rich condition; these data thus
strongly support Model I above. The changes in birch were
much less simple and may well only be explicable by a combination
of all three models, with the introduction of other factors, such
as defoliators. The data available do not permit so complex
an analysis.

V. v. Discussion

(a) Tree Litter Fall. The total fall of tree litter in 1966-7
was $273.476g/m^2$ and in 1967-8 was $282.685g/m^2$. Bray & Gorham
(1964) computed a mean value from the data then available to
them for the Cool Temperate Zone (Angiosperms and Gymnospersm)
of $350g/m^2$. This figure was for total litter, whereas those
given here are for tree litter alone. If the Wynyard tree

litter data are plotted onto Bray & Gorham's (op.cit.) graph
of total litter production vs. Latitude, they fall close to the
line through the zonal means.   In a later section of this thesis
litter production by ground vegetation will be shown to be
appreciable.   Thus the points for total litter production at
Wynyard lie well above Bray & Gorham's line.

Canopy leaf fall accounted for 65% and 61% of total
tree litter in 1966-7 and 1967-8 respectively.   This compares
with Bray & Gorham's mean of 79% for the Cool Temperate Zone.
The figures of around 18% for wood fall considerably exceed the
range (12-15%) calculated from work by five authors.   Subsequent
work by Carlisle, Brown & White (1966) and Traczyk (1967) has
given figures of 30.2% and 6.78 - 20.83% respectively.   In the
second of these the fraction contained all non-leaf litter but
fruits.   In both cases litter was collected throughout the year.
Many authors have not collected litter throughout the year,
whilst others have not estimated stem or large branch fall.
It seems likely that the difference between the Wynyard figures
and the zonal Angiosperm mean percentage leaf litter may be as
much due to the improved method used as to any other factor.
This conclusion is supported by an examination of the data of
Carlisle, Brown & White who collected litter right through the
year.   They found leaf litter to be 55.1% of total.

Litter fall was sharply seasonal, 35% of its biocontent falling in the month of October and 75% in the months August to November inclusive. The seasonal pattern of fall of the leaves of the two important tree species, alder and birch, was similar, although the birch fall declined rather more rapidly than the alder after peak. Although a significant proportion of the leaves of both species fell green, the July peak of green-leaf fall noted for <u>Alnus glutinosa</u> by Witkamp & Van der Drift (1961) in Holland was not observed in this case. The total litter fall in the second year was very similar to that in the first, excepting for the differences in percentage composition noted above. It would have been desirable to continue the litter fall studies for longer, but in any case the two years' results obtained were entirely consistent with one another.

The data available justify the statement that tree litter fall at Wynyard in 1966 and 1967 was lower (around $1,450Kcal/m^2$) than is generally the case in Angiosperms in the Cool Temperate Zone. For example, Carlisle et al (1966) report a tree litter fall of $1,863Kcal/m^2$ in a mature <u>Quercus petraea</u> woodland in North-West England. Traczyk (1967) reports values of $1,780Kcal/m^2$ and $1,623Kcal/m^2$ for a <u>Carici elongatae-Alnetum</u> and <u>Tilio-Carpinetum</u> respectively in Poland. His values may be an underestimate as he used the single value

of $4.35Kcal/m^2$ culled from Wiegert & Evans (1964) rather than

making direct calorific determinations as in the work of

Carlisle et al (op.cit.) and this study.   It is clear that a

truly meaningful comparison between litter fall data from

various studies cannot be made without reference to the

developmental stage or management history of the woodland

being studied, and to the contribution of other strata.

This will be dealt with further in Section VIII.

The canopy studies showed that maximum Leaf Area Index

(1966, $3.635m^2/m^2$;   1967, $3,053m^2/m^2$) was near the bottom of the

range for European Angiosperms as shown by Carlisle et al (1966)'s

Table I.   For such stands the total range of LAI was 2.24 to

8.44.   The lowest values were usually for younger stands, the

highest for older stands.   The Wynyard LAI values fell well

within the range for field crops (Black & Watson 1960) of 2

to 5, although they were not strictly comparable as not all

photosynthesising surfaces were included in them.   It should

further be noted that the maximum figures given here only

represent LAI for a very short part of the year.   As shown

in this section, tree LAI changes dramatically during the

summer in deciduous trees, the period of high LAI being short

in species where litter fall starts early, as in alder and birch.

It is to be expected that the low level of tree LAI will be

related to high Ground Vegetation production.   This effect is

particularly marked in early summer and perhaps in a large part

of the autumn (see Sections IX and X).

Not surprisingly, the maximum canopy biomass's
estimated at Wynyard (1966, 161.6g/m^2; 1967, 137.1g/m^2) are
near the bottom of the range of Bray & Gorham's collected data
(their Table XIX) of 120 to 530g/m^2 for temperate angiosperms.
This range becomes 170 to 520g/m^2 of stands younger than 20 years
are excluded.   They quote a mean of 260g/m^2 for two Alnus sites
(neither of them A.glutinosa) and 240g/m^2 for eight Betula sites
(three of them for Japanese species).   The most comparable are
Ovington & Madgwick's (1959) data for 24-55 year old Betula
verrucosa at Peterborough, England.   The figure given by Bray &
Gorham (op.cit.) is 170gms/m^2.

As with LAI, canopy biomass at Wynyard changed
dramatically throughout the season and as Bray & Gorham (op.cit.)
comment, there is a need for direct studies of maximum canopy
biomass (they use the term 'leaf production') and leaf litter
fall within one forest.   This has been attempted in a small
way in this study.   It is clear that intrinsic changes in
leaf weight or biocontent are important in this matter.
Mitchell (1936) reported for North American Hickory, Viro (1955)
for several European Angiosperms, a decrease in leaf weight
between high summer and autumn.   Similarly, Bray & Gorham (ibid)
report experiments in which they weighed leaflets of Tamarindus
indica before and after the formation of an abcission plane,
but before they fall.   The leaflets with abcission layers were
yellow and weighed on average 19% less than the other green leaves.

The same authors found a similar relationship using leaf discs
of _Ficus_.

In this study the weight per leaf of green attached
leaves did fall from August to October in both species
(cf. Tables XVI and XV). At all times of significant litter
fall, however, the weight of brown, falling leaves was greater
than that of leaves remaining on the canopy, contrary to the
findings of the authors quoted above. The same was true for
falling green alder leaves when they were important in early
autumn, but not for falling green birch leaves in early autumn.
Falling green birch leaves were heavier than those remaining on
the canopy in late autumn. This observation is consistent
with the fact that litter fall was greater than peak canopy
biomass at Wynyard, contrary to Bray & Gorham's (op.cit.)
expectation.

The calorific values reported in Section III indicated
that this effect would be even more marked when biocontent
rather than biomass was considered, because of the higher
calorific values of falling as against canopy leaf material.
The biomass effect could perhaps be explained in terms of
extrinsic factors such as defoliation, differential abcission
and so on, as discussed in this Section. A reference back to
Section III, Figures 13 and 14, will lend support to the
explanation of canopy biocontent change in the terms of Model I
given in this Section (V. iv). In particular, there is strong

evidence of a transfer of energy-rich material into the leaves of both species just before fall. If this simple model is valid, which seems more likely for alder than birch, it implies that most of the photosynthetic product bound for the non-leaf parts of the tree is instantaneously translocated out of the leaf on production. This would be a finding of importance for the type of analysis proposed by Olson (1964). It may imply that energy input to non-leafy parts of the tree depends directly on the rate of photosynthesis whereas energy accumulation in the leaf mass behaves in a modified exponential manner of the type discussed by Nichiporovich (1960), excepting for changes at the beginning and end of the summer imposed by net transfers from the rest of the tree. It is clear that further research into the growth of alder leaves in particular would be profitable in this context.

In summary, the methods used have enabled estimates of canopy biomass, biocontent and Leaf Area Index to be made. It has been possible to reconstruct seasonal changes of these quantities in such a way as to permit informed speculation on their causal basis. The estimates have allowed the character- ization of the canopy, and will be used to examine its effect on other ecosystem components in subsequent sections of this thesis. Furthermore, the canopy data have been compared with the litter fall data (on which they were partly dependent).

This comparison leads to the conclusion that for the purposes of an estimate of net primary production, litter fall, rather than maximum or other canopy biomass, should be used. Thus the inclusion of the same quantity twice in one summation may be avoided.

It is clear that litter fall represents a major proportion of the ecosystem's fixed energy. In both study years it was close to $1,450 Kcal/m^2$, the total accumulation as wood and branch material calculated in Section IV being $2,031.4 Kcal/m^2$. To return to the point made in the introduction to this section, the scale of the contribution of above-ground tree-parts to the energy required for the processes of mineralization and recycling has been estimated. It is clearly a very large contribution, and must represent a major fraction of total tree net production.

CHAPTER II - SECTION VI

The calculation of Tree Net Production

VI. i. Introduction

The measurement of wood increment and litter fall
were dealt with in Sections IV and V. This Section comprises
a collation of the data necessary to estimate measurable above-
ground tree net primary production.

VI. ii. Methods

As already described in IV. i. the basic method is
a modification of Newbould's (1967) Method I, where net primary
production is the sum of biomass change and losses to consumers,
either decomposers or herbivores. Biomass (and hence biocontent)
change data were obtained as described in Section IV for alder
and birch. Litter fall, and hence loss to decomposers, was
determined as described in Section V.

Loss to herbivores was not measured as a main part
of this study, although preliminary data were obtained in May -
June 1967. The data were based on the study of the winter-moth
caterpillar Operophtera brumata on birch and the bugs Psyllus alni
and Psyllus forsteri on alder. In both cases population samples
were taken with a high pruner on 29 May, 5 June and 15 June 1967.
These were chosen as for the leaf samples (cf. Section V) and put
onto a large white sheet. Hence the number of animals per leaf
was calculated. The ingestion of leaf material per animal per

day was calculated for animals of various dry weights.   In

fact, the populations of all three species concerned were

almost synchronous in the relevant period.   In the case of

O.brumata 20 individual caterpillars were placed on birch twigs

in jars under field conditions and the area of leaf missing after

one week measured.   Using area/weight ratios determined on fresh

material and calorific values from Section III, this allowed the

calculation of Kcal/ingested/caterpillar/day.   This, and the

population data, gave an estimate of ingestion by the population

of O.brumata.

The Psyllid bugs are not leaf-eaters but sucking bugs,

apparently living off translocate ambushed from the phloem of

leaf veins and petioles in alder.   They produce waxy threads

containing a honey-dew like substance.   These threads form a

white fluff which was a characteristic feature of the Study Area

in May and June.   The problems of determining their ingestion

directly were rather complex and therefore an indirect estimate

was made.   The weight distribution of the population on each of

the sampling dates was determined by weighing fifty specimens

which had been dried under a vacuum at $60^{o}C$.   From this data

growth was calculated following Wiegert (1964) in his study of

meadow spittle bugs.   Respiration data were available for

individuals of various dry weights at $10^{o}C$ (J. Richards, pers.

comm.).   These data were obtained using a simple capillary

respirometer. Hence population respiration was calculated, again following Wiegert (1964). Assuming that the sum of growth and respiration represented 35% of the total ingestion by the psyllid population, these figures were used to calculate energy taken from the alder by these bugs.

The period 29 May to 15 June 1967 represented the greater part of the time the first generation of psyllid bugs spent on the alder leaves. Subsequent generations were very much less noticeable. Similarly, in the case of birch, other observations suggest that little loss of leaf area to defoliators took place after this period, once the leaves were fully grown and harder. In fact, it is possible that much of the defoliation apparent at the end of the season is merely the result of the growth of holes made early in the season. Thus it is likely that the measurement of ingestion by O.brumata between 29 May and 15 June 1967 represents a significant proportion of the total defoliation of birch. Thus the total ingestion for O.brumata, P.alni and P.forsteri between 29 May and 15 June 1967 will be used as a minimum estimate of loss from trees to herbivores. It is clear that the unassimilated fraction of the O.brumata ingestion was also measured as part of the micro-litter, therefore this is excluded from the loss to herbivore term in Newbould's Method I. The unassimilated and excreted fractions were not separable in the Psyllids. They were not previously

measured, and therefore Psyllid ingestion is included <u>in toto</u>
in the estimate of net primary production.

Detailed production analyses were not made for
the trees and large shrubs of other species than alder or
birch present in the Study Area.   Instead ratios of litter
fall to total net primary production were calculated for the
two main species.   These were applied to the litter fall data
for the other species and hence the wood accumulation by these
other species was calculated.

VI. iii.   Results - Biomass

Table XXXVI gives a summary of the biomass production
data for the two study years, not including the estimates of
loss to herbivores.   The mean of the two years' figures was
713.6g/m^2 of which 435.5g/m^2 or 61% was as bole and branch
biomass change.

VI. iv.   Results - Biocontent

The results of the defoliator project are given here
because there is no reason to express trophic transfers in
other than energy terms.   Table XXXVII is a summary of these
data.

The total loss to these herbivores in the 18 day
period 29 May 1967 to 15 June 1967 was 25.9Kcal/m^2, or
1.44Kcal/m^2/day.   If this rate was maintained through May,
June, July and August, the total loss in this way would have been

TABLE XXXVI   Summary of tree above-ground net primary
                     production-biomass

g/m^2	1966-7	1967-8
Alder wood biomass change.	158.3	158.3
Birch wood biomass change.	267.7	267.7
Litter fall	273.5	282.7
Other tree wood biomass change.	8.9	10.2
TOTAL	708.4	718.9 g/m^2

TABLE XXXVII   Herbivore energetics

(a) Operophtera brumata on birch

Date	Caterpillars /leaf	Caterpillars /m^2	Ingestion (Kcal/caterpillar /day)	Total ingestion Kcal./m^2/day
29 May- 5 June	0.02	62.94	0.00264	0.165
5 June-15 June	0.02	62.94	0.00264	0.165
18 day total	-	-	-	2.96Kcal/m^2

Assuming 20% assimilation efficiency, the addition from this
source to the total estimate of net primary production should be

$$0.59Kcal/m^2$$

(b) Psyllus alni and P.forsteri on alder

Date	Psyllids /leaf	Psyllids /m^2	Biomass mg/m^2	Growth Kcal/m^2/ day	Respiration Kcal/m^2/ day	ε
29/5	1.772	2,500.0	175.0)			
			)	0.165	0.337	0.502
5/6	0.964	1,358.0	247.0)			
			)	0.208	0.198	0.406
15/6	0.502	710.0	395.0)			
18 day total	-	-	-	3.400	4.680	8.080

Assuming 35% assimilation efficiency, total ingestion =

$$23.00Kcal/m^2$$

177.50Kcal/m^2. The loss to herbivores minus <u>O.brumata</u> faeces during the 18 day period was 23.59Kcal/m^2 or 1.32Kcal/m^2/day. If this had continued through May - August the total correction to the net primary production estimate would be 162Kcal/m^2. It is clear that the figure based on the 18 day period only must be an underestimate, whilst that based on extrapolation to a four months period may be an overestimate. In neither case was the consumption by the other species of herbivores present included. The data justify a tentative addition of between 23 and 160Kcal/m^2 to the net primary production estimate.

Table XXXVIII summarises the biocontent production data for the tree stratum at Wynyard. If the minimum correction for herbivory is applied, it represents only 0.6% of the total. The maximum correction represents 4.4% of the total. In the interests of caution the total corrected for minimum herbivory is accepted. This was close to $3,575\text{Kcal/m}^2$ of which bole and branch biocontent change contributed $2,090\text{Kcal/m}^2$ (58%).

VI. v. Discussion

Of the mean biomass net production of 713.6g/m^2, 490.7g/m^2 (68.5%) was as wood production (wood accumulation plus wood fall). 179.1g/m^2 (25.0%) was as alder and birch leaves; 43.8g/m^2 (6.5%) as reproductive structures, bud scales, micro-litter and leaves of other woody species. (These figures are means for the two years).

TABLE XXXVIII   Summary of tree above-ground net primary production - biocontent

Kcal/m^2	1966-7	1967-8
Alder wood biocontent change	733.4	733.4
Birch wood " "	1,298.0	1,298.0
Other tree wood " "	62.1	55.4
Litter fall	1,479.9	1,440.1
Total before herbivory correction	3,574.4	3,526.9
minimum "	3,598.0	3,550.5
maximum "	3,736.4	3,688.9

The total of just over $700g/m^2$ compares with the
mean of $880g/m^2$ quoted by Bray & Gorham (1964) for ten deciduous
angiosperms. Of their total, $280g/m^2$ (32%) was as leaf
production, compared with 25% in this study. The difference
may be due partly to the careful measurement of minor components
in this study and partly to the developmental stage of the woodland
in question. That is, one would expect a higher proportion of
net primary production to be put into long-term store (i.e. wood)
in a developing woodland than in a mature, equilibrated forest.
The fact that the tree above-ground net primary production for
the Wynyard site was somewhat lower than the figures given by
Bray & Gorham may be related to the well-developed nature of
the ground vegetation at Wynyard.

The distribution of biocontent production amongst the
various components was rather similar to that of biomass. Cf
the mean total of $3,574.2Kcal/m^2$, $2,417Kcal/m^2$ (68%) was as
wood, $901.0Kcal/m^2$ (25.0%) as alder and birch leaves, $231.7Kcal/m^2$
(6.4%) as other litter and $23.6Kcal/m^2$ (0.6%) as loss to herbivores.
These data will be examined further in the discussion of energy
flow and accumulation in Section XI.

CHAPTER III

Ground Vegetation and the Forest Floor

General Introduction

The role of the Ground Vegetation and the Forest Floor in the trophic energetics of the Study Area are dealt with in three sections. In the first of these, Section VII, Serial Cropping, the basic biomass and biocontent studies are described. In the second, Section VIII, Disappearance, the loss of material from the Forest Floor by decomposition and other processes is examined. In the third, Section IX, Ground Vegetation Net Primary Production, a description is given of the determination of the net primary production of the above-ground parts of the ground vegetation. The ground vegetation and Forest Floor were physically intermeshed on the Study Area. At the same time, the methods of estimating biomass and accumulation for these two (ground vegetation and Forest Floor) were interdependent. Therefore they have been examined together in this chapter.

Section VII Serial Cropping

VII. i. Introduction

In order to characterize the role of the ground vegetation in the ecosystem energetics of this woodland it was necessary to investigate the changes in biocontent of the ground vegetation and the transfer of material and energy from the ground vegetation to the Forest Floor. In addition, information

was required on the changes in biocontent of tree litter on the Forest Floor. As the ground vegetation and Forest Floor are closely intermeshed, a sampling technique dealing with both simultaneously was considered desirable.

To elucidate the relationships between ground vegetation biocontent changes, litter fall and Forest Floor biocontent changes, estimates of biocontent were required at regular intervals throughout the year. The approach adopted was to sample a number of small areas (quadrats) within the Study Area (actually, on the Grid), throughout the year. The Forest Floor and above-ground ground vegetation materials thus obtained were dried and weighed. For each category of material the mean of the weights for the set of quadrats was taken as dry weight per unit area on that sampling occasion. The variance and standard error of the mean were also calculated. This technique of serial cropping has been used by many workers in studies of primary production (Golley 1965; Golley & Gentry 1966; Hadley & Kiekheffer 1964; Odum 1960; Traczyk 1967a; Traczyk 1967b; Wiegert & Evans 1964). The key decisions to be made in its application are :-

      a. method of cropping

      b. size of quadrats

      c. number of quadrats and their location

      d. frequency of cropping

As elsewhere (Frankland et al 1963) the Forest Floor and
Ground Vegetation on the Study Area were extremely heterogeneous
and these decisions had to be made with considerable care.   The
bases for these decisions are discussed in Sub-Section VII ii.)

VII. ii. Serial Cropping Methods

a). Method of Cropping.   No studies of roots were made.
Therefore the adopted procedure was as follows.   At each sampling
position a square metal quadrat of the appropriate internal
dimensions (cf. VII ii. (b)) was placed horizontally on the
vegetation.   Any material, such as Rubus fruticosus, that was
preventing the quadrat from lying on the Forest Floor was cut
with secateurs on the inside edge of the metal quadrat so that
the quadrat fell to the ground.   Then all other standing Ground
Vegetation whose shoots emerged from the mineral soil within the
quadrat was cut off at the soil surface.   For Rubus fruticosus
all material lying across and within the quadrat was harvested.
Wherever possible materials were clipped separately by species
from July 1966 on.   Following this, the remaining part of the
Forest Floor was cut with secateurs along the inside edge of
the quadrat and all recognizable plant parts in the form of
litter removed from within the quadrat.   All cropped and cleared
materials were placed in labelled polythene bags and taken to the
laboratory.   Once there, the material from each quadrat was
sorted into the following categories :   Green ground vegetation

by species or species groups;   ground vegetation litter, including attached dead (after December 1966 this was sub-divided into fern litter, <u>Rubus</u> litter, grass litter and <u>Chamaenerion</u> litter);

Current and old alder and birch leaves;

Alder and birch reproductive parts;

Litter from other trees and shrubs;

Woody material of diameter less than 2.5cm;

and bryophytes.

If any delay arose before sorting, the material was stored in a deep-freeze cabinet.   Once sorted, the material of each category from each quadrat was placed in an unglazed brown paper bag and dried for 24 hours at $105^{0}C$, excepting the bryophyte material which was dried at $85^{o}C$ (cf. Section III). After drying, the material was weighed on a torsion balance to 0.01 grams.   The dry weight of each category of material in each quadrat was recorded.   The dried materials were sub-sampled for calorific analysis as described in Section III.

b). Size of Quadrats.   The selection of optimal quadrat size for each category of material cropped was made using Wiegert's (1962) methods.   On 6 and 7 March 1966 sixteen sets of nesting quadrats were clipped and cleared on the Grid. Their positions were determined in a stratified, random manner so that two lay within each of the 20 x 20 metre squares.

A set of nesting quadrats is shown in Figure 35. The smallest quadrat had an area of $0.0156m^2$ (1), the next $0.0312m^2$ (2), and the largest $0.1250m^2$ (8). As may be seen from Figure 35 this gave by addition the following ratios of quadrat sizes for analysis :- 1, 2, 6, 7, 8. The cropped material was treated as in VII ii(a).

The data thus obtained were used to calculate the mean and variance of the dry weight of each category of material for each quadrat size. Each mean and variance was multiplied to give mean and variance of dry weight per m^2.

In addition to the weight determinations, the time involved in clipping, sorting and weighing the materials from each quadrat size was noted throughout the whole operation. Hence the relative time-cost of using each quadrat size was calculated. Taking the time-cost for the smallest quadrat size as unity, the following graphs were then plotted :-

- relative mean against quadrat size (x), taking the mean for size 1 as unity (Fig.36a & b).

- double-log plot of relative variance against quadrat size (Fig.37a & b).

- the product of relative variance (V_r) and relative time-cost (Cr) against quadrat-size (Fig.38a & b).

Using these graphs the optimal quadrat size for each category of material was determined as follows :-

Figure 35.

Nesting quadrats. An explanation is given on page 84.

NESTING QUADRATS
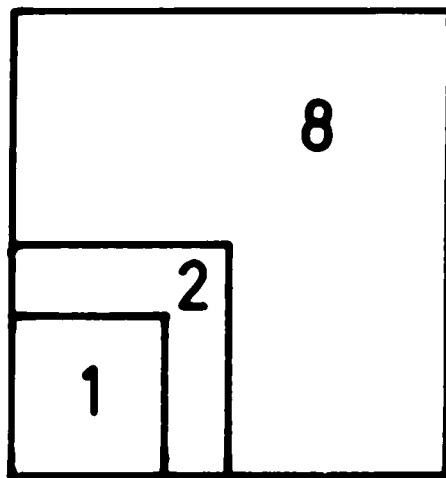
Figure 36.

Relative mean against quadrat size (x).

a. Other litter and vegetation.
b. tree litter.

Key: 1 - alder leaves.
     2 - birch reproductive structures.
     ② - birch wood.
     3 - other tree litter.
     4 - birch leaves.
     ⑤ - alder wood.
     6 - ground vegetation litter.
     7 - ground vegetation.
     8 - bryophytes.

RELATIVE MEAN VS QUADRAT SIZE (x)
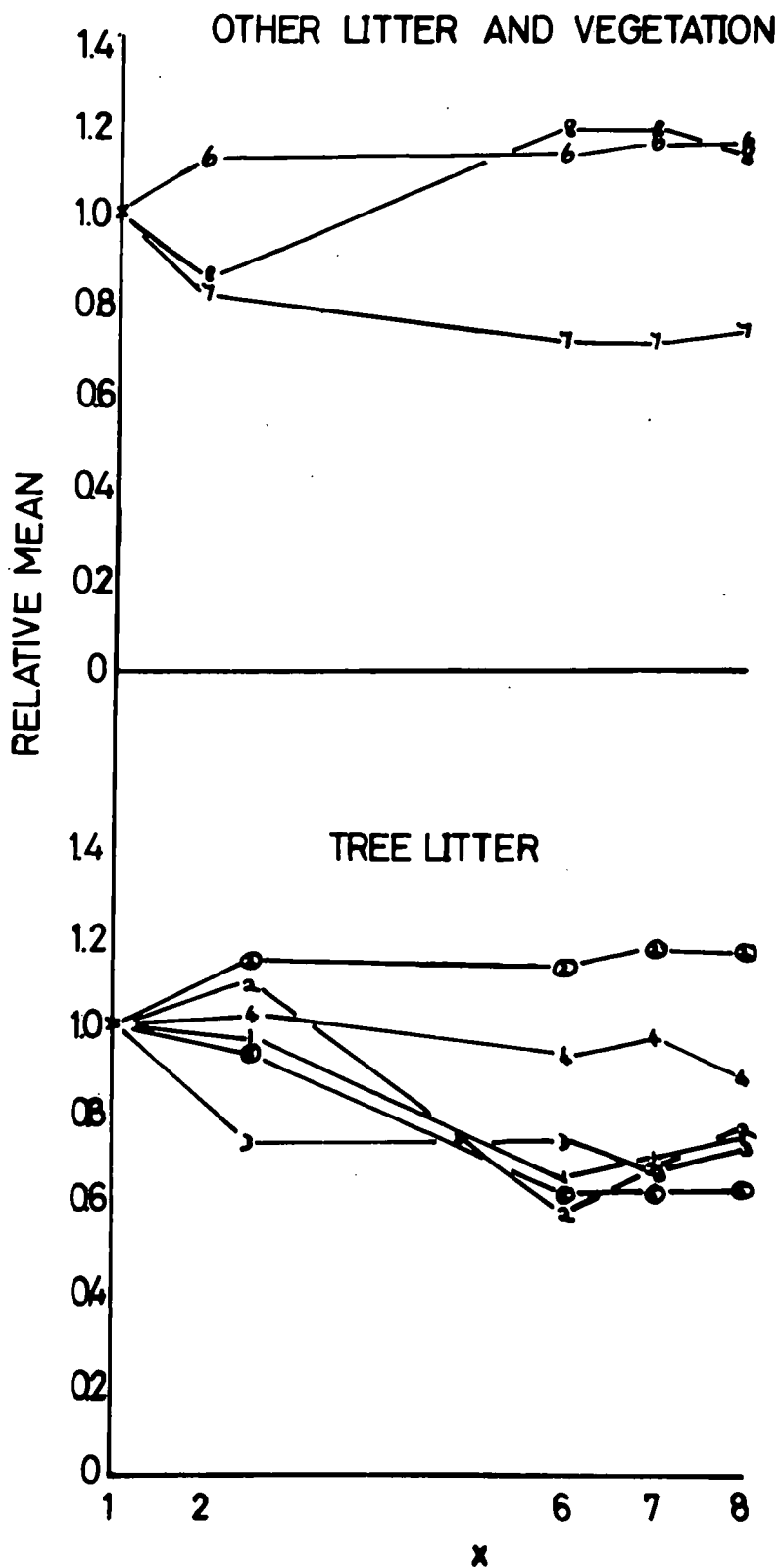
Figure 37.

Relative variance (Vr) against quadrat size (x).

a. Tree litter.
   Key: - open circles - birch leaves.
        closed circles - birch rep.
        open triangles - alder wood.
        closed triangles - alder leaves.
        open squares - other tree litter.
        plus signs - birch wood.

b. Ground vegetation and ground vegetation litter.
   Key: - open circles - bryophytes.
        open triangles - GV litter.
        plus signs - ground vegetation.

V_r vs X

TREE LITTER

GV AND GV LITTER
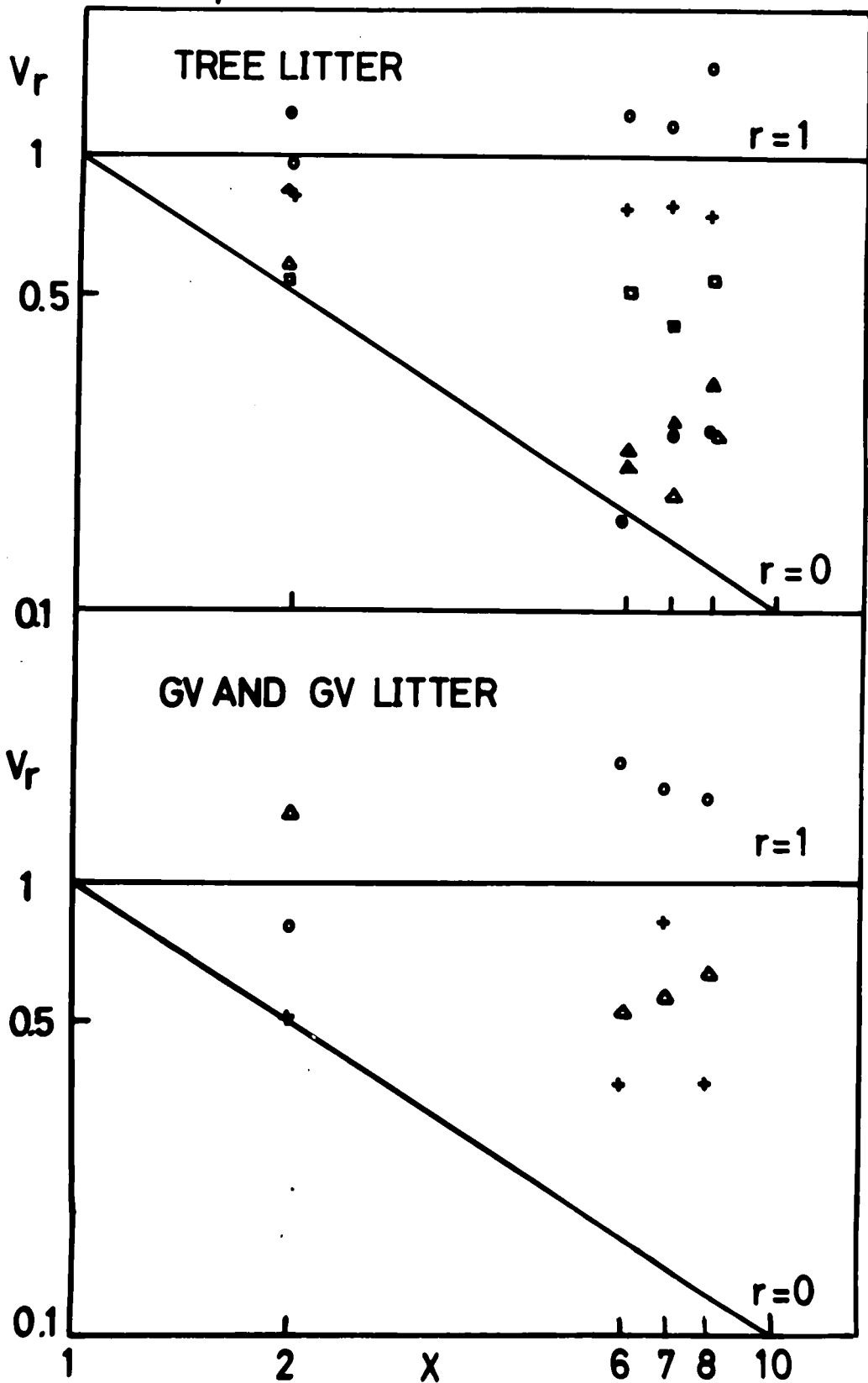
Figure 38.

The product of relative variance (Vr) and relative time-
cost (Cr) against quadrat size.
a. Other litter and vegetation.
b. tree litter.

Key as in Figure 36.

C_rV_r VS QUADRAT SIZE(x)
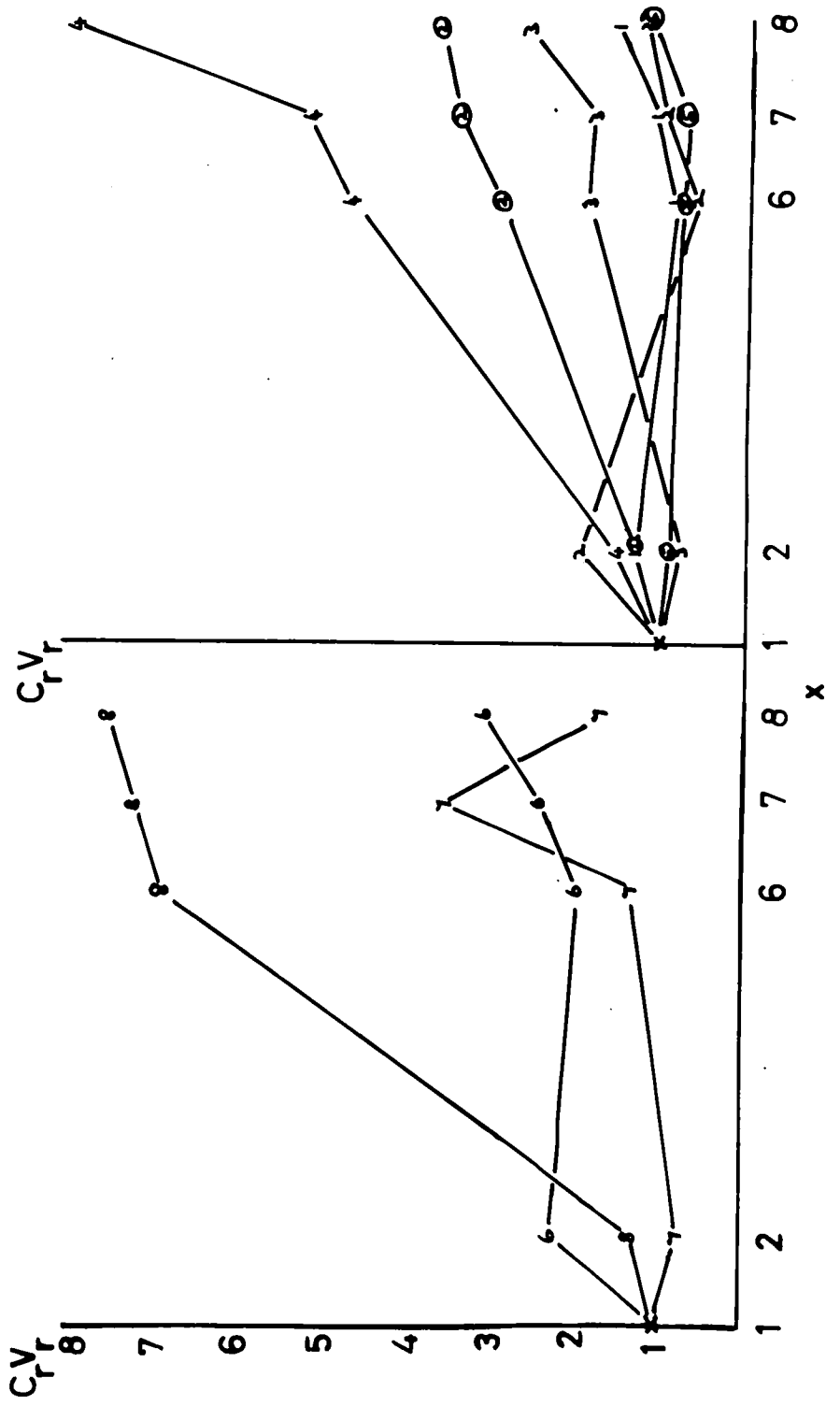
TABLE XXXIX   Optimal Quadrat Sizes

MATERIAL	(i)	(ii)	(iii)	(iv)
ALDER LEAVES	6	1, 2 out	6	6
ALDER REPRODUCTIVE	6	1, 2 out	6	6
ALDER WOOD	1	1 out	2	2
OTHER TREE LITTER	2	1 out	2	2
BIRCH LEAVES	1	1, 2 out	6	6
BIRCH WOOD	6 + 7	1, 2 out	6	2
GROUND VEGETATION LITTER	1	1 out	6 or 2	2
GREEN GROUND VEGETATION	2	1, 2 out	6	6
BRYOPHYTES	1	1, 2 out	2	2

An explanation is given in the text.

Wiegert's optimal quadrat size technique was used to help the construction of a sampling programme in which the least possible variance of each mean may be obtained in the time available. However, it should not be assumed that a more and more extensive sampling programme with more and bigger quadrats would lead to ever decreasing variances. In populations showing marked clumping, sample variance is at least in part a factor of the relationship between quadrat size, quadrat number and clump size and distribution, or 'scale of pattern'. Therefore, in the design of a biomass sampling programme, and in the evaluation of its results, this should be borne in mind.

The graph of relative variance (V_r) against quadrat size (x), Fig.37, can be used to examine the dispersion of the ground vegetation and litter categories on the Grid. In his treatment of similar data, Wiegert (op.cit.) constructs two hypothetical cases. In one there was no correlation between the biomass of a category in one quadrat and that in the next quadrat. In this case, random dispersal, relative variance (V_r) may be expected to decrease with increases in quadrat size (x). This hypothetical case is represented in Fig.37 by the line marked r = 0. In the other case, clumped dispersal, there was a high correlation between biomass in one quadrat and the next. Thus relative variance (V_r) did not change with increases in quadrat size (x). The extreme of this case is

represented by the line r = 1 in Figure 37. Wiegert shows
that where quadrat size (x) is equal to or smaller than clump
size for a given category the relationship between V_r and x
will approach that for r = 1. Once x is larger than clump
size, the relationship should correspond to that for r = 0.
Information on clump size can be of use at various stages of
sampling programme design.

If tree litter categories are considered first
it may be seen that the relationship between V_r and x corresponds
to that for r = 0 (random dispersal) for birch wood up to
x = 7 $(0.1092m^2)$. Above x = 7 it departs markedly from r = 0.
This may be explained either by a decrease in sampling efficiency
above this size, or by some real pattern effect. On the other
hand the relationship for alder wood corresponds closely to r = 1.
That is, alder wood has a clumped dispersal, clump size probably
being greater than x = 10 $(0.1560m^2)$. Birch wood litter consisted
largely of very small twig fragments, whereas alder wood litter
was composed to a greater extent of fallen branches. Above
x = 2 $(0.0312m^2)$ the relationship between V_r and x for alder
reproductive structures corresponds to r = 0. Therefore clump
size for this category is smaller than $0.0312m^2$. The relation-
ship for birch leaves approaches that for r = 1, that is birch
leaves are highly clumped on the Forest Floor, and their clump
size is greater than $0.1560m^2$. On the other hand, alder leaves

appear to have a clump size between $x = 1$ and $x = 2$, and also shows an increase in V_r above $x = 6$ $(0.0936m^2)$. This phenomenon of increases in V_r at higher values of x was noted by Justeson (1932) working on field crops and Wiegert (op.cit.) working on an old field. Whether it is an artefact of inadequate observational technique or the product of the real dispersal characteristics of the materials concerned is not a question that can be definitively answered here. The only tree litter category that does not show this effect at all is alder wood.

The relationship between V_r and x for ground vegetation litter suggests a clump size below $x = 2$ $(0.0312m^2)$ and again an increase in V_r above $x = 6$ is shown. The behaviour of the ground vegetation itself is more complex. Up to $x = 2$ it corresponds closely to $r = 0$, from $x = 2$ to $x = 6$ it approaches $r = 1$, and then V_r increases and decreases sharply. Ground vegetation is an aggregate category, including many species of plants with many clump sizes and indeed many dispersal patterns. The key to the understanding of the dispersal of most of the other categories probably lies in this, the least clear case. The dispersal of green ground vegetation biomass will change for each species through the year and will no doubt dictate the three-dimensional structure of the Forest Floor.

Examination of Figure 37 shows the complexity of biomass dispersal on the Grid. Almost all the categories

cropped show clumping on at least one level of pattern; if

not on several. Therefore no sampling technique can be

reasonably expected to give estimates of mean biomass with

small confidence limits for any ground vegetation or Forest

Floor category. However, the following conclusions were drawn.

First, when considered in isolation, limited confidence should

be placed in the results of serial cropping on the Grid.

Second, as many quadrats as possible should be clipped so as

to give some indication of spatial variation of biomass.

Third, any calculations based on serial cropping results should

be cross-checked by independent methods wherever possible.

c) Number of quadrats and their location. The question of

how many quadrats should be clipped was dealt with in part

in VII ii(b). It was decided to take only that number of

quadrats which could be dealt with in one or one and a half

days field work and five or six days laboratory work. For

this reason sixteen quadrats were clipped on each sampling

occasion from April 1966 to March 1967 inclusive.

During this period the quadrat positions were chosen

as follows. Each of the eight 20 x 20m squares comprising

the Grid was divided into four 10 x 10m squares, which were

subdivided into 100m squares, which were subdivided into

100m squares, which were subdivided into $0.25m^2$ (Fig.39).

Each 10 x 10m square was labelled by a single digit - 1, 2, 3 or 4.

On its North-South and West-East side it was marked off at each metre, being labelled 0 to 9. Within each square metre each quarter was labelled 1 - 4. Thus any $0.25m^2$ on the Grid could be designated by a letter (A - H for the 20 x 20m square) and a four digit number. On each sampling occasion, two such positions were chosen within each 20 x 20m square using a table of random numbers (Snedecor 1956) to obtain the four-digit place-number. In the field the positions were found by using the posts marking the Grid and a system of marked cross-strings. Within the quarter-metre the size 6 quadrat was placed in the centre. The size 2 quadrat was placed within the size 6 quadrat and to its south-east corner, these being the two quadrat sizes chosen (cf. Table XXXIX, column iv). If some obstacle, such as a tree, was found at the chosen position, the position was moved one metre to the west. If still obstructed, it was moved one metre north, and so on. All square metres from which any sample had been taken were marked on a full chart of the Grid. Future selection of that square metre as a sampling position was ruled out.

It will be noted that this method of stratified random sampling did not take cognizance of the differentiation of the Grid into Alder and Birch Zones. From April 1967, due to experience in clipping and sorting of material, it was possible to increase the number of quadrats clipped on each occasion

Figure 39.

A Grid square (A – H).
An explanation is given on page 89.

20 x 20 METRE SQUARE (A-H)

10 m

1	2
3	4

10m

0 1 2 3 4 5 6 7 8 9

0 1 2 3 4 5 6 7 8 9

1m

1	2
3	4
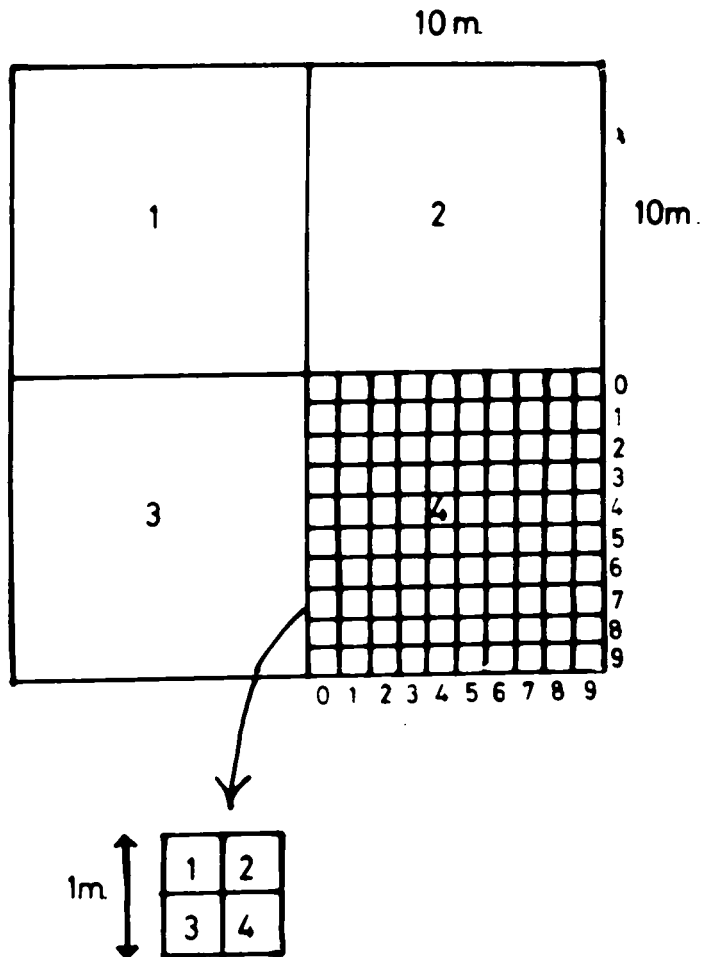
squares from the calculation of biomass variance.   The
results of this calculation are given in VII iii.   The data
thus obtained allowed the calculation of biomass mean, variance
and standard error for the Alder and Birch Zones considered
separately, and when combined, with appropriate weighting,
for the two zones taken together, that is the Grid.   Whenever
biomass data are reported for the Grid from April 1967 on, they
refer to a combination of the data from the Alder and Birch
Zones achieved in this way.

d) Frequency of cropping.   From April 1966 through September
1967 cropping was carried out as near monthly as possible.
Thereafter it was done bi-monthly until April 1968.   More
frequent cropping would have been desirable, but because of the
limited time available, this was not possible.

VII. iii.   Results, April 1966 to March 1967

a) Green Ground Vegetation and Bryophytes.   Table XXXX shows
the mean biomass and standard error for each of the sorted
categories on each sampling occasion.   Unfortunately, the
ground vegetation material was not separated into species or
species groups until July 1966.   Thereafter it was sorted into
the categories shown in Table XXXX, "Forbs" being a residual
category for the several species of herbs only represented
by occasional small individuals.

TABLE XXXX   BIOMASS OF GREEN GROUND VEGETATION AND BRYOPHYTES 1966-7 (BIOMASS G.O.DwT/M^2 (1 S.E.)

DATE	FERNS	RUBUS	CHAMAENERION ANGUSTIFOLIUM	FORBS	DESCHAMPSIA CAESPITOSA	AGROSTIS TENUIS	H.LANATUS	H.MOLLIS	TOTAL	BRYOPHYTES
20. 4.66	-	-	-	-	-	-	-	-	25.17 (7.90)	13.76 (5.92)
16. 5.66	-	-	-	-	-	-	-	-	55.54(12.20)	9.92 (3.70)
10. 6.66	-	-	-	-	-	-	-	-	99.90(14.79)	17.60 (8.74)
1. 7.66	25.90 (10.30)	45.60 (12.90)	6.30	4.90	-	-	12.76 (4.80)	22.60	117.38 (14.05)	49.41 (15.94)
1. 8.66	75.26 (27.36)	31.90 (9.50)	4.78	0.71	-	3.52	4.82	16.12	137.70 (25.30)	17.18 (8.80)
5. 9.66	36.89 (29.27)	56.14 (14.78)	9.73	2.21	3.05	9.58	3.92	7.97	129.56 (28.53)	22.75 (6.34)
5.10.66	34.36 (15.31)	51.78 (14.78)	0.81	0.53	0.12	1.73	3.73	10.30	104.27 (19.31)	18.20 (8.99)
31.10.66	27.88 (14.67)	49.06 (5.65)	-	2.04	0.13	3.56	1.73	12.36 (7.05)	97.02 (17.02)	14.88 (6.08)
1.12.66	0.26	22.01 (8.42)	-	1.37	1.55	1.43	-	1.51	28.29 (8.40)	14.18 (6.50)
16. 1.67	+	19.73 (4.79)	-	+	-	+	-	4.45	25.96 (5.05)	18.66 (8.92)
15. 2.67	+	14.85 (5.53)	-	0.79	-	-	3.25 (1.56)	1.57	20.59 (5.21)	20.70 (8.22)
15. 3.67	-	12.68 (4.19)	-	+	---	-	3.34	-	16.05 (4.94)	14.89 (7.02)

Figure 40a shows the change in green ground vegetation biomass and bryophyte biomass through the 12 month period. The ground vegetation biomass showed a clear seasonal pattern, with a peak in August declining to a low figure in April 1967. The bryophyte biomass lay between 10 and $20g/m^2$ for most of the year, only deviating sharply in July when it approached $50g/m^2$. This change was not significant at the 95% level and may simply be the result of quadrat location. For most of the summer, apart from July, the bryophyte biomass amounted to less than 18% of the green ground vegetation biomass (of which it did not form a part). During the winter, from December through March, the two were almost equal.

Figures 40b, c and d show the changes in biomass of ferns and Rubus, Chamaenerion and forbs, and the grass species respectively. The highest biomass reached by each species or species group here may not represent peak biomass, for this may have occurred before July. However, the data did show certain peaks, and these did not all coincide with the overall peak ground vegetation biomass in August. The highest recorded values for Forbs, Holcus lanatus and Agrostis tenuis fell in July. Those for Rubus fruticosus, Chamaenerion angustifolium, Deschampsia caespitosa and Holcus mollis came in September, whereas that for Ferns fell in August. Thus the apparently simple changes in total green ground vegetation biomass

Figure 40.

Biomass (g/m^2) 1966-7.

a. top left - total ground vegetation (crosses) and
         bryophytes (open circles).
b. top right - ferns (plus signs) and Rubus (open circles).
c. bottom right - forbs.
d. bottom left - total grasses.

BIOMASS (g/m²) 1966-7

TOTAL GROUND VEGETATION +BRYOPHYTES

FERNS + RUBUS

GRASSES

FORBS
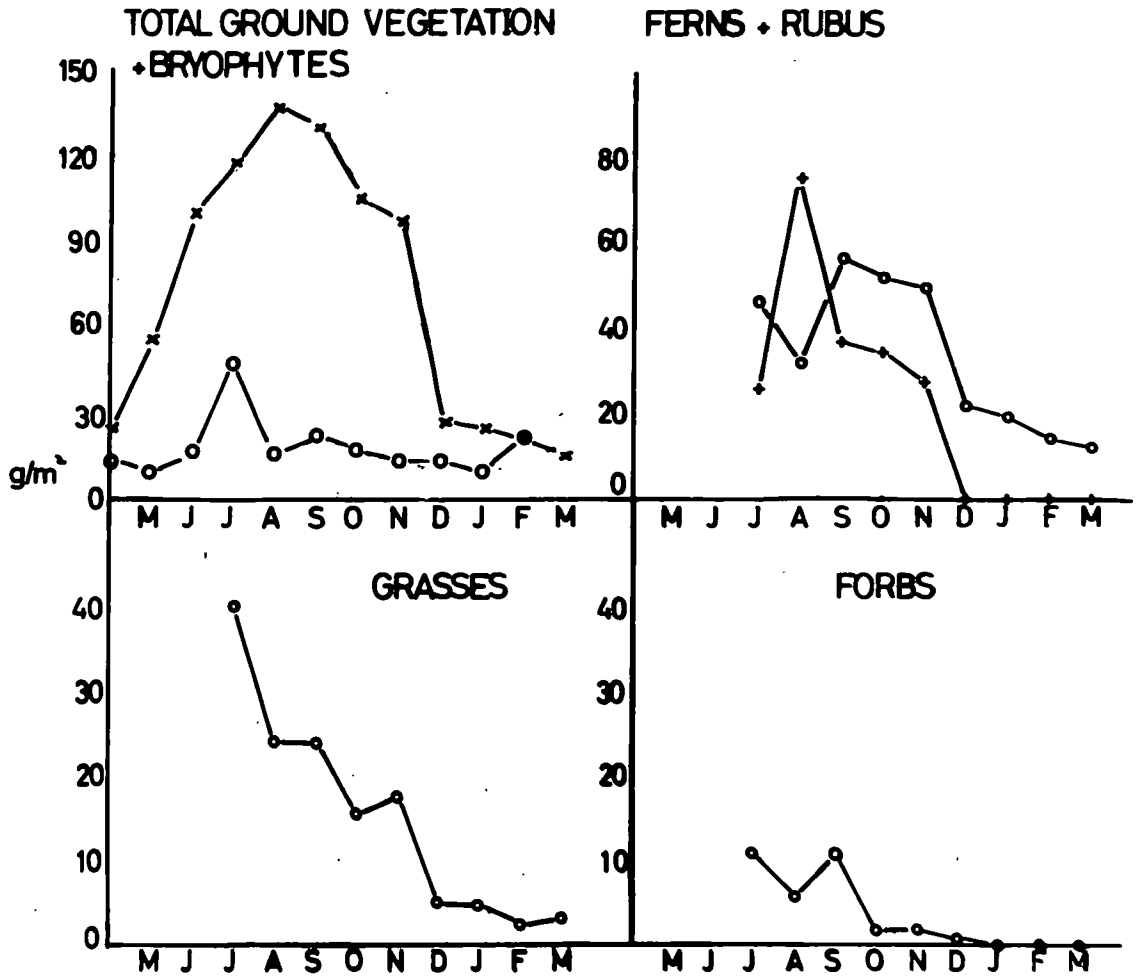
concealed a complex pattern of species and species group biomass changes. However, the confidence limits of many of the species and species group biomass estimates were wide, and only limited trust can be placed in them. The confidence limits placed on the estimate of overall green ground vegetation biomass were more acceptable, one standard error usually representing 20% or less of the mean. These figures were comparable to those of Frankland et al (1963) and Whittaker (1962), obtained in similarly heterogeneous vegetation.

Although the Fern category showed the highest peak biomass, Rubus fruticosus formed the most consistently important biomass component. It formed the major part of the overwintering material because of its persistent woody shoots. In July the grasses contributed 29% of the green ground vegetation biomass, but by December they had fallen to 5%.

b) Ground Vegetation Litter. Table XXXI shows the mean biomass and its standard error for the ground vegetation litter on each sampling occasion. Figure 41 shows the changes in ground vegetation litter biomass through a 12 month period. The biomass dropped from nearly $450g/m^2$ in April to just over $200g/m^2$ in July. After an increase in August and another in October, it remained between 200 and $250g/m^2$ for the rest of the study period. It is of interest to note that the winter of 1965-6 was particularly hard, snow covering the ground for

TABLE XXXXI

Biomass of Ground Vegetation Litter 1966-7
(g/m^2 $\pm$ 1 S.E.)

DATE	TOTAL	FERN	RUBUS	GRASS
20. 4.66	448.00 (51.90)	-	-	-
16. 5.66	373.44 (59.10)	-	-	-
10. 6.66	284.38 (37.94)	-	-	-
1. 7.66	207.01 (41.15)	-	-	-
1. 8.66	288.32 (47.36)	-	-	-
5. 9.66	257.32 (42.72)	-	-	-
5.10.66	284.45 (53.18)	-	-	-
31.10.66	217.15 (31.65)	-	-	-
1.12.66	225.57 (26.72)	-	-	-
16. 1.67	250.83 (38.43)	133.25 (40.82)	88.02 (23.73)	29.57 (17.07)
15. 2.67	229.69 (46.89)	137.82 (48.18)	50.79 (14.71)	42.08 (13.91)
15. 3.67	229.96 (35.43)	143.16 (43.36)	48.34 (5.19)	37.94 (17.98)

many weeks.   These severe conditions probably slowed up the
breakdown of ground vegetation litter formed in 1965.   The
litter surplus thus formed was broken down once spring conditions
arrived.   The increase in ground vegetation litter biomass from
1 August 1966 to 1 September 1966 was probably due to the die-
back of those species known to have an early peak biomass, e.g.
Agrostis tenuis and Holcus lanatus.   The high October value was
probably due to the mortality of species having September peaks,
for example, Rubus fruticosus, Chamaenerion angustifolium,
Deschampsia caespitosa and Holcus mollis.   The ground vegetation
litter biomass figures do not reflect any decrease in Fern
biomass from 1 August 1966 to 5 September 1966.   The standard
error of the ground vegetation litter biomass estimate as a
percentage of the mean ranged from 11.60% to 20.52%, the period
average of this statistic being 15.95%.   For green ground
vegetation the range was 11.95% to 31.14%, the period average
being 21.80%.   Because the lowest value of ground vegetation
litter biomass was much higher than the highest value of green
ground vegetation biomass, the narrower confidence limits of
the former probably represented greater amounts of material
than the broader limits of the latter.

From January 1967 the ground vegetation litter was
sorted into Fern and Chamaenerion litter, Rubus litter, and
Grass litter.   The Fern and Chamaenerion litter formed 53%

Figure 41.

Biomass (g/m^2) 1966-7. Total ground vegetation litter.

BIOMASS (g/m^2) 1966-7
GROUND VEGETATION LITTER

of this litter in January, and rose to 62% in March. The <u>Rubus</u>

litter formed 35% in January, and fell to 21% in March, whereas

the Grass proportion rose from 12% to 16%. The Fern material

clearly comprised the most important ground vegetation Litter

component, followed by <u>Rubus,</u> and then the grasses. This order

of importance followed that for the green ground Vegetation categories'

peaks and suggests that the persistence on the Forest Floor of each of

these three types of material was of the same order of magnitude.

c) Tree Litter. Table XXXXII shows mean biomass and standard

error for each tree litter category on the Forest Floor on each

sampling occasion. Figures 42a,b,c and d show respectively the

changes in biomass of alder leaves and birch leaves; reproductive

structures and other tree litter; and wood through this period.

It was possible to separate the fallen tree leaves into

old (1965 crop) and new (1966 crop) on the basis of colour, texture

and fragility. In the case of alder the old leaves were usually

highly skeletonised, whilst in birch, the old leaves were mid-brown

and very brittle. It is clear from Figures 42b and c that the

seasonal changes in Forest Floor tree Leaf Litter biomass corresponded

to autumnal leaf fall, and the subsequent disappearance of almost all

the year's leaf fall within twelve months. However, the estimate

of the old leaf biomass after new leaf fall had begun may have been

an underestimate, because of sorting inefficiency. The alder

TABLE XXXXII   Biomass of Tree Litter on the Forest Floor, 1966-7 $(g/m^2 \pm 1 \text{ S.E.})$ Grid

DATE	ALDER LEAVES - NEW	ALDER LEAVES - OLD	ALDER REP	OTHER TREE	BIRCH LEAVES - NEW	BIRCH LEAVES - OLD	BIRCH REP	WOOD
20. 4.66	–	35.67 (9.30)	11.50 (4.60)	1.28 (0.80)	–	50.10 (10.70)	–	239.00 (55.75)
16. 5.66	–	19.76 (7.45)	6.66 (2.86)	1.60 (0.84)	–	53.24 (13.11)	–	254.08 (43.93)
10. 6.66	–	26.52 (12.10)	9.82 (3.57)	2.19 (–)	–	23.46 (8.76)	–	278.78 (92.80)
1. 7.66	1.16 (0.17)	7.28 (3.05)	9.62 (3.22)	2.59 (–)	1.75 (0.50)	20.66 (8.48)	–	221.79 (48.16)
1. 8.66	3.60 (0.86)	10.70 (4.70)	6.70 (2.90)	0.33 (–)	3.40 (0.24)	16.70 (5.80)	–	411.52 (78.72)
5. 9.66	9.47 (3.07)	1.40 (0.65)	2.67 (0.83)	+	8.23 (2.11)	13.26 (6.16)	0.35 (0.15)	298.37 (64.77)
5.10.66	27.15 (6.10)	9.29 (4.23)	3.44 (1.13)	4.06 (–)	34.85 (7.27)	2.83 (1.10)	0.73 (–)	342.30 (67.07)
31.10.66	69.39 (16.38)	0.96 (–)	5.20 (2.04)	5.08 (–)	75.89 (19.37)	0.62 (–)	0.98 (–)	182.69 (42.85)
1.12.66	97.58 (21.05)	–	6.27 (2.28)	23.06 (–)	71.02 (18.25)	–	0.19 (–)	180.86 (40.51)
16.1.67	76.89 (23.04)	–	3.78 (1.31)	5.39 (2.23)	46.62 (13.26)	–	0.34 (–)	318.57 (80.03)
15.2.67	50.24 (14.48)	–	3.79 (1.49)	11.24 (7.69)	69.54 (16.23)	–	0.75 (0.21)	215.23 (45.38)
15.3.67	25.53 (8.79)	–	5.91 (2.49)	1.74 (–)	51.12 (13.42)	–	0.77 (–)	231.90 (29.04)

Forest Floor leaf litter biomass reached a peak of 97.58g/m^2 at

the beginning of December, and declined steadily from this time through

to March. The birch leaf peak of 75.89g/m^2 was reached at the beginning

of November. Although some fluctuations took place, due no doubt to

quadrat location, no great decrease took place until after the middle

of February. These data are compared with the litter fall and

disappearance data in Section VIII. The biomass of alder reproductive

structures on the Forest Floor (Fig.42c) remained between 6.5 and

11.5g/m^2 from April to August. From September to March it lay between

2.6 and 6.3g/m^2. No birch reproductive structures were recorded

between April and August, but from September to March a small biomass

of less than 1g/m^2 was recorded. The other tree litter (also Fig.42c)

showed a peak of 23.06g/m^2 in December and declined to around 1g/m^2

the following spring. These data are considered further in Section VIII.

The wood litter biomass fluctuated greatly around a figure

of approximately 250g/m^2. The confidence limits of each of the

monthly figures were large, the standard error representing from 12.5%

to 33.3% of the mean, the period average of this statistic being 21.7%.

There was little difference (7.10g/m^2) between the wood litter biomass

estimates for April 1966 and March 1967. The disappearance of wood

litter is dealt with in Section VIII.

d) Quadrat apportionment for 1967-8 as calculated from 1966-7 data.

The apportionment of quadrats for clipping between the Alder and Birch

Zones from April 1967 on was decided on the basis of Snedecor's (1956)

Figure 42.

Biomass (g/m^2) 1966-7.
Forest floor tree litter.

a. top left - alder leaves, old (plus signs) and new (open
            circles).
b. top right - birch leaves, old (plus signs) and new (open
            circles).
c. bottom left - miscellaneous litter;
                alder rep. (open circles).
                other tree (closed circles).
                birch rep. (plus signs).
d. bottom right - wood litter.

BIOMASS (g/m²) 1966-7

FOREST FLOOR LITTER

ALDER LEAVES

BIRCH LEAVES

g/m²

MISC. LITTER

WOOD LITTER

M J J A S O N D J F M   M J J A S O N D J F M
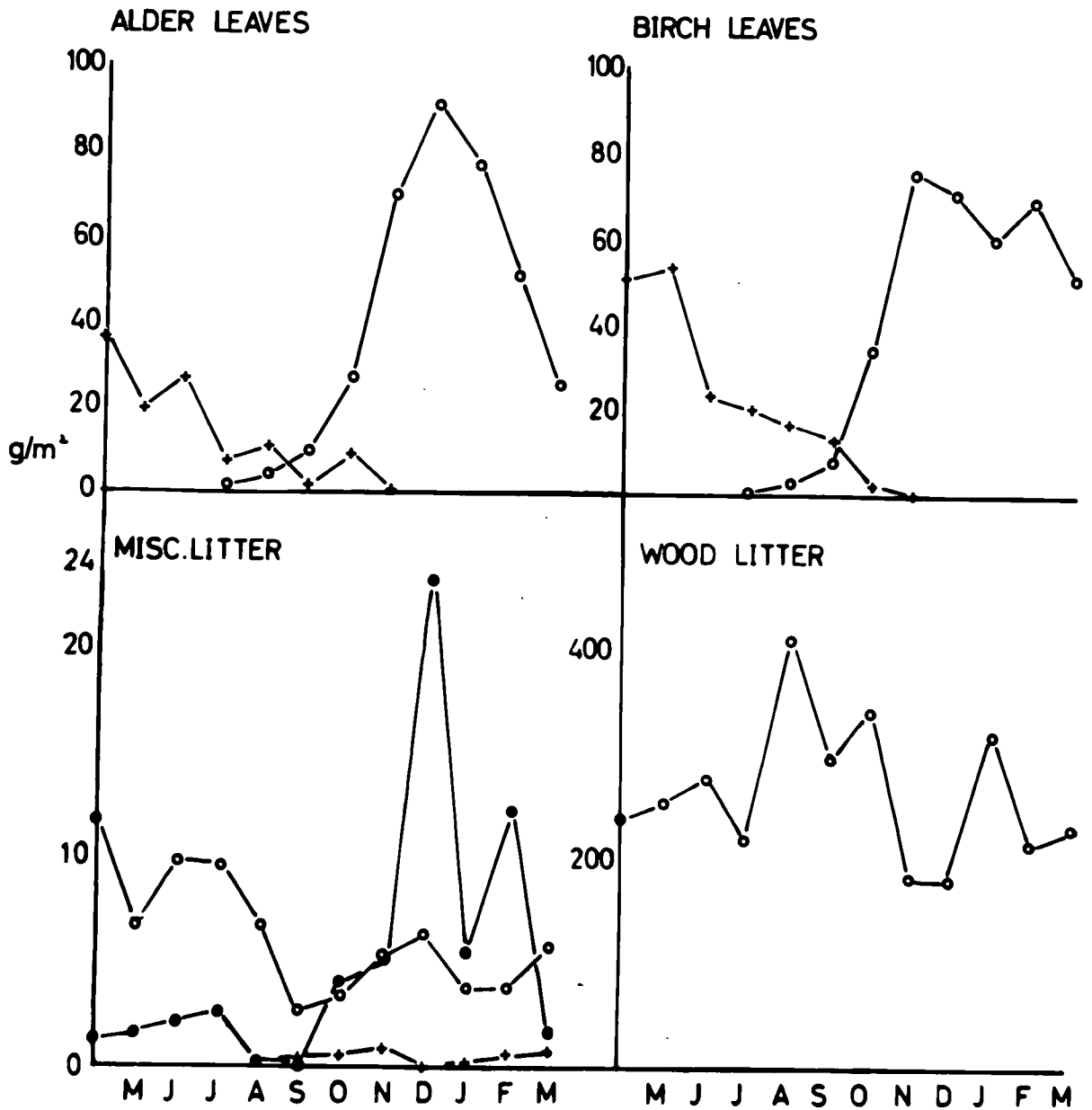
method (see Section VII ii(c)). The data obtained by serial cropping

from April 1966 to March 1967 were used. An example using the biomass

data for green ground vegetation on 10.6.66 is given below. In this

case, δ_h and hence relative "variance", may be calculated for the

Alder and Birch Zones as follows :-

	δ_h	W_h	$W_h\delta_h$	$\dfrac{W_h\,\delta_h}{\Sigma\,W_h\,\delta_h}$
ALDER ZONE	12.42	0.51	6.21	0.529
BIRCH ZONE	11.05	0.49	5.52	0.471
			11.73	1.000

$$\therefore\quad 24\,\frac{\delta_A\,W_A}{\Sigma\,\delta_h\,W_h} \;=\; 24 \times 0.529 = 12.69$$

$$\text{and } 24\,\frac{\delta_B\,W_B}{\Sigma\,\delta_h\,W_h} \;=\; 24 \times 0.471 = 11.31$$

The calculations indicate that 13 quadrats should be clipped in the

Alder Zone and 11 in the Birch Zone. The same calculations on data

for different categories of material on different sampling occasions

gave the same result. Therefore, from April 1967 to April 1968

13 quadrats were clipped in the Alder Zone of the Grid and 11 in the

Birch Zone of the Grid.

e) To test the effectiveness of mapping the Grid into the Alder and

Birch Zones. This was done using the results of serial cropping

from April 1966 to March 1967. The percentage deviation from the

monthly mean biomass for each category of material in each quadrat

was calculated using an Elliott 805 computer. This made possible

the mapping of the positions of quadrats where the percentage

deviation for a particular category of material was greater than

20%.   This was essentially the same technique as that used by

Golley (1965).   Figure 43 shows the distribution of these positions

for Forest Floor alder leaves, Forest Floor birch leaves and green

Agrostis tenuis.   Locations where percentage deviation exceeded

+ 20% for alder leaves and -20% for birch leaves were most common

in the Alder Zone.   The reverse was true in most of the Birch Zone.

All but three of the Agrostis tenuis locations lay in the Birch Zone,

so that this acted as a reasonably reliable indicator species.

This map suggests that the physiognomic division of the Grid into

Alder and Birch Zones effectively reflects the differentiation of

the vegetation and its biomass structure into two main types.

VII   iv.   Results, April 1967 through April 1968

Using the data obtained by serial cropping during the

second year of sampling mean biomass, variance and standard error

were calculated for each category of material for the Alder and Birch

Zones separately on each sampling occasion.   These values were weighted

according to the relative areas of the Alder and Birch Zones and hence

mean biomass and standard error for each category of material calculated

for the two zones taken together, that is, the Grid taken as a whole.

The reasons for adopting this procedure were given in VII ii (c).

These calculations were carried out on the Northumbrian Universities

Table 43.

Seasonal distribution. Explanation is given on pages
9/..

Key: > + 20   > - 20μ

  Agrostis tenuis   ●   ─○─

  Forest floor alder leaves   ◐   ◖

  Forest floor birch leaves   ◑   D

BIOMASS DISTRIBUTION
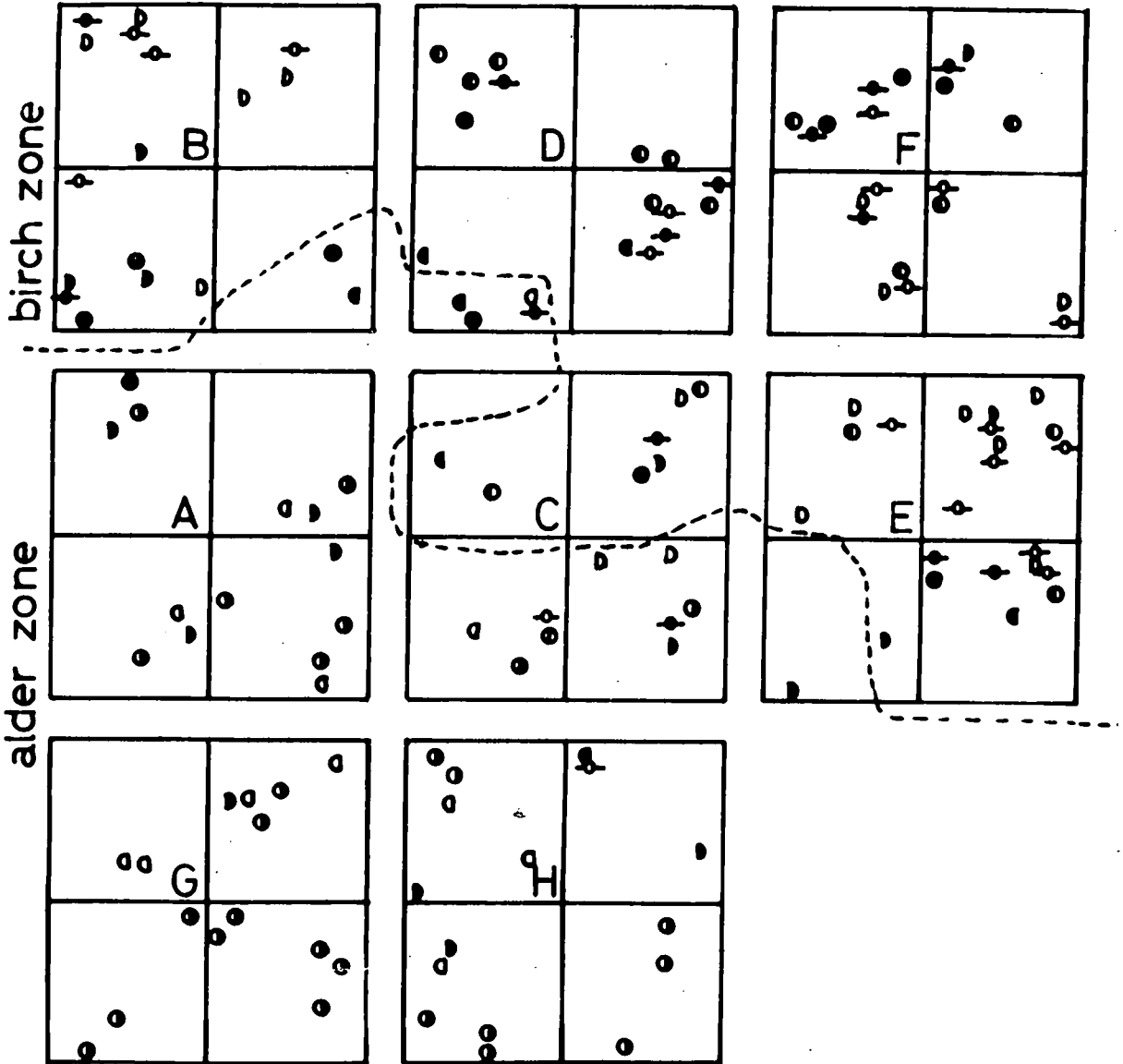
Multiple Access Computer (NUMAC), IBM 360/375. The programme, 'MEANWTS', was written for this purpose in Programme Language One by J. Ollason of the Department of Zoology, University of Durham. Appendix II contains a specimen of the print-out, and a description of the punched-card format of the data input.

During the 1967-8 sampling period, the subdivision of ground vegetation litter into Fern + Chamaenerion, Rubus, and grass litter was continued. Some of the green ground vegetation categories were further subdivided. In particular, the Fern category was split into Dryopteris, Polystichum and Pteridium. Although the collection and handling of the serial cropping data in this period was different to that in 1966-7, it is possible to compare biomasses on the Grid taken as a whole for the two periods.

a) Green Ground Vegetation and Bryophytes, Alder Zone, Birch Zone and whole Grid, 1967-8. Table XXXXIII shows the serial cropping data for the green ground vegetation and bryophytes from April 1967 through April 1968. The data for the Alder and Birch Zones are dealt with separately, and then the resulting values for the whole Grid are discussed.

i. Alder Zone. Figure 44a shows the changes of green ground vegetation biomass and bryophyte biomass for the Alder Zone. The green ground vegetation biomass showed a clear seasonal pattern, rising to a peak of $104.66 g/m^2$ in July and showing a secondary peak of $78.67 g/m^2$ in October. It then declined to a winter value of

TABLE XXXXIII

Biomass of Green Ground Vegetation and Bryophytes 1967-8

A : Alder Zone   B : Birch Zone   E : Grid as a whole   (Biomass G.O.D.WT/M^2 (1 S.E.))

CATEGORY		APRIL	MAY	JUNE	JULY	AUGUST	SEPTEMBER	OCTOBER	DECEMBER	FEBRUARY	APRIL
DRYOPTERIS	A	1.81 (1.37)	20.67(12.53)	25.35(14.66)	31.69(24.68)	34.22(18.30)	35.32(15.32)	48.46(35.30)	3.23 (2.23)	-	-
	B	1.70 (0.73)	11.74 (5.89)	20.79(15.31)	25.68(17.47)	47.27(47.27)	54.16(50.13)	70.97(64.68)	0.37 (0.37)	-	-
	E	1.76 (0.78)	16.30 (7.20)	23.12(10.59)	28.75(15.22)	40.78(17.85)	44.93(20.23)	59.71( )	1.84 (1.15)	-	-
POLYSTICHUM	A	-	-	-	8.72 (7.56)	1.19 (0.76)	0.93( )	1.07 (0.51)	0.67 (0.67)	-	-
	B	0.33 (0.19)	0.37 (0.28)	1.03 (0.66)	2.31 (2.31)	-	0.62 (0.49)	-	-	-	-
	E	0.17 (0.09)	0.19 (0.12)	0.19 (0.08)	0.38 (0.18)	1.75 (1.20)	4.96 (3.87)	0.46	0.84	0.33	0.56 (0.38)
PTERIDIUM	A	-	-	-	-	0.15 (0.15)	-	-	-	-	-
	B	-	-	-	-	8.75 (8.75)	-	-	-	-	-
	E	-	-	-	5.31 (5.15)	4.53	-	-	0.33	-	-
RUBUS	A	37.63(10.88)	25.83 (8.10)	21.62 (7.61)	41.64(14.20)	30.22(11.85)	29.50 (6.90)	28.72 (6.72)	17.95 (5.15)	18.97 (4.59)	20.71 (6.13)
	B	8.60 (3.61)	43.95(17.73)	30.31 (9.42)	26.13(14.22)	20.34 (5.50)	20.50 (8.89)	20.74 (8.94)	7.99 (6.10)	23.78 (9.50)	15.30 (4.25)
	E	23.41 (5.82)	34.89(15.72)	25.88 (6.03)	33.73(10.20)	25.38 (6.62)	24.90 (5.01)	24.56 (5.03)	13.08 (3.99)	21.33 (5.21)	17.95 (3.56)
C. ANGUSTIFOLIUM	A	-	0.43 (+)	0.87 (0.87)	-	7.98 (5.68)	-	-	-	-	-
	B	-	0.86 (0.86)	0.62	2.60	4.07	-	-	-	-	-
	E	0.21 (+)	0.87 (0.62)	-	5.31 (5.15)	-	-	-	-	-	-
FORBS	A	-	0.49 (+)	0.30 (0.30)	4.41 (4.19)	1.72 (1.47)	0.32 (0.25)	0.07 (0.05)	0.23 (0.23)	0.04 (0.04)	0.54 (0.54)
	B	2.94 (1.86)	0.51 (+)	2.24 (0.87)	-	1.83 (1.00)	1.03 (0.76)	0.70 (0.44)	0.45 (0.45)	0.70 (0.70)	0.22 (0.22)
	E	1.50 (0.92)	1.00 (+)	1.25 (0.45)	2.16	1.78 (0.89)	0.68	0.39 (0.22)	0.34 (0.25)	0.37 (0.34)	0.39 (0.29)
VIOLA	A	0.71 (0.71)	-	0.02 (0.02)	0.06 (0.04)	0.05 (0.05)	-	0.08 (+)	-	0.15 (0.15)	0.07 (0.07)
	B	0.36 (0.35)	0.24 (+)	1.18 (0.90)	-	0.34 (0.26)	-	-	-	-	-
	E	-	0.12 (+)	0.59 (0.44)	0.03	0.19 (0.13)	-	0.04	-	0.07 (0.07)	0.03
AGROSTIS TENUIS	A	0.03 (0.03)	0.46 (0.45)	6.02 (2.50)	-	-	16.50( )	0.02 (0.02)	1.24 (1.23)	0.01 (0.01)	0.24 (0.16)
	B	2.92 (2.49)	11.13 (4.84)	10.17 (7.12)	44.84(22.33)	32.52(19.20)	3.18 (1.19)	0.47 (0.42)	-	-	0.13 (0.12)
	E	1.45 (1.22)	5.68 (1.01)	8.14	22.87	16.58	8.41	1.57 (0.58)	0.87 (0.66)	-	0.19 (0.10)
D. CAESPITOSA	A	-	-	10.95 (1.41)	-	-	-	-	-	-	-
	B	0.82 (0.56)	0.26 (+)	-	-	-	0.38 (0.38)	0.19	-	0.16 (0.16)	1.13 (0.81)
	E	0.42 (0.28)	0.13 (-)	5.37	-	-	0.19	-	-	0.82	0.58
H. LANATUS	A	-	10.73 (4.10)	9.81 (3.80)	12.83 (5.92)	5.29 (2.09)	3.20 (1.80)	0.25 (0.11)	-	-	-
	B	-	7.52 (3.62)	10.87 (6.09)	0.33 (0.22)	6.21 (4.56)	2.90 (1.51)	0.01 (0.01)	-	-	-
	E	-	9.12 (3.97)	10.33 (3.56)	6.71 (3.02)	5.74 (2.45)	3.05	0.14 (0.06)	-	-	-
H. MOLLIS	A	3.47 (1.92)	3.44 (1.81)	9.35 (4.88)	-	2.56 (1.83)	0.90 (0.53)	0.01 (0.01)	-	0.71 (0.16)	2.82 (1.52)
	B	5.63 (2.77)	3.77 (1.92)	4.77 (2.89)	9.94 (5.82)	1.74 (1.31)	1.10 (0.91)	0.12 (0.12)	0.58 (0.55)	3.33 (1.78)	1.79 (1.19)
	E	4.35 (1.67)	3.60 (1.75)	7.11 (2.87)	5.07	2.17 (1.14)	1.00	0.06	0.29 (0.27)	2.05	1.29 (0.94)
TOTAL G.V.	A	42.97(10.71)	61.62(14.52)	84.29(14.57)	104.66(28.02)	75.40(18.35)	70.17(15.30)	78.67(28.57)	23.33 (4.45)	19.88 (4.59)	24.38 (5.96)
	B	23.68 (5.57)	79.92(12.97)	81.57(13.03)	107.95(31.83)	129.29(28.22)	96.19(25.20)	96.72(62.90)	9.86 (6.14)	28.53 (8.95)	18.48 (4.98)
	E	33.13 (6.11)	70.95 (9.97)	82.90 (9.85)	106.33(21.48)	102.89(17.52)	83.44(14.52)	87.88(34.48)	16.46 (3.68)	24.29 (4.99)	21.37 (4.35)
BRYOPHYTES	A	8.19 (4.10)	19.35 (8.81)	18.38(10.71)	12.72 (9.71)	15.45 (7.40)	12.82 (9.72)	7.60 (4.29)	5.16 (3.28)	6.10 (3.78)	5.90 (2.73)
	B	16.31(10.17)	6.66 (3.51)	17.77 (6.41)	13.06 (9.30)	11.14 (4.05)	12.99 (9.20)	12.88 (8.83)	12.27 (4.43)	9.86 (4.62)	1.57 (0.70)
	E	12.18 (5.41)	13.13 (5.53)	18.09 (6.31)	12.89 (6.73)	13.34 (4.26)	12.90 (6.74)	10.19 (4.85)	8.65 (2.74)	7.94 (2.98)	3.78 (1.44)

$19.88g/m^2$ in February 1968. The bryophyte biomass showed a peak

of $19.35g/m^2$ in May, staying between this value and $12.70g/m^2$ until

September. For the rest of the year bryophyte biomass in the Alder

Zone lay between 5.16 and $8.19g/m^2$. The bryophyte biomass never

amounted to more than 31% of the green ground vegetation biomass

(i.e. of green ground vegetation without bryophytes). The bryophytes

had the greatest relative importance in May 1967 (31%) and February

1968 (30%). On the first occasion this was due to low green ground

vegetation biomass.

Figure 44b shows the biomass changes of the Fern categories

in the Alder Zone. For Dryopteris there was a steady rise from near

zero in April to $48.46g/m^2$ in October. Following this, the Dryopteris

biomass declined almost to zero by December. No Polystichum was

recorded in the Alder Zone until July, when a 'peak' value of $8.72g/m^2$

was recorded. After that, Polystichum biomass remained at approximately

$1g/m^2$. The July value was almost certainly the product of quadrat

location. Pteridium was only recorded once in the Alder Zone, with

a very low value of $0.15g/m^2$.

Figure 44c shows the biomass changes of Rubus fructicosus

and Chamaenerion angustifolium in the Alder Zone. The Rubus biomass

was between $17.9g/m^2$ and $30.2g/m^2$ for the whole year excepting April

($37.63g/m^2$) and July ($41.64g/m^2$), when it peaked. The April high

value was probably due to the superimposition of new growth on the

second-year material. The die-back of second-year material could

account for the May - June trough, only to be overtaken by new

growth to form the July peak. The confidence limits were wide,

and so any conclusions drawn from these data must be viewed with

caution. The Rubus biomass contributed 39% of the green ground

vegetation in July, when both peaked, and over 85% from December

to April. Thus Rubus provided the most important overwintering

component of green ground vegetation. When compared with Rubus,

Chamaenerion was a much less prominent component of the green ground

vegetation biomass in the Alder Zone. It was only recorded twice,

in June and July. In June the biomass was less than $1g/m^2$ and in

July a higher value of $5.31g/m^2$ was recorded. The standard error

in July was almost as great as the mean. Thus the sampling method

was not adequate to deal with species such as Chamaenerion

angustifolium represented by a few widely dispersed individuals

in the Alder Zone.

Figure 44d shows the biomass of Viola riviniana and

the other forb categories in the Alder Zone. The biomass of the

two combined never exceeded $4.47g/m^2$, the July figure. Apart from

the forb figure for August ($1.72g/m^2$) and this, neither exceeded

$0.49g/m^2$ at any time in the year, usually approaching zero. In

spite of limitations in the sampling technique, it seems reasonable

to suppose that these species contributed little to the biomass of

the green ground vegetation of the Alder Zone in 1967-8.

Figure 44.

Biomass (g/m^2) 1967-8. Alder Zone.

a. top left - total ground vegetation (open circles) and
      bryophytes (plus signs).
b. top right - ferns; total ferns (plus signs) and Dryopteris
      filix-mas.
c. middle left - Rubus fruticosus (open circles) and C.angust-
      ifolium (plus signs).
d. middle right - forbs.
e. bottom - grasses; Holcus spp. (open circles), D. caespetosa
      (closed circles) and Agrostis tenuis (plus signs).

BIOMASS(g/m²) 1967-8 ALDER ZONE

GROUND VEGETATION + BRYOPHYTES

FERNS

g/m²

RUBUS+C.ANGUSTIFOLIUM

FORBS

GRASSES
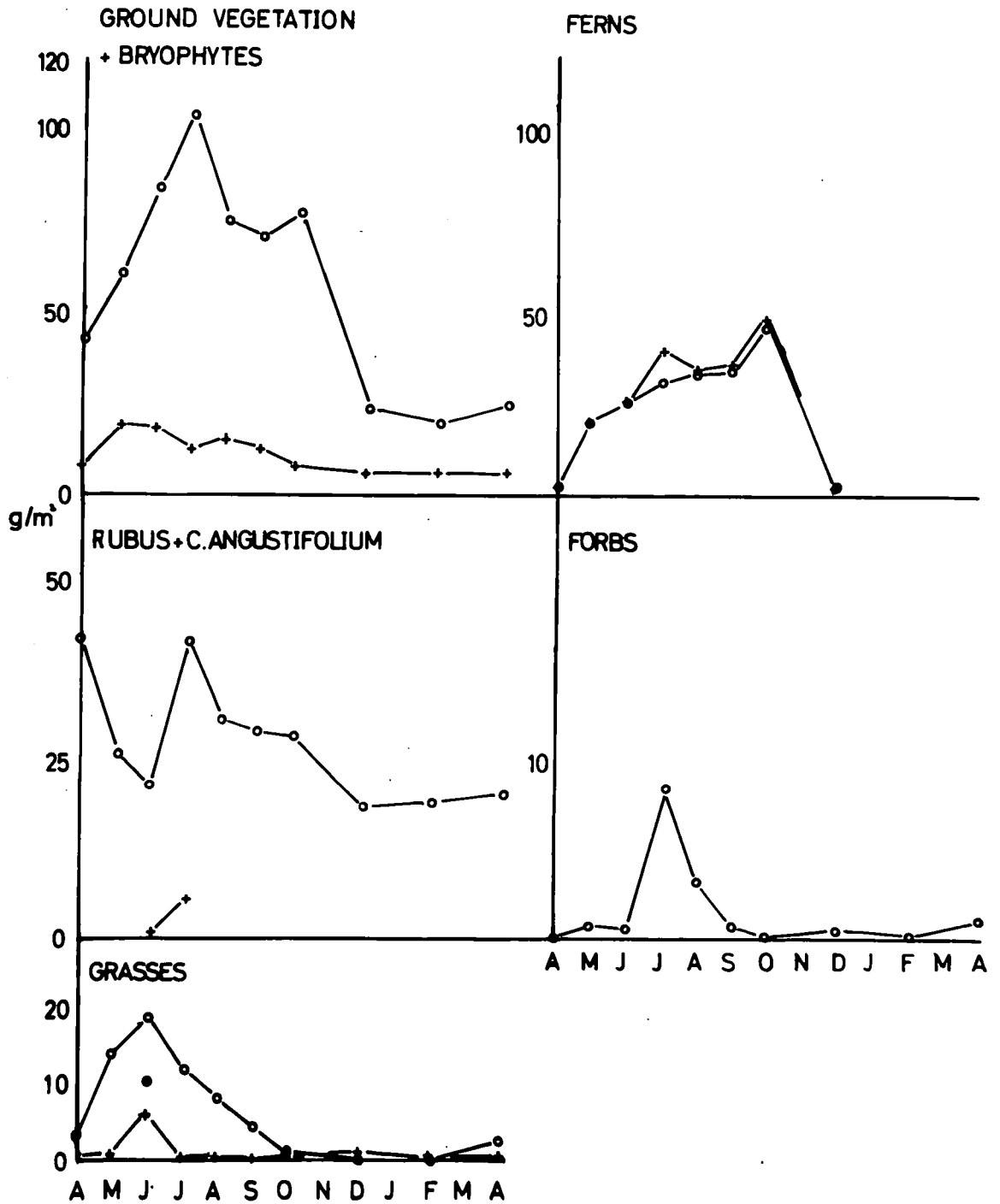
Figure 44e shows the biomass changes of the grass species in the Alder Zone. Apart from a single, high value for Deschampsia caespetosa in June, the two Holcus spp. always contributed the major part of the grass biomass. It was only possible to sort the Holcus into Holcus mollis and Holcus lanatus from May to October inclusive. During this period Holcus lanatus showed values around $10g/m^2$ from May to July, reaching a peak of $12.83g/m^2$ in July. After that it steadily declined to near zero in October,; H.mollis showed more erratic behaviour, with a peak of $9.35g/m^2$ in June. A simpler pattern appeared when Holcus was considered as one. It increased to a peak of $19.16g/m^2$ in June, decreasing to near zero in October. Agrostis tenuis was much less important than Holcus in the Alder Zone. It reached a peak of $6.02g/m^2$ in June, showing values of around $1g/m^2$ or less for the rest of the year. The grasses contributed 43% of the green ground vegetation biomass of the Alder Zone in June, but less than 10% for most of the year.

ii. Birch Zone. Figure 45a shows the changes in green ground vegetation biomass and bryophyte biomass for the Birch Zone from April 1967 through April 1968. As in the Alder Zone, the green ground vegetation showed a clear seasonal pattern reaching a higher peak of $129.29g/m^2$ in August, one month later. It declined to $96g/m^2$ in September and October and then fell sharply to a December value of $9.86g/m^2$. The February and April figures were higher ($28.53g/m^2$ and $18.48g/m^2$), but the difference was not significant at the 95% level.

The bryophyte biomass peaked at $16.31g/m^2$ and $17.77g/m^2$ in April and June respectively. Apart from a very low value $(1.57g/m^2)$ in April 1968, bryophyte biomass lay between $6.66g/m^2$ and $13.06g/m^2$ for the rest of the year. The bryophyte biomass was greater (124%) than the green ground vegetation biomass in December, and amounted to 66% of it in April 1967, thereby showing a marked contrast with the Alder Zone situation. For the rest of the year Bryophyte biomass was between 8% and 35% the size of the green ground vegetation biomass.

Figure 45b shows the biomass changes of the Fern categories in the Birch Zone. For Dryopteris the pattern was much as in the Alder Zone, excepting that the October peak was much higher $(70.97g/m^2)$. Polystichum appeared more frequently in the cropped quadrats than in the Alder Zone, showing a low peak of $2.31g/m^2$ in August. Pteridium was cropped on a single occasion, August, when a single quadrat contained a clump of Pteridium giving a mean biomass estimate of $8.75g/m^2$. At the time of the Dryopteris peak in October the Fern categories contributed 74% of the green ground vegetation biomass in the Birch Zone.

Figure 45c shows the biomass changes of Rubus fruticosus and Chamaenerion angustifolium in the Birch Zone. The Rubus biomass in the Birch Zone showed much greater fluctuation than in the Alder Zone. It rose from $8.60g/m^2$ in April to a peak of $43.95g/m^2$ in May. Then it declined to around $20g/m^2$ in August, September and October. A low value of $7.99g/m^2$ was recorded in December, rising to $23.78g/m^2$

and $15.30g/m^2$ in February and April respectively. It seems likely that these winter fluctuations were largely the result of quadrat location. The Rubus biomass came to 55% of green ground vegetation biomass in May and between 81% and 83% from December through April. It contributed between 16% and 36% for the rest of the year. Thus Rubus was the most important contributor to the winter biomass of green ground vegetation, in the Birch Zone as in the Alder Zone. Chamaenerion angustifolium appeared only sporadically in the serial cropping of the Birch Zone, the highest biomass ($7.88g/m^2$) being recorded in August.

Figure 45d shows the biomass of Viola riviniana and the other forb categories in the Birch Zone 1967-8. As in the Alder Zone these biomasses were very low. The forbs showed peaks in April and June as did Viola riviniana.

Figure 45e shows the biomass changes of the grass species in the Birch Zone. Deschampsia caespetosa was only sporadically recorded, almost all values being less than $1g/m^2$. Agrostis tenuis was by far the most important contributor to grass biomass in the Birch Zone, peaking at $44.84g/m^2$ in July. The Holcus species showed complex changes of biomass when considered separately. H.lanatus showed a peak in June and H.mollis in July, both being close to $10g/m^2$. As in the Alder Zone, a clearer pattern emerged when these two species were considered together, rising to a maximum of $15.64g/m^2$ in June.

Figure 45.

Biomass (g/m^2) 1967-8. Birch Zone.

a. top left - total ground vegetation (crosses) and bry-
            ophytes (open circles).
b. top right - ferns; D.filix-mas (crosses), Pteridium
            aquilinum (closed circle) and Polystichum
            setiferum (open circles).
c. middle left - Rubus (crosses) and C.angustifolium (open
            circles).
d. middle right - V.riviniana (crosses) and other forbs (circles).
e. bottom - grasses; D.caespetosa (crosses), Agrostis tenuis
            (open circles), Holcus lanatus (plus signs),
            H.mollis (closed circles).

BIOMASS (g/m²) 1967-8. GROUND VEGETATION AND BRYOPHYTES
BIRCH ZONE

TOTAL GV AND BRYOPHYTES

FERNS

RUBUS AND C.ANGUSTIFOLIUM

VIOLA AND OTHER FORBS
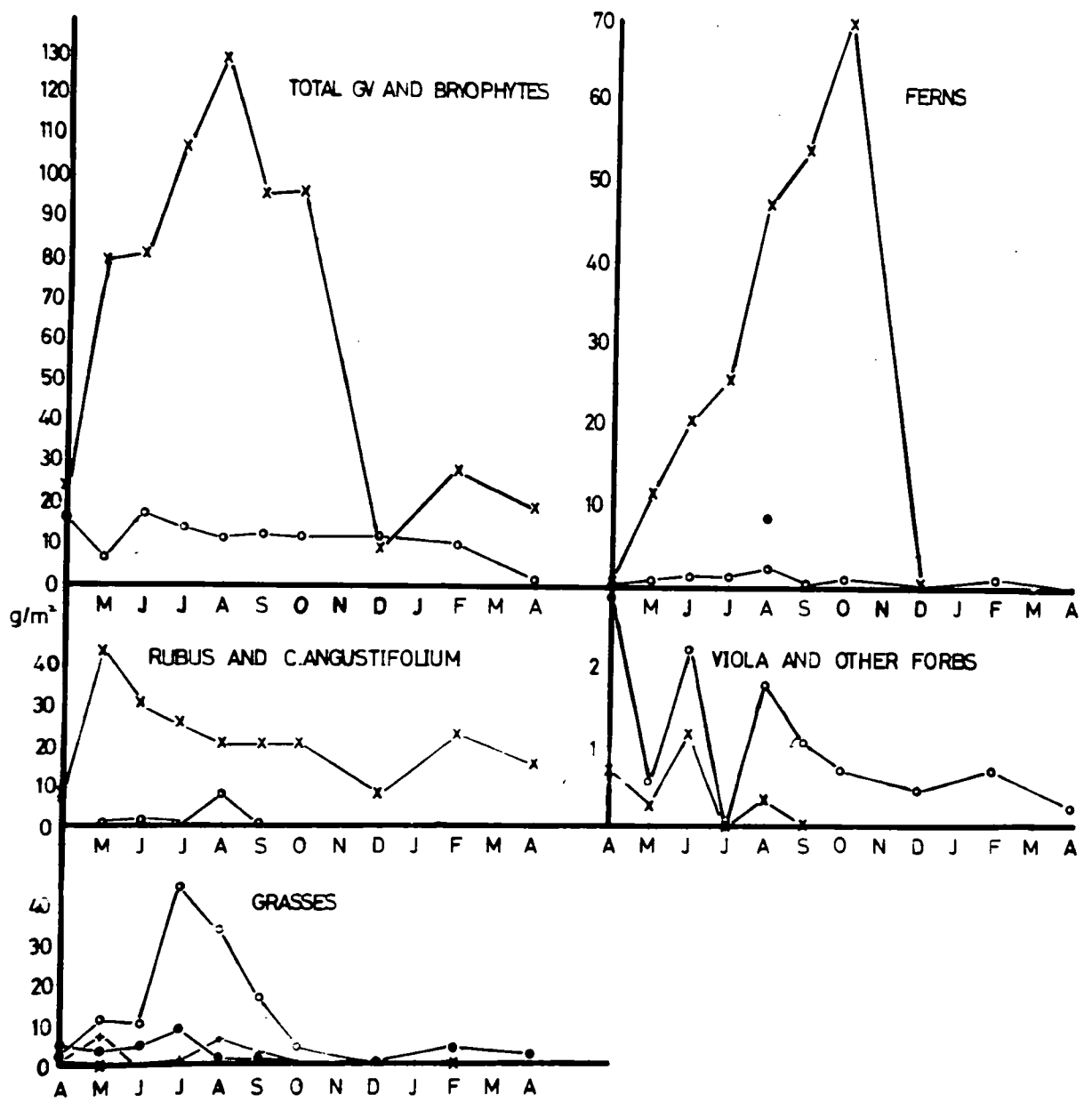
GRASSES

The grasses contributed 51% of the green ground vegetation biomass of the Birch Zone in June, between 28% and 40% for the rest of the summer and less than 21% from September on. The grasses were, overall, more important contributors to the green ground vegetation biomass in the Birch Zone than in the Alder Zone.

iii. Grid. The values presented here were calculated from those for the Alder and Birch Zones as outlined at the beginning of VII iv. Therefore, they will be intermediate between those of the two Zones.

Figure 46a shows the changes in green ground vegetation biomass for the whole Grid (referred to below as simply the Grid). The peak biomass of green ground vegetation was recorded in July, at the same time as the Alder Zone green ground vegetation biomass peak. A secondary peak occurred in October, again as in the Alder Zone. This secondary peak was probably due to the increase in Dryopteris biomass, which occurred in October in both zones. The winter biomass (December and February) lay between $16.46g/m^2$ and $24.29g/m^2$ as did that for April 1968, although it should be noted that the April 1967 figure was $33.13g/m^2$. For most of the year Bryophyte biomass was between $10.19g/m^2$ and $13.34g/m^2$. In June it peaked at $18.09g/m^2$ and from December on it lay below $10g/m^2$. When considered for the whole Grid, the bryophytes did not achieve the winter importance they had in the Birch Zone taken alone. Their biomass was equal to 11.6% to 21.0% of that of the green ground

vegetation biomass in all months except April 1967 and December
and February, when it lay between 32.7% and 52.6%.

Figure 46b shows the biomass changes of the Fern categories
for the Grid in 1967-8. As explained above, the Grid biomass values
are necessarily intermediate between those for the Alder Zone and the
Birch Zone. Thus the pattern for Dryopteris was similar to that
observed in both zones. Due to the method employed (i.e. the
scattered nature of the zone data), Polystichium was more consistently
present and reached a peak of just under 5g/m^2 in July. Pteridium
was only present in August. During the Dryopteris peak in October
the Fern categories contributed 69% of the green ground vegetation
biomass on the Grid taken as a whole.

Figure 46c shows the biomass changes of Rubus fruticosus
and Chamaenerion angustifolium on the Grid. The fluctuations in
Rubus biomass were, of course, less marked than in either zone taken
alone. The Rubus biomass lay between 23.41g/m^2 and 33.73g/m^2 from
April 1967 until October. From December until April 1968 it lay
between 13.08g/m^2 and 21.33g/m^2. In April 1967 the Rubus biomass
was 71% of the green ground vegetation biomass. It fell to 49%
in May and lay between 25% and 32% until December. From December
through April 1968 it lay above 79% of green ground vegetation biomass.
Rubus was the most important green ground vegetation biomass component
in winter over the whole Grid. Chamaenerion was relatively unimportant,

the highest value being just over $4g/m^2$.

Figure 46d shows the biomass of <u>Viola riviniana</u> and the other forb categories on the Grid. Neither of these was of much importance, the highest values being $0.59g/m^2$ (<u>Viola</u>) and $2.16g/m^2$ (forbs).

Figure 46e shows the biomass changes of grass species for the whole Grid. <u>Deschampsia caespetosa</u> occurred only sporadically, with a peak value of $5.37g/m^2$ in June. <u>Agrostis tenuis</u> was the most important single species, peaking at $22.87g/m^2$ in July. The <u>Holcus</u> species taken separately showed peaks of $10.33g/m^2$ (<u>H.lanatus</u>) and $7.11g/m^2$ (<u>H.mollis</u>) in June. Taken together, they rose to a peak of $17.44g/m^2$ in June. Expressed as a percentage of green ground vegetation biomass, grass biomass rose to a peak of 37% in June, and then fell steadily to 2% in October. It then climbed back to 14% by April 1968, that is to say, the grasses do not form an important part of the overwintering green ground vegetation biomass.

b) Ground Vegetation Litter; Alder Zone, Birch Zone and whole Grid 1967-8. Table XXXXIV shows the biomass changes of ground vegetation litter categories of material from April 1967 through April 1968. The data for the Alder and Birch Zones are dealt with separately and then those for the whole Grid are discussed.

i. Alder Zone. Figure 47a shows the biomass changes of ground vegetation litter in the Alder Zone. The total fell from almost $180g/m^2$ in April 1967 until June. Then it increased in June - July

TABLE XXXIV

Biomass of Ground Vegetation Litter g/m² (± 1 S.E.) 1967-8

		APRIL		MAY		JUNE		JULY		AUGUST	
Fern	A	130.43	(75.69)	75.02	(25.25)	60.03	(16.91)	58.14	(27.92)	43.19	(20.74)
	B	94.19	(54.66)	87.32	(39.67)	85.49	(39.67)	67.37	(41.96)	73.86	(59.30)
	E	112.68	(46.98)	81.29	(22.34)	72.51	(21.27)	62.66	(25.01)	58.22	(30.92)
Rubus	A	34.60	(10.72)	35.30	(10.72)	36.89	(11.28)	79.65	(30.34)	40.46	(16.18)
	B	42.44	(13.02)	51.49	(20.12)	101.00	(31.50)	117.14	(57.99)	57.86	(24.29)
	E	38.54	(7.65)	43.35	(11.50)	69.52	(19.56)	98.03	(32.36)	48.99	(14.48)
Grass	A	8.24	(3.81)	10.32	(3.90)	12.40	(3.74)	9.69	(4.46)	22.03	(7.82)
	B	27.89	(9.09)	41.89	(20.19)	41.07	(14.28)	49.71	(20.66)	57.25	(19.04)
	E	17.87	(4.86)	26.42		26.45	(7.25)	29.31	(10.38)	39.29	(10.15)
C.angustifolium	A	4.38	(3.31)	-		-		-		-	
	B	8.58	(7.04)	1.44		0.58	(0.58)	-		-	
	E	6.44	(3.84)	0.73		0.29		-		-	
Total	A	177.67	(69.98)	120.64	(22.93)	109.34	(12.84)	147.49	(33.45)	105.69	(22.68)
	B	173.10	(55.48)	182.14	(65.30)	228.14	(46.11)	234.23	(56.45)	188.97	(77.26)
	E	175.34	(43.96)	152.00	(35.59)	169.93	(28.27)	190.00	(32.49)	146.50	(39.59)

		OCTOBER		DECEMBER		FEBRUARY		APRIL	
Fern	A	58.06	(21.74)	88.31	(31.22)	73.23	(25.25)	64.66	(27.56)
	B	39.15	(26.83)	67.25	(29.53)	99.72	(55.59)	132.88	(54.96)
	E	48.80	(17.20)	77.57	(21.72)	86.21	(30.14)	98.09	(30.38)
Rubus	A	45.78	(10.97)	34.14	(13.49)	26.43	(8.63)	31.70	(8.73)
	B	29.93	(10.19)	44.77	(12.45)	63.21	(18.73)	26.93	(8.79)
	E	38.02	(7.50)	39.35	(9.20)	44.46	(10.18)	29.37	(6.20)
Grass	A	12.84	(5.59)	31.50	(21.40)	38.62	(11.13)	23.67	(8.76)
	B	93.00	(32.29)	84.59	(25.52)	90.61	(22.40)	61.55	(22.68)
	E	52.12	(16.08)	57.52	(16.60)	64.10	(12.36)	42.24	(11.98)
C.angustifolium	A	2.26	(1.72)	-		0.09	(0.09)	0.07	(0.07)
	B	-		-		0.61	(0.41)	-	
	E	1.11		-		0.35	(0.21)	0.03	
Total	A	121.42	(22.93)	151.53	(27.25)	138.38	(23.38)	119.38	(21.05)
	B	162.09	(20.99)	196.61	(35.61)	257.07	(44.97)	221.38	(55.09)
	E	141.35	(18.78)	174.52	(22.34)	196.54	(25.06)	169.36	(29.05)

A Alder Zone
B Birch Zone
E Grid

Figure 46.

Biomass (g/m^2) 1967-8. Grid.

a. top left - total ground vegetation (crosses) and
           bryophtes (circles).
b. top right - ferns; D.filix-mas (crosses), Polystichum
           setiferum (open circles), Pteridium aquilinum
           (closed circles).
c. middle left - Rubus (crosses) and C.angustifolium (circles).
d. middle right - V.riviniana (crosses) and other forbs
           (circles).
e. bottom - grasses; A.tenuis (open circles), H.lanatus
           (plus signs), H.mollis (closed circles) and
           D.caespitosa (crosses).

BIOMASS (g/m²) 1967-8   GROUND VEGETATION AND BRYOPHYTES
GRID
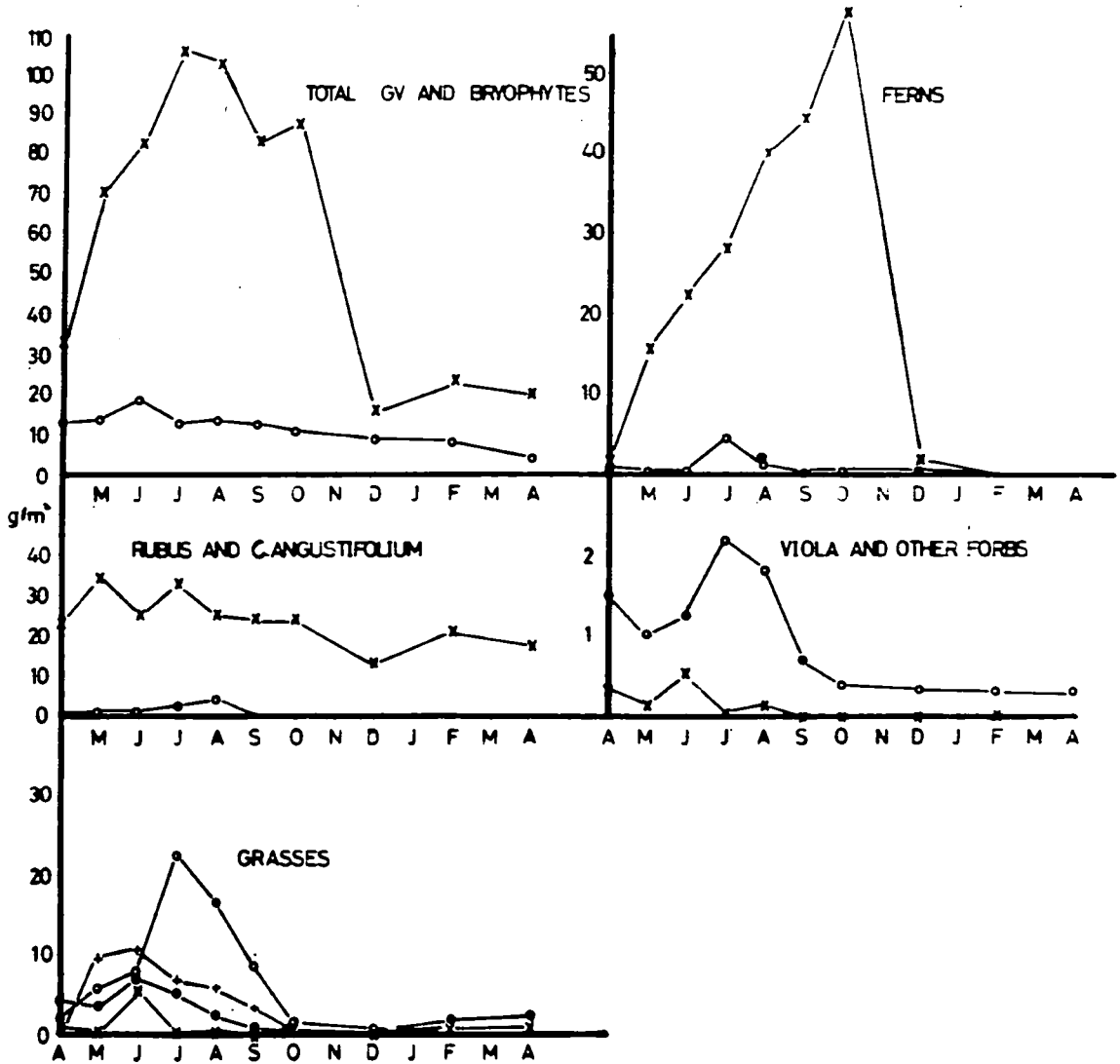
and decreased in July - August. Figures are not available for September 1967, due to mechanical failure of the storage facilities containing the ground vegetation litter samples. The total ground vegetation litter biomass in the Alder Zone increased from August to December, when it just exceeded $150g/m^2$, followed by a slow decline until April 1968. A greater understanding of the biomass change processes may be gained from an examination of biomass changes in the three components of the ground vegetation litter. The April - June decline can be accounted for by a decrease in fern litter biomass. The July peak was almost entirely made up of an increase in _Rubus_ litter biomass and was probably due to the die-back of overwintered _Rubus_ parts, despite the fact that the increase in litter occurred later than the decrease in green _Rubus_ biomass. The increase in total ground vegetation litter, August to December, can be explained by the increases in fern and grass litter biomasses. These increases did coincide with decreases in green fern and grass biomasses. Despite the fluctuations of the three litter components, the ground vegetation litter biomass remained between $105g/m^2$ and $178g/m^2$ throughout the year. There was a net decrease of $58.29g/m^2$ between April 1967 and April 1968.

ii. Birch Zone. The biomass changes of ground vegetation litter in the Birch Zone are shown in Figure 47b. The total rose to almost $235g/m^2$ in July and then fell to near $160g/m^2$ by October. It then

rose to almost $260g/m^2$ in February, declining in the spring to just over $220g/m^2$ in April. The general level was higher than in the Alder Zone and the fluctuations were greater. As in the Alder Zone, the April to July increase in ground vegetation litter biomass can be attributed to die-back of <u>Rubus</u> and was correlated with the decrease in green <u>Rubus</u> biomass from May to July. There was a steady decline in Fern litter from April to October, and in <u>Rubus</u> litter from July to October. The increase in total ground vegetation litter biomass from October to February corresponded with the increase in Fern and <u>Rubus</u> litter biomass during this period. The grass litter biomass rose to a plateau in October - February, after which it declined, as did the <u>Rubus</u> litter, between February and April 1968. There was a net increase of $48.28g/m^2$ in the total ground vegetation litter biomass between April 1967 and April 1968.

iii. Grid. Biomass changes in ground vegetation litter biomass on the whole Grid in 1967-8 are shown in Figure 47c. There was a net decrease of only $5.98g/m^2$ in the ground vegetation litter biomass on the grid between April 1967 and April 1968. Neither in the data for the zones taken separately, nor together as the Grid, was it always possible to relate biomass changes of live and dead categories of material on a month to month basis. Although, on a seasonal basis the two sets of data show consistent relationships with one another and the known natural history of the Study Area.

Figure 47.

Biomass (g/m^2) 1967-8. Grid. Ground Vegetation Litter.

a. top left – Alder Zone.
b. top right – Birch Zone.
c. bottom – Grid.

Key:- open circles – total.
    closed circles – Rubus litter.
    crosses – fern litter.
    plus signs – grass litter.

BIOMASS (g/m²)   1967-8

GROUND VEGETATION LITTER

ALDER ZONE
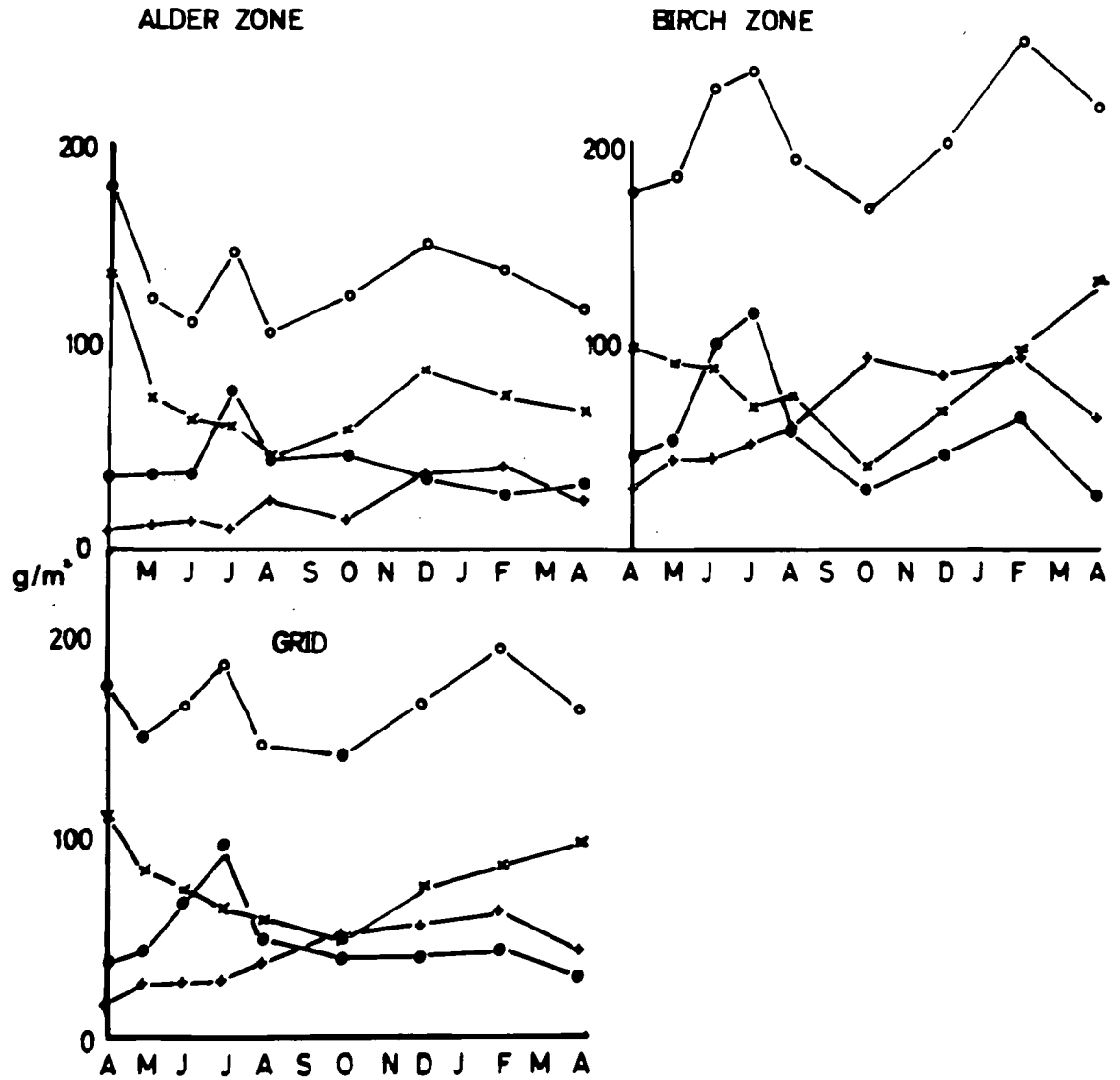
BIRCH ZONE

GRID

c) Tree Litter; Alder Zone, Birch Zone and the whole Grid, 1967-8.

Table XXXXV shows the biomass of tree Litter on the Forest Floor from April 1967 through April 1968. The data for the Alder and Birch Zones are dealt with separately and then the figures for the Grid taken as a whole are dealt with.

i. Alder Zone. Figures 48a,b, show the biomass changes of alder leaves, birch leaves,

The expected seasonal pattern emerged quite clearly for alder leaves. The newly fallen leaves began to accumulate in June, reaching a peak of almost $120g/m^2$ in February, rather later than might be expected from the litter trap data. The choice of quadrat location no doubt intruded here, and the December figure of $101.31g/m^2$ may well represent a more realistic estimate of peak standing crop. After February there was a rapid decline in alder leaf biomass and it is clear that the greater part of a year's alder leaf fall appears to break down within 12 months of fall. The biomass of birch leaves in the Alder Zone (Fig.48b) was, as might be expected, much smaller than that of alder leaves, reaching a peak of under $25g/m^2$ in December - February. The litter of other trees showed two peaks, one ($23.23g/m^2$) in October, the other ($41.40g/m^2$) in February. Birch reproductive structures were almost completely absent until April 1968, when a high value of $2.63g/m^2$ was recorded. Alder reproductive structures were much more important, peaking at over $16g/m^2$ in May 1967 and April 1968.

TABLE XXXV

Biomass of Tree Litter Categories (g/m²) ± 1 S.E.   1967-8

		APRIL	MAY	JUNE	JULY	AUGUST	OCTOBER	DECEMBER	FEBRUARY	APRIL
Old Alder leaves	A	23.67(6.63)	6.30(1.49)	11.76 (5.08)	14.96 (5.77)	8.56 (2.35)	—	—	—	—
	B	1.71(0.78)	1.77(1.05)	0.46 (0.28)	1.01 (0.69)	0.14 (0.1)	—	—	—	—
	E	12.92(3.41)	4.08(0.55)	6.23 (2.59)	8.13 (2.96)	4.26 (1.22)	—	—	—	—
New Alder leaves	A	—	—	—	7.45 (2.60)	17.50(10.63)	67.34 (9.90)	101.31(23.75)	119.72(22.54)	48.71(14.41)
	B	—	—	—	0.26 (0.26)	19.31(18.84)	29.93(11.52)	36.91(24.92)	21.49(10.63)	4.30 (2.31)
	E	—	—	—	3.93 (1.37)	18.42(10.70)	49.01 (7.57)	69.76(17.20)	71.59(12.62)	26.95 (7.44)
Other Tree Litter	A	0.14(0.09)	0.48(0.37)	1.59 (1.20)	0.22 (0.19)	1.50 (1.46)	23.23(15.63)	11.91 (9.40)	41.40(18.48)	9.32 (4.94)
	B	1.07(0.95)	1.16(0.48)	1.71 (1.22)	0.23 (0.23)	0.40 (0.27)	8.46 (3.4)	21.29(16.82)	2.93 (1.31)	2.79 (2.16)
	E	0.60(0.47)	0.82(0.39)	1.65 (0.86)	0.23 (0.15)	0.96 (0.76)	15.99 (8.15)	16.51 (9.54)	22.56 (9.45)	6.13 (2.73)
Old Birch leaves	A	7.26(3.57)	10.62(3.50)	3.19 (1.93)	1.77 (1.24)	—	—	—	—	—
	B	36.21(10.88)	25.31(18.20)	19.51 (7.65)	15.70 (7.70)	2.26 (2.26)	—	—	—	—
	E	21.45(5.64)	18.11(9.29)	11.19 (3.88)	8.60(3.83)	1.15 (1.15)	—	—	—	—
New Birch leaves	A	—	—	—	3.24 (2.33)	6.44 (3.99)	16.24 (5.40)	22.89 (7.77)	25.08 (8.71)	8.66 (1.89)
	B	—	0.14(0.68)	0.98 (0.52)	2.47 (1.09)	32.40(19.13)	126.66(19.67)	94.77(10.81)	109.84(15.43)	114.79(16.77)
	E	—	0.07	0.50	2.87 (1.31)	19.17 (9.59)	70.35(10.00)	58.11 (6.62)	66.62 (8.77)	60.67 (8.28)
Wood	A	167.03(40.93)	214.99(29.91)	219.76(57.63)	270.15(45.97)	130.70(27.19)	230.25(65.90)	195.39(51.90)	240.98(50.94)	206.10(32.06)
	B	202.00(51.13)	160.04(40.61)	138.96(26.51)	122.99(35.64)	188.88(78.40)	126.34(34.57)	105.68(28.34)	189.64(30.87)	133.06(17.32)
	E	184.17(32.61)	200.19(25.01)	180.17(32.14)	198.05(29.24)	159.21(40.85)	179.34(37.64)	151.44(29.89)	215.83(30.06)	170.31(18.43)
Alder Rep	A	10.59 (2.64)	16.76(4.91)	7.47 (2.04)	8.97 (2.85)	3.30 (1.14)	4.52 (1.06)	5.91 (2.42)	12.87 (3.69)	17.62 (5.18)
	B	2.30 (1.41)	1.21(2.18)	1.03 (0.57)	0.45 (0.36)	0.95 (0.48)	0.92 (0.31)	1.75 (0.96)	2.32 (1.22)	0.45 (0.31)
	E	6.53 (1.52)	8.79(2.47)	4.31 (1.08)	4.80 (1.47)	2.15 (0.63)	2.76 (0.56)	3.88 (1.32)	7.70 (1.98)	9.21 (2.65)
Birch Rep	A	0.14 (0.10)	—	—	0.01 (0.01)	0.05 (0.05)	0.48 (0.48)	0.07 (0.01)	0.18 (0.18)	2.63 (1.33)
	B	1.03 (0.46)	1.00(0.20)	0.73 (0.29)	0.15 (0.10)	—	0.65 (0.30)	—	0.19 (0.16)	0.33 (0.22)
	E	0.58 (0.23)	0.51	0.37	0.08 (0.05)	0.03 (0.03)	0.56 (0.29)	0.03	0.19 (0.12)	1.51 (0.69)

A Alder Zone
B Birch Zone
E Grid

Figure 48.

Biomass (g/m^2) 1967-8.   Alder Zone.   Alder and birch leaves.

a. Alder leaves.
b. Birch leaves.

Key: plus signs – old crop.
     circles – new crop.

BIOMASS (g/m²) 1967-8 ALDER ZONE
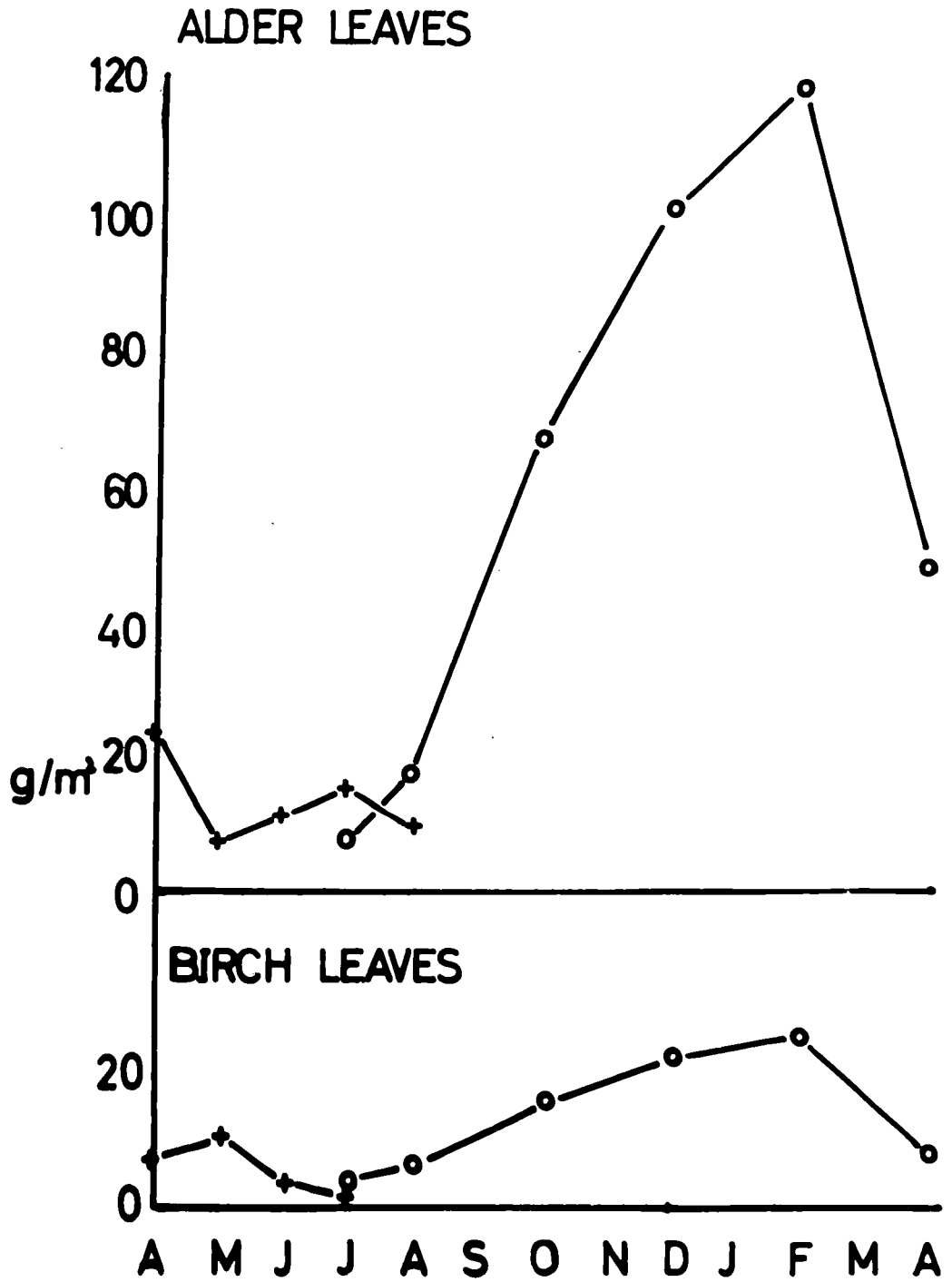
There was a marked decline from May to August, a steady increase

until December, and a sharp increase to April 1968. The wood litter

showed erratic variations around $220g/m^2$, and was always

the most important tree litter category on the Forest Floor of the

Alder Zone.

ii. Birch Zone. Figures 49a,b, ·for the Birch Zone can be

compared with Figure 48 for the Alder Zone. Alder leaves were much

less important than birch leaves. Their respective peak values were

$26.91g/m^2$ and $126.66g/m^2$. The alder leaves reached a peak in December,

the birch in October. There were fluctuations in birch leaf biomass

after October, which would only have been due to sampling error,

probably through quadrat location. It is possible that the

aggregation pattern of fallen leaves could have changed through the

autumn, increasing the probability of sampling errors. That is,

fallen leaves may have been blown into small depressions in the ground,

or against small obstacles, forming patches of high biomass. After

this, it is possible that the leaves in these aggregations may have

disappeared at a different rate to those not so aggregated. This

would accentuate the clumping of biomass. The litter of other trees

reached a peak of $21.2og/m^2$ in December but had almost gone by April.

The biomass of birch reproductive structures   ·   only once

.(April 1967) exceeded $1g/m^2$, whereas that of alder reproductive

structures exceeded $2g/m^2$ on two occasions (April 1967 and February 1968).

The biomass of wood litter   varied erratically as in the Alder

Zone, but around a lower level of about $140g/m^2$.

Figure 49.

Biomass (g/m^2) 1967-8.   Birch Zone.   Alder and Birch leaves.

a. Alder leaves.
b. Birch leaves.

Key: plus signs – old crop.
     circles – new crop.

BIOMASS(g/m²) 1967-8 BIRCH ZONE

ALDER LEAVES

BIRCH LEAVES

g/m²

A M J J A S O N D J F M A
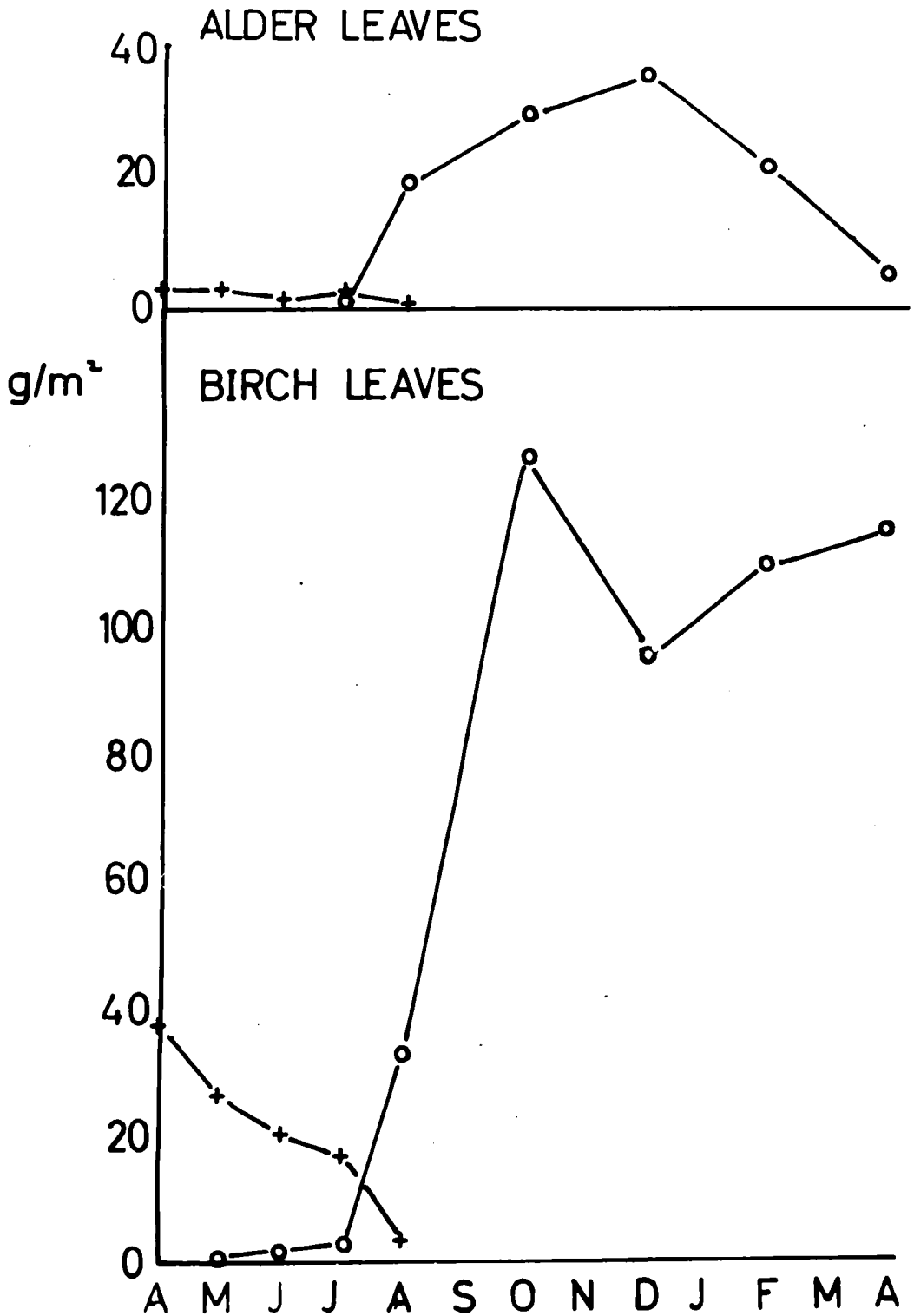
iii. Grid. Figures 50a,b, correspond to Figures 48 and 49. Alder leaves reached a peak of $71.59g/m^2$ in February although the December value was within $2g/m^2$ of this. The birch leaves showed a peak of $70.35g/m^2$ biomass in October. Thus, for the Grid as a whole, both alder and birch leaf litter contributed about $70g/m^2$ each to the litter biomass on the Forest Floor. The litter of other trees reached a peak of $22.56g/m^2$ in February along with the alder leaves. The biomass of fallen birch reproductive structures was $1.5g/m^2$ or less, whereas that of alder reproductive structures showed a seasonal decline from around $8g/m^2$ in late spring to near $2g/m^2$ in August and October. Then it increased to over $9g/m^2$ by April 1968. As for the zones considered separately, the biomass of wood litter on the Forest Floor of the Grid as a whole fluctuated greatly from month to month, although some of the fluctuations were less marked. The level around which wood litter biomass fluctuated was $180g/m^2$.

d) Comparison of Grid data for 1966-7 and 1967-8.

The data obtained for the whole Grid during the two sampling years are comparable. Comparing Figures 46 and 40, it can be seen that the peak biomass of green ground vegetation was greater $(137.70g/m^2)$ in 1966 than in 1967 $(103.33g/m^2)$. The 1966 peak was recorded on 1st August, the 1967 peak two weeks earlier on 17th July. The bryophyte biomass did not show a sharp summer peak in 1966 as it did in 1967. In 1966 the Fern biomass peak $(75.26g/m^2)$

Figure 50.

Biomass (g/m^2) 1967-8. Grid. Alder and birch leaves.

a. Alder leaves.
b. Birch leaves.

Key: plus signs – old crop.
     circles – new crop.

BIOMASS (g/m²) 1967-8   GRID
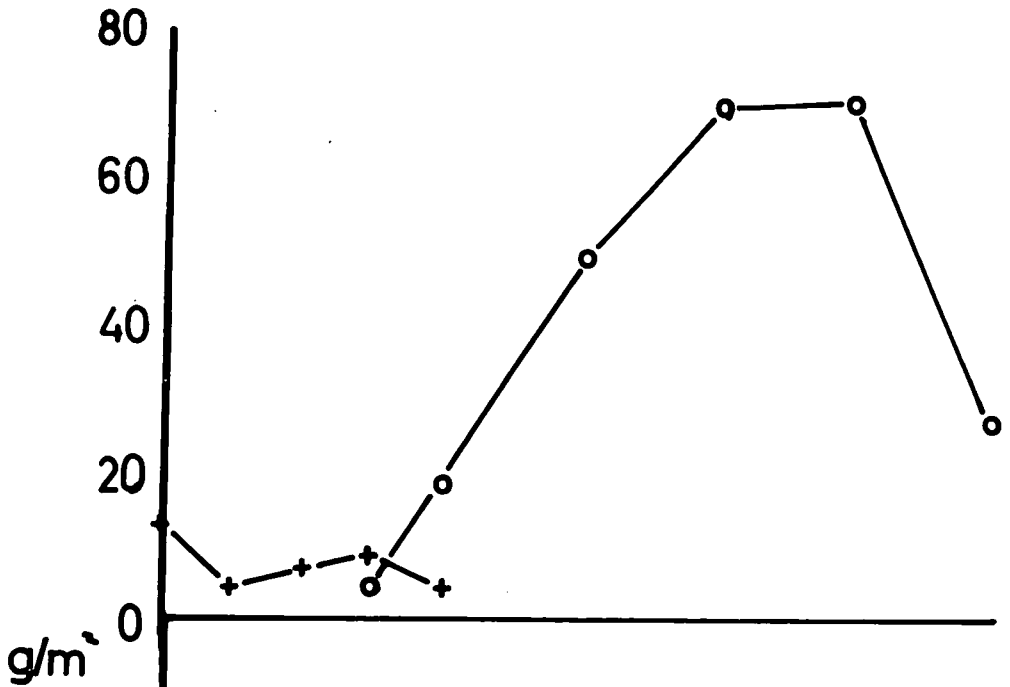
came in August but in 1967 it came in October ($59.71g/m^2$). No

separate Rubus data were recorded before July 1966, but the peak

Rubus biomasses in 1967 were reached in May and July. In 1966 a

peak was reached in September. Green grass biomass reached a peak

($34.65g/m^2$) in July 1967, which closely corresponded to the highest

value in 1966. This was $35.36g/m^2$ in July. The same holds true

for Agrostis tenuis, although the Holcus species showed peaks in

June 1967, and as division into species was not started until July 1966,

a direct comparison was not possible between the two years' data for

these species.

If the data for ground vegetation litter (Figs. 41 & 47c)

for the two periods are compared, a general decrease in biomass from

$448.00g/m^2$ in April 1966 to $169.36g/m^2$ in April 1967 will be noted.

The reasons for the decrease during 1966-7 have already been discussed

(VII iii (b)). It can only be supposed that the excess litter

accumulated in the winter of 1965-6 was not all broken down in 1966-7

and equilibrium was not reached until 1967-8. Alternatively, the

decrease represented a genuine decrease in litter production by the

ground vegetation, and perhaps a decrease in that proportion of it

made up of more persistent materials. This in turn demands that

ground vegetation mortality was markedly lower during the sampling

period than some point in the recent past.

Figures 42 and 50 show the data for tree litter biomass on

the Forest Floor. The pattern was quite similar in both years.

Birch leaf biomass reached a slightly higher peak one month later in 1966 than in 1967. Alder leaves reached a higher peak in December 1966 as compared with December 1967 - February 1968. The litter of other trees reached a similar peak two months earlier in 1966 than in 1967. The biomasses of fallen reproductive structures were similar during the two periods. Wood litter biomass showed similarly large fluctuations in both periods, its general level being a little higher in 1966-7 than in 1967-8.

e) Relative Reliability of the 1966-7 and 1967-8 biomass estimates.

The purpose of the changes made in the serial cropping sampling procedure from April 1967 on (increased number of quadrats, apportionment by vegetation zone rather than Grid blocks etc.) was to increase the reliability of the biomass estimate. Bearing in mind the discussion of the relationship between biomass dispersal and sampling in VII ii (b), the relative size of the standard error should provide some indication of the reliability of an estimate. Table XXXXVI shows the standard error as a percentage of the mean biomass of green ground vegetation on comparable occasions in the two sampling periods. Apart from the values for July and October, the 1967-8 values based on the revised sampling technique showed lower standard errors than those for 1966-7. In most cases, however, this improvement was not particularly great. To make a fair comparison between the two sampling programmes, e.g. using the ground vegetation

TABLE XXXXVI   Standard error as % of mean for Grid biomass

Total green ground vegetation

	1966-7	1967-8
20. 4.66/6.7.68	31.7	18.4/20.3
16. 5.66	22.0	-
20. 5.67	-	14.1
10. 6.66	14.8	-
18. 6.67	-	11.9
1. 7.66	12.0	-
17. 7.67	-	20.2
1. 8.66	18.4	-
2. 8.67	-	17.1
5. 9.66	22.0	-
21. 9.67	-	17.4
5.10.66	18.5	-
23.10.66	-	39.2
31.10.66	17.6	-
1.12.66	29.7	-
18.12.67	-	22.3
16. 1.67	19.5	-
15. 2.67	25.3	-
26. 2.68	-	20.5
15. 3.67	30.8	-

litter data, occasions must be chosen when the biomass estimates approached one another at a corresponding time of year. This was the case for July, when standard error represented 19.9% of the mean in 1966 and 17.7% of a slightly lower mean in 1967. Similarly, in February the 1967 value was 20.4% and the 1968 value (from a lower mean) 12.8%.

It is clear that some advantage was gained from the increased number of quadrats clipped and their stratal apportionment by vegetation zones rather than by Grid blocks. In addition, it should be borne in mind that the revised technique made possible a comparison of biomass and biomass change in the two vegetation zones. The standard error of a biomass estimate was usually higher for either zone than for the whole Grid; because of the smaller number of quadrats clipped, 11 or 13 as against 24 for the whole Grid, these biomass estimates were more subject to fluctuations caused by quadrat location. However, the separate biomass estimates for the two zones pointed to the different dynamics of growth, mortality and disappearance which pertained in the two zones. These data also made possible an analysis of the different species - distribution of the biomass in the two zones.

VII v. Results - Biocontent

The biomass results were converted to biocontent results using the calorific equivalents given in Section III. The results for green ground vegetation biocontent and bryophyte biocontent for

the Grid taken as a whole are given in Table XXXXVII.   The information

is summarized in graph form in Figure 51 and shows that the seasonal

pattern of biocontent change is very similar to that for biomass change.

The peak biocontent reached in 1966 was just under 600Kcal/m^2, whereas

that in 1967 was about 430Kcal/m^2.   The relative roles of the species

groups as biomass contributors were similar in both years.   In both

winters the green ground vegetation biocontent lay between 75 and

115Kcal/m^2, and consisted largely of _Rubus_ material.   The relative

importance of the bryophytes was reduced in the biocontent analysis,

because of the low calorific equivalent used for them.

Table XXXXVIII gives the biocontent data for tree litter

and ground vegetation litter for the whole Grid.   The information

is summarized in Figure 52.   The overall litter biocontent was between

5 and 20 times that of the green ground vegetation.   The sharp

fluctuations in litter biocontent in the first period (20.4.66 to

20.4.67) can be accounted for by the changes in the wood litter

biocontent.   The pattern of total litter biocontent change in the

second period (20.4.67 to 22.4.68) was largely determined by the

normal seasonal march of tree litter fall and ground vegetation die-back.

The large fluctuations in wood litter biomass and hence biocontent

during the first period were possibly due to quadrat location effects.

In spite of these fluctuations it was possible to discern a general

decline in the litter biocontent through the first period, this being

most marked from April 1966 to July 1966.   The possible causes of

this were discussed in VII iv.(d).   The ground vegetation litter

TABLE XXXXVII   Green Ground Vegetation Biocontent (Kcal/m²)   20.4.66 to 22.4.68   GRID

1966/67

	20/4	16/5	10/6	1/7	1/8	5/9	5/10	31/10	1/12	16/1	15/2
Fern	?	?	?	103.6	324.9	159.2	138.7	112.5	1.0	-	-
Rubus	?	?	?	197.1	138.0	231.7	213.7	202.5	89.9	80.7	60.7
Forbs	?	?	?	26.7 / 19.1	20.3 / 2.8	41.3 / 8.6	3.4 / 2.1	8.0	5.3	-	3.1
D.caespitosa	?	?	?	-	-	12.4	0.5	0.5	6.3	-	-
Agrostis tenuis	?	?	?	88.4	63.1	31.2	40.3	48.4	5.9	17.4	6.1
Holcus spp.	?	?	?	50.5	32.2	53.4	21.6	20.9	5.6	-	12.8
Total	97.6	226.7	367.6	485.4	581.3	537.8	420.3	392.8	114.0	98.1	82.7
Bryophytes	48.2	34.8	61.7	173.3	60.2	79.8	63.8	52.2	49.7	65.4	72.6

	15/3	20/4	20/5	18/6	17/7	21/8	21/9	23/10	18/12	26/2	22/4
Fern	-	7.6	65.1	93.3	145.5	203.1	195.9	244.4	8.8	1.1	-
Rubus	51.8	95.7	141.3	104.8	145.8	109.7	107.6	101.4	53.9	87.2	72.7
Forbs	-	-	0.9 / 7.3	3.7 / 4.4	11.0 / 7.2	17.3 / 7.7	- / 2.6	- / 1.7	- / 1.3	- / 1.7	- / 1.5
D.caespitosa	-	1.7	0.5	21.8	-	-	-	0.8	-	3.3	2.3
Agrostis tenuis	-	6.2	24.2	8.1	89.5	64.9	32.9	6.1	3.4	-	0.7
Holcus spp.	13.2	17.2	50.3	69.0	46.6	24.7	16.0	0.8	1.1	8.1	9.0
Total	65.0	128.4	289.6	305.1	445.6	427.4	355.0	355.2	68.5	101.4	86.2
Bryophytes	52.2	42.7	46.0	63.4	45.2	46.8	45.2	35.7	30.3	27.8	13.2

TABLE XXXXVIII   Litter (Forest Floor) Biocontent (Kcal/m^2)   20.4.66 to 20.4.68   GRID

1966/67

	20/4	16/5	10/6	1/7	1/8	5/9	5/10	31/10	1/12	16/1	15/2
Ground veg.litter Fern	–	–	–	–	–	–	–	–	–	528.1	458.9
Rubus	–	–	–	–	–	–	–	–	–	377.2	217.6
Grass	–	–	–	–	–	–	–	–	–	119.1	169.5
C.angustifolium	184.84	–	–	–	–	–	–	–	–	–	85.9
Total ground veg.litter	1848.4	1535.9	1165.4	854.7	1185.6	1058.1	1132.4	864.5	915.4	1024.4	931.9
Tree litter–Alder lvs.	166.8	92.4	124.0	39.5	67.3	52.9	177.6	342.9	447.8	376.8	246.2
Birch "	240.1	255.2	112.4	107.0	95.9	102.6	176.8	359.1	321.8	224.2	334.4
Other tree	5.7	7.1	9.8	11.6	1.5	–	18.1	22.7	103.1	24.1	50.2
Alder rep	60.9	35.3	52.0	50.9	35.5	14.1	18.2	27.6	33.2	20.0	20.1
Birch rep	–	–	–	–	–	1.8	3.7	4.9	0.9	1.7	3.8
Wood	1195.0	1270.4	1393.9	1108.9	2057.6	1691.6	1711.5	913.5	904.3	1592.8	1076.1
Total Tree Litter	1668.5	1660.4	1692.1	1317.8	2257.8	1663.0	2105.9	1670.7	1811.1	2239.6	1730.8
Total Litter (Forest Floor)	3516.9	3196.3	2857.5	2172.5	3443.4	2721.1	3238.3	2535.2	2720.5	3264.0	2662.7

1967/68

	15/3	20/4	20/5	18/6	17/7	21/8	21/9	23/10	18/12	26/2	20/4
Ground veg.litter Fern	539.4	465.4	335.7	299.5	258.8	240.4	–	201.5	320.3	341.6	405.1
Rubus	207.1	160.2	180.2	289.1	407.6	203.7	–	158.1	168.6	190.5	122.1
Grass	152.8	72.0	106.4	106.6	118.1	158.3	–	198.7	219.3	244.4	170.2
C.angustifolium	28.2	25.8	2.9	1.2	–	–	–	4.4	–	1.4	0.1
Total ground veg.litter	927.5	723.4	625.2	696.4	784.5	602.4	–	562.7	708.2	777.9	697.5
Tree litter–Alder lvs.	125.1	60.4	29.1	19.1	56.4	106.0	–	239.0	320.2	350.8	126.0
Birch "	244.9	102.8	87.1	56.0	54.8	97.0	–	330.1	263.3	301.9	290.8
Other tree	7.8	2.7	3.7	7.4	1.0	4.3	–	71.5	73.8	100.9	27.4
Alder rep	31.3	34.6	46.6	22.8	25.4	11.4	–	14.6	20.6	40.8	48.8
Birch rep	3.9	2.9	2.6	1.9	0.4	0.1	–	2.8	0.1	0.9	1.7
Wood	1159.5	920.8	1000.9	900.8	990.2	796.0	–	896.7	757.2	1079.1	851.6
Total Tree Litter	1572.5	1124.2	1432.2	1008.0	1128.2	1014.8	–	1554.7	1435.5	1874.4	1346.3
Total Litter (Forest Floor)	2500.0	1847.6	2057.4	1704.4	1912.7	1617.2	–	2117.4	2143.7	2652.3	2043.8

Figure 51.

Ground Vegetation biocontent (Kcal/m^2), 20/4/66 to 22/4/68.

Key: crosses - <u>Rubus</u>.

closed circles - <u>Rubus</u> + forbs.

plus signs - <u>Rubus</u> + forbs + grasses.

open circles - <u>Rubus</u> + forbs + grasses + ferns.

BIOCONTENT (kcal/m²)   GROUND VEGETATION
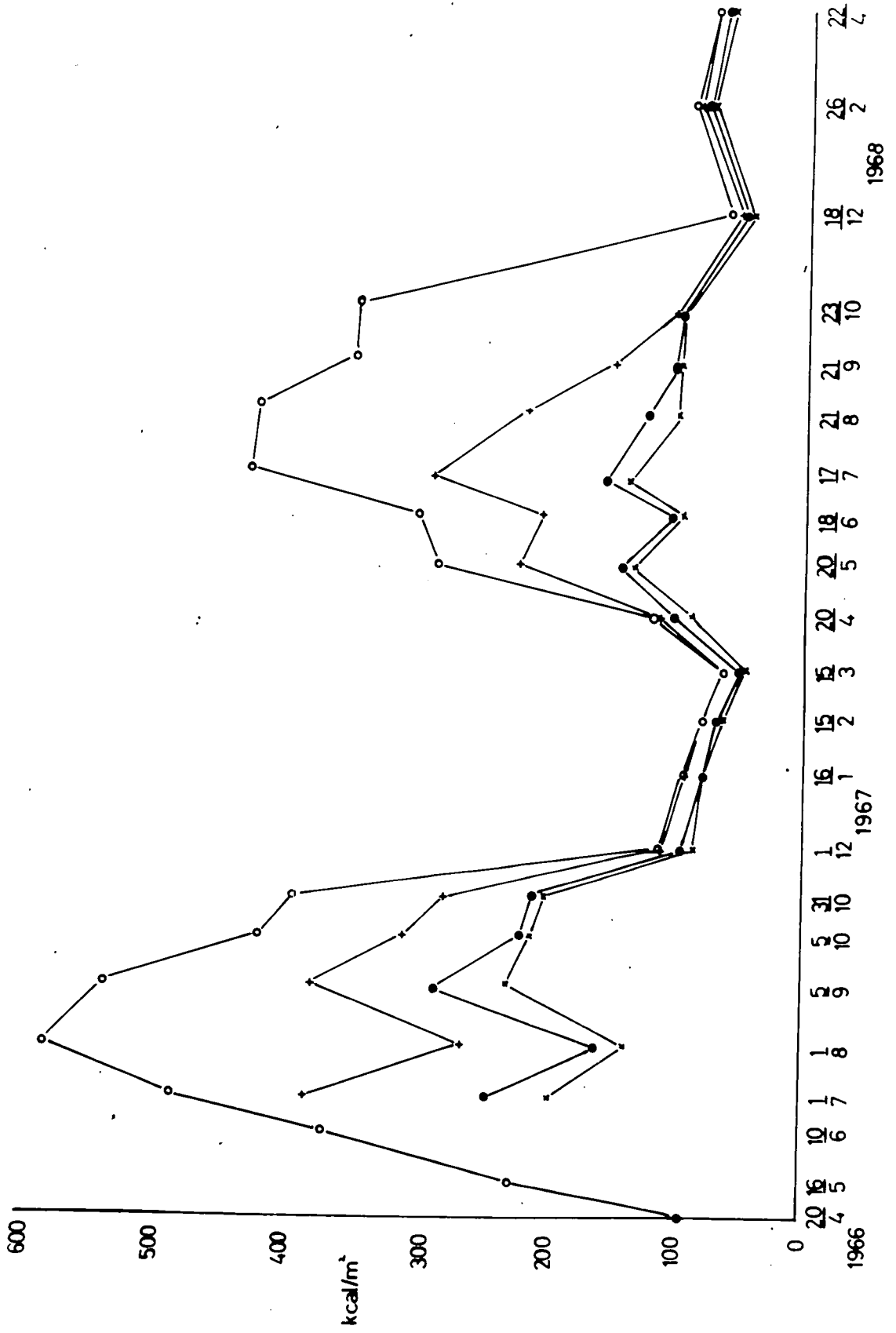
Figure 52.

Forest Floor litter biocontent (Kcal/m^2), 20/4/66 to 22/4/68.

Key: closed circles - ground vegetation litter.
     plus signs - GV litter + leaf litter.
     open circles - GV litter + leaf litter + woody litter.

BIOCONTENT(kcal/m²)   FOREST FLOOR LITTER
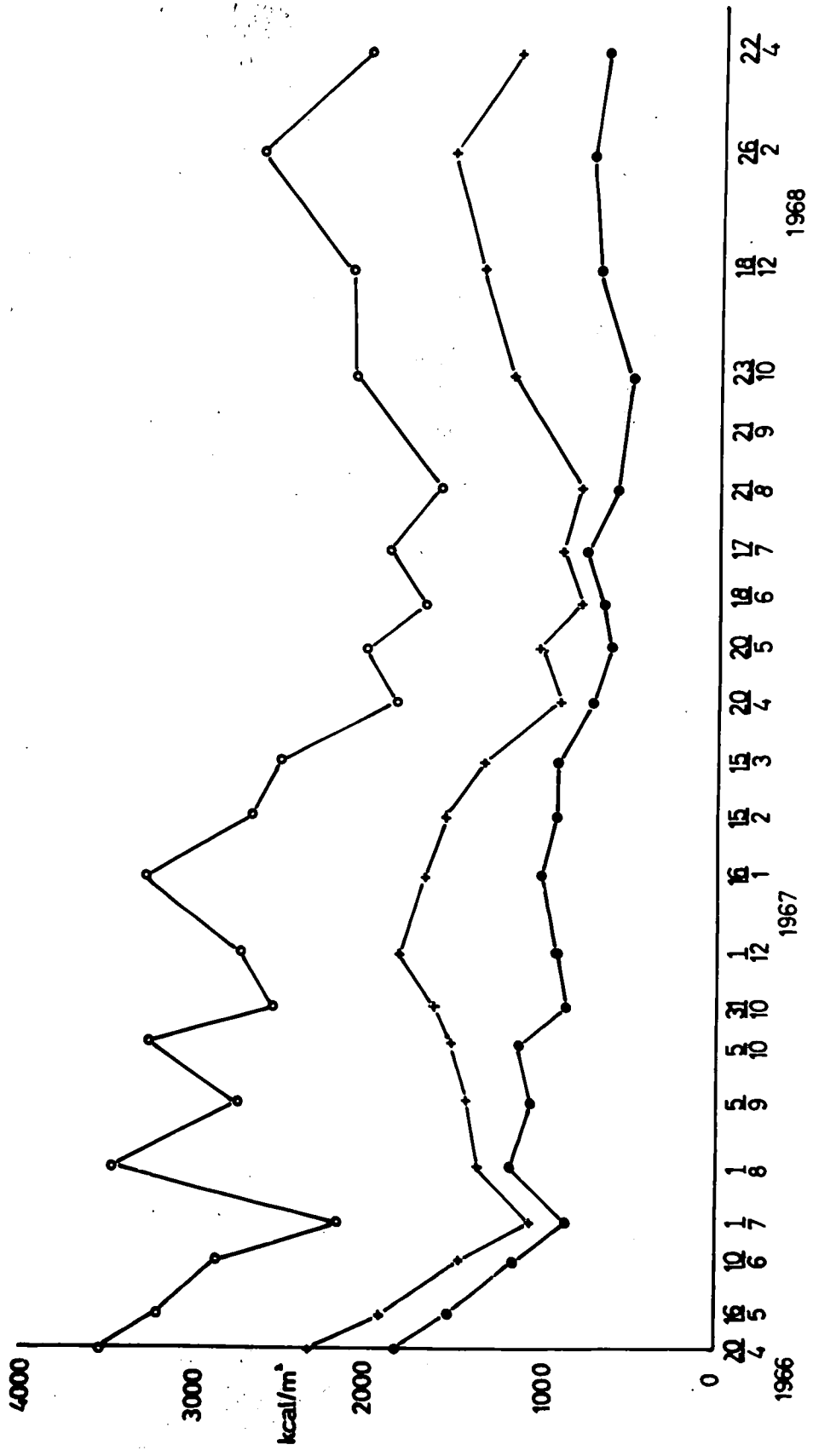
came to between 25% and 35% of the total litter biocontent, excepting

for the period April 1966 to July 1966. The wood litter made up

most of the tree litter biocontent, only being approached in

importance by the leaf litter at and after the time of leaf fall.

Tables XXXXIX and L give the biocontent data for the Alder

and Birch Zones from April 1967 through April 1968. These data are

summarized in Figures 53a & b, and 54a & b. As for the Grid taken

as a whole, the patterns were essentially similar to those for biomass.

The differences between the zones corresponded to those for biomass.

The total litter biocontent was quite similar in both, but wood litter

was more important in the Alder Zone than in the Birch Zone, whereas

the opposite was the case for ground vegetation litter.

VII vi. Discussion

The basic problem of estimating quantities such as those

dealt with in this Section is that the samples, however, apportioned,

however processed, represent only a diminutive fraction of the area

studied. For example, the 16 quadrats clipped on each occasion up

to March 1967 had a total area of $1.54m^2$. In the second year the

24 quadrats had an area of $2.30m^2$. Thus the total area clipped was

only 0.048% and 0.072% of the Grid area on each occasion in 1966-7

and 1967-8 respectively. Quadrat size and number were limited by

the time available for processing cropped material. On the other

hand, the technique of serial cropping required that the quadrats

TABLE XXXXIX

Biocontent (Kcal/m²) - Alder Zone

	20.4.67	20.5.67	18.6.67	17.7.67	21.8.67	21.9.67	23.10.67	18.12.67	26.2.68	22.4.68
Ground vegetation										
FERNS	7.2	81.7	101.4	161.7	152.9	156.5	199.9	15.7	-	-
RUBUS	152.4	104.6	87.6	179.9	130.6	127.5	118.6	74.1	78.3	83.9
FORBS	-	1.9	4.8	39.9	6.91	1.2	0.6	0.9	0.7	2.4
D.CAESPITOSA	-	-	44.4	-	-	-	-	-	-	-
AGROSTIS TENUIS	0.1	1.9	25.7	-	-	-	0.1	4.8	-	0.9
HOLCUS Spp.	13.7	56.0	75.8	44.8	31.0	16.2	1.0	+	2.8	11.1
TOTAL	173.4	246.1	339.7	426.3	383.6	301.4	320.2	95.5	81.8	98.3
Ground vegetation litter										
FERNS	538.7	309.8	247.9	240.1	178.4	-	239.8	364.7	290.2	267.0
RUBUS	143.9	146.8	153.4	331.2	168.2	-	190.3	141.9	113.3	131.8
GRASS	33.2	41.6	49.9	39.0	88.7	-	48.9	120.1	147.3	95.4
C.ANGUSTIFOLIUM	17.5	-	-	-	-	-	9.0	-	0.4	0.3
TOTAL	733.3	498.2	451.2	610.3	435.3	-	488.0	626.7	551.2	494.5
BRYOPHYTES	28.7	67.9	64.5	44.6	54.2	44.9	26.6	18.1	21.4	20.7
Tree litter										
ALDER LEAVES	110.7	29.5	54.9	104.8	121.8	-	328.2	465.0	586.6	227.8
OTHER TREE	6.3	2.1	7.1	1.0	6.7	-	103.9	53.2	185.1	41.7
BIRCH LEAVES	34.8	50.9	15.3	23.9	30.8	-	76.2	107.4	120.6	41.5
WOOD	835.2	1,209.9	1,098.8	1,350.7	653.5	-	1,151.2	976.9	1,204.9	1,030.5
ALDER REP	56.1	88.8	39.6	47.5	17.5	-	23.9	31.3	68.2	93.4
BIRCH REP	0.7	-	-	+	0.2	-	2.4	0.4	0.9	13.3
TOTAL TREE LITTER	1,043.8	1,381.2	1,215.7	1,527.9	830.5	-	1,685.8	1,634.2	2,166.3	1,448.2
TOTAL LITTER	1,777.1	1,879.4	1,666.9	2,138.2	1,265.8	-	2,173.8	2,260.9	2,717.5	1,942.7

TABLE I

Birch Zone biocontent $(Kcal/m^2)$

	20.4.67	20.5.67	10.6.67	17.7.67	21.8.67	21.9.67	23.10.67	18.12.67	26.2.68	22.4.68
Ground Vegetation										
FERN	8.0	47.8	84.7	106.9	251.8	233.8	288.9	1.5	2.3	-
RUBUS	34.8	177.9	122.7	105.8	87.9	88.6	85.6	32.9	97.2	61.9
FORBS	14.2	2.9	13.3	-	8.5	4.0	2.7	1.8	2.7	0.9
V.RIVINIANA		1.8	3.6	-	33.9	-	-	-	-	-
D.CAESPITOSA	3.3	1.1	-	-	-	-	1.6	-	0.6	4.6
AGROSTIS.TENUIS	12.5	47.5	43.4	175.5	127.3	64.6	12.4	1.8	-	0.5
HOLCUS Spp.	22.3	44.7	61.8	40.6	31.4	15.8	0.5	2.3	13.2	6.7
TOTAL	95.1	323.7	329.5	428.8	540.8	406.8	391.7	40.3	116.0	74.6
Ground Vegetation Litter										
FERN	373.3	360.6	353.1	278.2	305.0	-	155.1	266.4	395.2	526.6
RUBUS	176.5	214.1	419.9	487.1	240.6	-	128.2	191.8	270.8	115.4
GRASS	112.4	168.8	165.5	200.3	230.6	-	354.6	322.5	345.5	234.7
C.AUGUSTIFOLIUM	34.3	57.6	2.3	-	-	-	-	-	2.4	-
TOTAL	696.5	801.1	940.8	965.6	776.2	-	637.9	780.7	1,013.9	876.7
BRYOPHYTES	57.2	23.4	62.3	45.8	39.1	45.6	45.2	43.0	34.6	55.1
Tree Litter										
ALDER LEAVES	8.0	8.3	2.1	5.9	90.9	-	145.9	169.4	105.3	20.1
OTHER TREE	4.8	5.2	7.6	1.0	1.8	-	37.8	95.2	13.1	12.5
BIRCH LEAVES	173.6	121.9	98.2	86.8	165.5	-	594.4	429.4	528.2	550.2
WOOD	1,010.0	800.2	694.8	614.9	944.4	-	631.7	528.4	948.2	665.3
ALDER REP	12.2	6.4	5.5	2.4	5.0	-	4.9	9.3	12.3	2.4
BIRCH REP	5.2	5.1	3.7	0.8	-	-	3.4	-	1.0	1.7
TOTAL	1,213.8	947.1	811.9	711.8	1,207.8	-	1,418.1	1,231.7	1,608.1	1,252.2
TOTAL LITTER	1,910.3	1,748.2	1,752.7	1,677.4	1,984.0	-	2,056.0	2,264.7	2,622.0	2,128.9

Figure 53.

Biocontent (Kcal/m^2). Alder Zone 1967-8.

a. Ground vegetation.

Key: crosses - <u>Rubus</u>.
closed circles - <u>Rubus</u> + forbs.
plus signs - <u>Rubus</u> + forbs + grasses.
open circles - <u>Rubus</u> + forbs + grasses + ferns.

b. Forest Floor litter.

Key: closed circles - ground vegetation litter.
plus signs - GV litter + leaf litter.
open circles - GV litter + leaf litter + woody litter.

BIOCONTENT(kcal/m²) 1967-8 ALDER ZONE

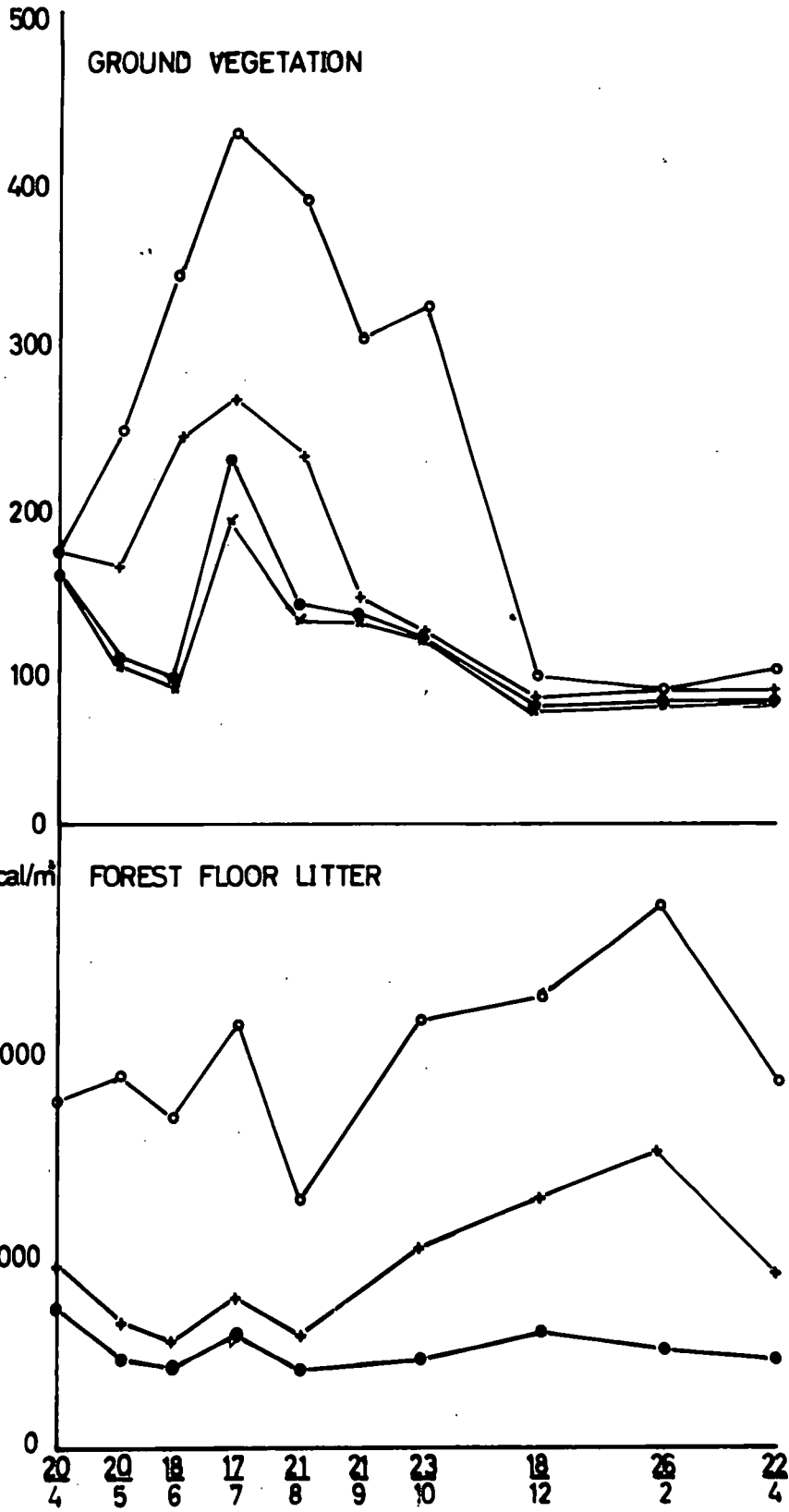GROUND VEGETATION

kcal/m² FOREST FLOOR LITTER

Figure 54.

Biocontent (Kcal/m^2). Birch Zone 1967-8.

a. Ground Vegetation.
b. Forest floor litter.

Keys as in Figure 53.

BIOCONTENT(kcal/m²) 1967-8 BIRCH ZONE
GROUND VEGETATION

FOREST FLOOR LITTER

should be small relative to the area studied, so that it was possible
to sample on successive occasions without the taking of one set of
samples affecting the results of subsequent sampling. The combination
of vegetational heterogeneity and the inherent limitations of the
serial cropping technique resulted in estimates with rather wide
confidence limits. This gave rise to two problems of interpretation.
Firstly, how closely does an individual calculated biomass approximate
to that actually existing in the field at the time of sampling?
Secondly, do these successive calculated biomasses correspond closely
enough to reality for the cycle of changes they show to bear any close
relationship to the annual sequence of events in the field? In
particular, is the use of differences between successive estimates in
calculations in any way justified? This particular problem is dealt
with further in Section IX. The relationship between changes in
biomass estimate and annual cycles of biomass is determined in a two-
fold way. On the one hand there is the question of the reliability
of the estimates at the time they were made. On the other hand
there is the question of sample timing. That is, the biomass
estimates may be extremely accurate, but made at inappropriate times.
The answer is clearly very frequent sampling, but there are practical
difficulties here, and a monthly sampling was the most frequent possible.

These criticisms of the serial cropping technique are,
indeed, very serious. However, an ecologist should have more than
statistical criteria in his critical armoury. The reasonableness

of the biomass and biocontent estimates made in this Section may be
assessed by relating the changes in biomass indicated to the known
natural history of the Study Area (this Section); to the observed
phenology of litter-fall and die-back (this Section and Section V);
and to other estimates of input and output for the litter components
(Sections V and VIII). In particular, the simultaneous estimation
of green ground vegetation biomass (by species or species groups)
and ground vegetation litter biomass (by species groups) made possible
a further examination for internal consistency in these data (this
Section). The subdivision of the Grid into Alder and Birch Zones
made possible a more detailed analysis of this kind.

Throughout this Section the data have been examined in
these ways. No glaring discrepancies appeared and it thus seems
reasonable to assume that the biomass and biocontent estimates
presented in this Section bear a close relation to those actually
taking place in the Study Area.

The litter of the Forest Floor may be seen as an aggregate
energy store, whose total size does not fluctuate greatly during the
year. The most important seasonal changes are probably those in
its physical and chemical composition. These must be closely related
to its species composition. The study has indicated in which forms
(as wood, leaves, woody ground vegetation, or grass litter etc.) this
energy is locked up and therefore an examination of this data should
give first information about the role of the litter in ecosystem

energetics. It seems likely that the litter formed a medium term energy store (see Section VIII) existing above the longer-term humus energy-store. A large number of food types for decomposer organisms were present in a whole range of conditions, being formed over a large part of the year.

The ground vegetation species litter was a large part of the total litter for much of the year and although dominated by a few species, added greatly to the diversity of forms of stored energy in the litter.

Existing in close physical relationship with the Forest Floor was the ground vegetation. Its biomass and biocontent was made up of Rubus fruticosus and some grasses in winter, with the emergence of other grasses, forbs and Dryopteris filix-mas as very important parts of the biocontent in spring and summer. There appeared to be little or no accumulation of green ground vegetation biomass and biocontent from year to year, almost all of a year's increment falling the few centimetres to the Forest Floor. If the sharp decline of ground vegetation litter biomass in spring 1966 was assumed to be atypical, it would seem that there is little, if any, accumulation or loss of energy or material by the litter from year to year. Therefore, unlike the tree stratum, the ground vegetation did not appear to be accumulating energy either in itself or its litter on an annual basis.

Clearly, the views expressed are based on two years' sampling only and the conclusions can only be applied to the two years in question, although the present picture might reflect a longer term situation for woods of similar age and structure.

CHAPTER III

Section VIII   Disappearance

VIII. i. <u>Introduction</u>

        This section is concerned with the loss of material from the Forest Floor and although this certainly took place in several ways, e.g., by microbial breakdown, leaching etc., it will be assumed that the total disappearance from the Forest Floor equalled the total energy released by the breakdown of litter formed by the above-ground parts of the vegetation. For this to be the case there must be no significant change in the biocontent of organic matter derived from this litter in lower horizons.

        The concept of the 'Forest Floor' is commonly taken to include the L, F, and H layers. Both the lateral heterogeneity of the Forest Floor in the Study Area (cf. Section II) and the practicalities of sampling (cf. Section VII) led to the restriction of the use of this term to the L layer in this study.

        There is a vast literature concerned with the breakdown of litter on and in soils in various ecosystems. Much of it is concerned with qualitative analysis of the chemistry of decomposition and humus formation (for example, many papers in the IAEA symposia 'The Use of Isotopes in Soil Organic Matter Studies' 1966 and 'Isotopes and Radiation in Soil Organic Matter Studies' 1968). Another approach used by several workers has been to estimate fractional disappearance of litter of various types under varying

conditions using some kind of mesh enclosure (Attiwill 1968;

Bocock & Gilbert 1957;   Heath et al 1964;

Kucera, Dahlman & Koelling 1967; Mikola 1954,   Shanks

& Olson 1961; Thomas 1968; Witkamp & Olson 1963; Wittich 1939).

A few workers have attempted to make an absolute measure of litter

decomposition as part of an ecosystem study (Golley 1965; Kucera

et al 1967; Ovington 1961; Wiegert & Evans 1964; Witkamp & van

derDrift 1966).   In most of these studies, litter decomposition was

estimated as either the residual term in an energy budget, or as the

sum of input to the litter and the litter biocontent or biomass change.

Wiegert & Evans (1964) and Witkamp & van der Drift (1961) measured

litter breakdown directly.   Wiegert & Evans (op.cit.) compared the

mesh bag method and the Paired Plots technique, and it is discussed

in detail below.   Witkamp & van der Drift (op.cit.) weighed dried

litter from permanent plots in December, replaced the material and

weighed it again the following September;   they also weighed fresh

litter monthly from permanent quadrats.   Attiwill (1968) used both

the mesh bag method and the determination of an annual decomposition

constant, k, (Jenny et al 1949) from litter fall and soil organic

matter data.   In a Eucalyptus forest in Victoria he determined k as

16.3% by Jenny et al's (1949) method, but as 10% by the mesh bag

method.   He attributed this lower value to incomplete incorporation

of the bagged material into the L layer.   This point was also

emphasized by Witkamp & Olson (1963).

An alternative approach was suggested by Jenkinson (1966) and attempted by Dutch & Stout (1968). This utilizes an increase in C^{14} incorporated into plant material in the early 1960s as a result of atom bomb fall-out. Thus the flow of the C^{14} pulse from foliage leaves through the various soil horizons may be traced. However, the authors found considerable disparities between this method and results from other methods. Clearly there is a possibility of C^{14} input to the soil from the tree roots as well as in falling litter.

In their 'paired-plots method' Wiegert & Evans (op.cit.) removed the dead material from a given area of a field and weighed (W_o) at a time t. At time t they removed the dead material (W_1) from a second area identical in size. Thus they calculated the instantaneous rate of disappearance of dead material as :-

$$r = \frac{\ln(W_o/W_1)}{t_o - t_1}$$

where r = disappearance rate in g/g/day and $t_o - t_1$ is in days.

This equation assumes that the rate of disappearance from the two plots are equal; that the biomass and species composition of the dead material on the two plots is identical; that no additional material can be added to the dead material of the second quadrat during the interval $t_o - t_1$. In order to justify these assumptions, Wiegert & Evans (op.cit.) took two small contiguous plots whose dead vegetation appeared to be identical. To prevent the addition of newly dead material the living vegetation was removed from both plots at the

beginning of the procedure. In addition to this 'Paired-Plots' method, mesh-bag studies were also made. The authors pointed out that in both cases a considerable disturbance to the system takes place, but that in the case of fairly sparse vegetation this will be of less importance than in a dense vegetation in the case of the paired-plots method. It was their opinion that the 'rates of disappearance measured with paired-plots appear to approximate the natural condition better than do rates of disappearance measured with litter bags'.

In the case of litter on the Forest Floor, there seems good reason to use the Paired Plots method. It seems unlikely that the removal of the living ground vegetation will have as drastic an effect on litter microclimate as would be the case in a grassland. Moreover, the Paired Plots technique allows the study of disappearance rate of litter mixed up with that of other species, rather than separated off into an enclosure of abnormal homogeneity. Two important problems exist. First, how to 'pair' plots effectively. Second, how to adapt the method for fall of litter during the experiment.

The other parameter on which this estimate of disappearance is based is the standing crop of litter. The standing crop data must be precise so that the calculation of disappearance is accurate and reliable in that it may reasonably be used in the study of ecosystem energetics. The considerations discussed in VII v. & vi suggest that this may be true in this study; thus a modified version of the

Wiegert & Evans Paired Plot technique was used to estimate the disappearance of various types of Forest Floor Litter in 1966-7 and 1967-8.

VIII. ii. <u>Methods</u>

The standing crop data used in the calculation of disappearance were obtained as described in VII ii. The instantaneous rate of disappearance of ground vegetation litter and tree litter categories was estimated by a modification of the Paired Plots technique (Wiegert & Evans op.cit.).

First, a square metre was selected at random in each of the eight 20 x 20m^2 squares of the Grid. Secondly, an apparently homogeneous area of Forest Floor was chosen within it. Then two 0.0312m^2 plots were marked out contiguously within that area as in Figure 55. On the first sampling occasion (t_o) the following procedure was adopted :-

(1) All green vegetation was clipped from the two plots and discarded.

(2) One of the plots was chosen by tossing a coin. This was Plot I.

(3) All litter was carefully harvested from Plot I. It was then taken to the laboratory, sorted, dried for 24 hours at 105°C and weighed. Hence the weight, W_o, of litter on Plot I on this occasion - time t_o - was found. On the second sampling occasion, t_1, the following procedure was used :-

Fig. 55

PLOT I | PLOT II

— apparently homogeneous
area of forest floor

Paired Plots ($0.0312m^2$ each)
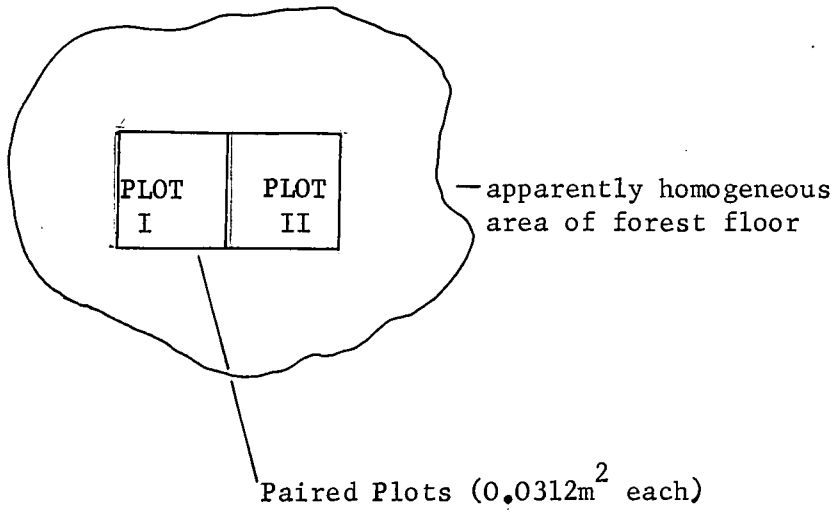
(1) All litter that had fallen onto Plot I since t_o was harvested, sorted, dried and weighed. This was W_A.

(2) All litter was harvested from Plot II, taken to the laboratory, sorted, dried and weighed. This was W_B.

(3) It was assumed that W_A represents the amount of litter that was also deposited on Plot II and that it disappeared at the same rate as that on Plot II. Hence $W_B - W_A = W_1$.

Assuming that :

(a) at t_o the weight and composition of litter on Plots I and II was identical

(b) the litter on Plot II disappeared at the same rate as if Plot I had not been cleared and the live material had not been removed.

(c) the correction for deposition of material on the plots during $t_1 - t_o$) was valid, then the ~~instantaneous~~ mean rate of disappearance (g/g/day) of the litter was calculated as follows :-

$$r = \frac{\ln (W_1/W_o)}{t_1 - t_o}$$

At (t_1) a new set of plots was chosen and harvested as on the first sampling occasion (t_o). One of the most important criticisms of this technique is that plots are seldom correctly paired. In this study the correlation co-efficient for the weights of litter cleared from the randomly assorted components of pair is 0.913 for sets of

eight pairs. Hence t = 5.49, df7, P<0.01, >0.001. This suggests effective pairing.

The amount of litter disappearing during an interval was calculated as the product of the mean standing crop in g/m^2, the time in days and the ~~instantaneous~~ mean rate of disappearance in g/g/day.

The paired plots procedure was carried out at intervals usually of about two months from April 1966 until May 1968.

VIII. iii. <u>Results - Biomass</u>

The results for disappearance in terms of biomass are given first for 1966-7. In that year data for total ground vegetation litter (undivided), alder and birch leaves were obtained. For the period 1967-8, the ground vegetation litter was divided into <u>Rubus</u>, Fern, and grass litter, as in the serial cropping. Rates of disappearance were calculated from the Forest Floor litter biomass estimates for both alder and birch zones as well as from the whole Grid biomass estimates.

(a) 1966-7. Table LI. shows the ~~instantaneous~~ mean rates of disappearance of ground vegetation litter and the amounts of material disappearing as calculated from these and the ground vegetation litter standing crops from 20.4.66 to 20.4.67. The total disappearance of ground vegetation litter during that period was 544.14gms/m^2; this was not evenly spread through the year. Large amounts of material disappeared in the period 20.4.66 to 10.6.66, the period after this until 1.8.66 being marked by very low rates of disappearance. From 1st August to 1st December

TABLE LI   Ground vegetation disappearance data 1966-7

DATE	INTERVAL	MEAN ~~INSTANTANEOUS~~ RATE (mg/g/day)	DISAPPEARANCE (gms.O.D.wt/m^2)
20/4	-	-	-
16/5	26	7.19	76.77
10/6	25	7.19	59.12
1/7	22	1.30	7.02
1/8	31	1.30	9.98
5/9	36	6.30	61.88
5/10	30	6.30	51.21
31/10	26	10.37	67.60
1/12	32	10.37	73.44
16/1	46	0	0
15/2	30	4.66	33.59
15/3	28	4.66	29.99
20/4	33	11.00	73.56

TOTAL DISAPPEARANCE OF GROUND VEGETATION LITTER = 544.14gms/m^2

the rates were similar to those in early summer, falling to zero in the period 1st December to 16th January. In February, March and April the rate of disappearance once again increased. In fact the period 20.4.66 to 1.7.66 was marked by a fall of almost $250g/m^2$ in the ground vegetation litter biomass although the total calculated disappearance for this period was only $142.91g/m^2$. The standard errors of the biomass estimates were wide enough to allow this smaller amount as a possibility, if not a probability. The high spring rates of disappearance were thus associated with high litter biomass, and the summer low perhaps with drying out of the litter.

Table LII shows similar data for Forest Floor alder and birch leaves for the period 20.4.66 to 20.4.67. For alder, the total disappearance was $109.47g/m^2$, for birch, $140.81g/m^2$. Litter fall estimates (Section V) for that year were $110.61g/m^2$ for alder and $75.74g/m^2$ for birch. There was a decline of $22.75g/m^2$ and $28.65g/m^2$ in the Forest Floor biomass of alder and birch leaves respectively in the year concerned. Disappearance calculated as the sum of fall and Forest Floor decline was $133.36g/m^2$ for alder and $104.39g/m^2$ for birch, making a total of $237.75g/m^2$ as compared with $250.28g/m^2$ by the paired plots method. Assuming the estimate from litter fall and decline of biomass to be the more correct, the paired plots estimate for alder leaves was an underestimate of $23.89g/m^2$ (18.2%) and an overestimate of $36.42g/m^2$ (34.0%) for birch.

<u>TABLE LIT</u>   <u>Calculation of Disappearance for Tree-leaf material</u>
<u>Grid 1966-7</u>

ALDER LEAVES

DATE	DAYS	RATE (mg/g/day)	DISAPPEARANCE (g/m^2)
20. 4.66	-	-	-
16. 5.66	26	3.68	2.65
10. 6.66	25	8.97	5.19
1. 7.66	22	16.90	6.50
1. 8.66	31	16.90	5.96
5. 9.66	36	6.27	3.83
5.10.66	30	6.27	4.45
31.10.66	26	6.27	8.70
1.12.66	32	3.14	8.45
16. 1.67	46	3.14	12.62
15. 2.67	30	23.01	43.88
15. 3.67	28	4.27	4.53
20. 4.67	33	4.27	2.71
	365		109.47

Net change in S/C = -22.75 .˙. Estimate of Alder leaf fall = 86.72g/m^2

BIRCH LEAVES

DATE	DAYS	RATE (mg/g/day)	DISAPPEARANCE (g/m^2)
20. 4.66	-	-	-
16. 5.66	26	7.21	9.69
10. 6.66	25	9.61	9.21
1. 7.66	22	13.20	6.66
1. 8.66	31	13.20	8.70
5. 9.66	36	13.20	9.88
5.10.66	30	13.20	11.72
31.10.66	26	12.46	18.50
1.12.66	32	7.01	16.54
16. 1.67	46	7.01	18.96
15. 2.67	30	7.45	12.98
15. 3.67	28	4.40	7.43
20. 4.67	33	8.80	10.54
	365		140.81

Net change in S/C = -28.65 .˙. Estimate of Birch leaf fall = 112.16g/m^2

.˙. from disappearance + S/C, estimated leaf fall = <u>196.88g/m^2</u>

The weakness of paired plots estimates for tree litter lies in the relatively small amounts of tree litter present for much of the year. Just as the biomass estimates of forest floor tree litter had large standard errors, so there were greater possibilities of error in the paired plots experiment than for ground vegetation litter. Even so, the estimate for alder leaves did not appear to be wildly wrong, and that for birch leaves was of the right order of magnitude.

Total disappearance of other categories of forest litter could only be calculated from their litter fall and forest floor biomass change. In 1966-7 these two figures were $76.94g/m^2$ and $59.90g/m^2$. The total disappearance of this material was thus $136.84g/m^2$.

If the paired plots estimate is taken as correct for both ground vegetation and alder and birch leaf litter, the total disappearance from the forest floor from 20.4.66 to 20.4.67 was $931.26g/m^2$. If the alternative, more reliable estimate of alder and birch leaf litter disappearance is used, the total was $918.73g/m^2$. There was a net loss of $385.56g/m^2$ from the Forest Floor during this year, so that an input of $545.70g/m^2$ is implied.

(b) 1967-8. Table LIII shows the ~~instantaneous~~ mean rate of disappearance of total ground vegetation litter and the amount of this material disappearing as calculated from these and the total ground vegetation litter standing crops from 20.4.67 to 20.4.68. The total disappearance

TABLE LIII   Disappearance of total ground vegetation/$\underline{\text{litter}}$ from the Grid
                              1967-8

DATE	DAYS	RATE (mg/g/day	DISAPPEARANCE (g/m^2)
20/ 4/67	-	-	-
20/ 5	31	11.00	55.81
18/ 6	28	4.52	20.37
17/ 7	29	1.54	8.37
21/ 8	35	6.86	40.39
21/ 9	31	6.86	30.60
23/10	32	1.00	4.60
18/12	56	5.74	50.74
26/ 2/68	70	0.50	6.49
20/ 4	54	8.16	80.57
		TOTAL	297.94

of ground vegetation litter as calculated by this method was 297.94g/m^2. This method used the Grid values for biomass and treated the ground vegetation litter as though undivided.

Similar estimates were made using the biomass data for the Alder and Birch Zones taken separately. The total disappearance of ground vegetation litter for the Alder Zone was given as 235.03g/m^2, whilst that for the Birch Zone was much higher at 361.61g/m^2. The weighted mean of these two estimates, 299.58g/m^2, was very close to that obtained directly from the Grid biomass data. Table LIV shows disappearance of ground vegetation litter from the Grid calculated by species group. The total of 331.71g/m^2 was higher than that calculated from total ground vegetation standing crop data. During some intervals the disappearance estimated in this way was greater than that estimated from undivided litter. During other intervals it was less. This was largely because the proportional composition of the litter in the eight paired plots need not have been the same as that in the site as a whole at the same time. However, the overall difference was only 11% between the two estimates. Fern, Rubus and Grass litter made up 47, 30 and 23% respectively of the decomposition of total ground vegetation litter calculated for the grid as a whole.

If the two zones are considered separately (Table LV), the total disappearance of ground vegetation litter in the Alder Zone, calculated from species groups, was 276.03g/m^2; of this, Fern, Rubus

TABLE LIV

Disappearance of ground vegetation litter by species groups from the Grid 1967-8 (g/m²)

DATES	DAYS	FERN		RUBUS		GRASS		TOTAL
		RATE (mg/g/day)	DISS. (g/m²)	RATE (mg/g/day)	DISS. (g/m²)	RATE (mg/g/day)	DISS. (g/m²)	(g/m²/yr)
20/4	-	-	-	-	-	-	-	-
20/5	31	13.80	41.49	12.40	15.74	5.40	3.71	60.94
18/6	28	5.50	11.84	4.89	7.73	6.36	4.71	24.28
17/7	29	7.98	15.64	1.42	3.45	7.20	5.82	24.91
21/8	35	8.96	18.95	6.86	17.65	8.51	10.22	46.82
21/9	31	8.96	15.52	6.86	9.83	8.51	11.21	36.56
23/10	32	7.58	12.41	5.34	6.97	8.51	13.32	32.70
18/12	56	7.58	26.82	5.34	11.57	1.00	3.07	41.46
26/2	70	0.93	5.33	0.62	1.82	0.10	0.43	7.58
20/4	54	1.86	9.26	12.40	24.72	7.85	22.54	56.52
TOTAL	366		157.26		99.48		75.03	331.77

TABLE LV   Summary of disappearance of ground vegetation litter by species groups from Alder and Birch Zones, 1967-8

$g/m^2/yr$	FERN	RUBUS	GRASS	TOTAL
ALDER ZONE	155.21	84.43	36.39	276.03
BIRCH ZONE	161.47	114.89	116.82	393.18
		mean of totals		333.50

and Grass litter contributed 56, 31 and 13% respectively. In the Birch Zone the total was 393.18g/m^2, apportioned among the same three groups as 41, 29 and 30%. It is clear that the grasses were much more important in the litter disappearing from the Birch Zone than the Alder Zone.

Table LVI shows the data for decomposition of alder and birch leaf litter for the whole Grid in 1967-8. The ~~instantaneous~~ _mean_ rates were taken from the 1966-7 Paired Plots data, as those for 1967-8 were on several occasions improbably large. The total disappearance of alder leaves was 62.03g/m^2. The first estimate for birch leaves was 137.24g/m^2. However, 54.11g/m^2 of this total appeared to disappear between 18.12.67 and 20.4.68, a period in which there was no change in litter standing crop and no addition of litter by fall, therefore a corrected total of 83.13g/m^2 was used. This gave a total disappearance of alder and birch leaves of 145.16g/m^2. The alternative estimates calculated from litter fall and litter standing crop change were 74.76g/m^2 for alder, 43.80g/m^2 for birch, giving a total of 118.56g/m^2.

The estimate of decomposition of other litter components was made in the same way as for 1966-7. Their litter fall was 100.68g/m^2, and their biomass declined by 4.72g/m^2. Thus their disappearance from the litter layer was estimated as 95.96g/m^2.

When paired plots estimates were used, as in 1966-7, the estimate of total disappearance in the period 20.4.67 to 20.4.68 was

TABLE LVI   Calculation of Disappearance of Tree-leaf material
                              Grid 1967-8

ALDER LEAVES

DATE	DAYS	RATE (mg/g/day	DISAPPEARANCE (g/m^2)
20/4	-	-	-
20/5	31	3.68	0.97
18/6	28	8.97	1.29
17/7	29	16.90	4.47
21/8	35	6.27	3.81
21/9	31	6.27	6.97
23/10	32	6.27	7.19
18/12	56	3.14	10.44
26/2	70	3.14	15.53
20/4	54	4.27	11.36
Total	365		62.03

Net change in S/C = + 14.03 $\therefore$ estimate of Alder leaf fall = 76.06g/m^2

BIRCH LEAVES

20/4	-	-	-
20/5	31	7.21	4.43
18/6	28	9.61	4.02
17/7	29	13.20	4.43
21/8	35	13.20	7.34
21/9	31	13.20	18.55
23/10	32	13.20	19.15
18/12	56	7.01	25.21
26/2	70	7.01	(30.60)
20/4	54	6.84	(23.51)
	366		(137.24)(83.13)

Using 83.13g/m^2 as disappearance, net change in S/C = + 39.22

$\therefore$ Estimate of Birch leaf fall = 122.35g/m^2

539.06g/m^2 (A). If the same figures were used, but with the disappearance of ground vegetation litter calculated by species group, the total was 573.83g/m^2 (B). If the litter fall/standing crop estimates of tree leaf litter disappearance were used, these two estimates became 512.26g/m^2 (C) and 556.03g/m^2 (D) respectively. There was a net addition of 42.55g/m^2 to the Forest Floor in this year, and so an input of 598.58g/m^2 was implied when estimate (D) was used. If (A) was used, because it was directly comparable with the 1966-7 figure, the input to the Forest Floor was calculated as 581.61g/m^2. The input figures for the two years were rather similar however calculated, the ratio between the two most comparable estimates being 1966 : 1967 - 0.94 : 1.00. The excess of disappearance over input of 385.56g/m^2 in 1966-7 was due to the breakdown of the large excess of litter in spring 1966 remaining from the previous autumn.

VIII. iv. <u>Results as Biocontent</u>

Table LVII gives a summary of the calculation of the biocontent of disappeared material. The values for ground vegetation method (A) were calculated using the mean calorific content of this material. The method (B) estimates were multiplied by the appropriate calorific value for each category of material. The tree litter figure C + D) was calculated from the total litter fall biocontent (cf. Section V) and the net change in biocontent of the forest floor

<u>Table LVII</u>   <u>Biocontent (Kcal/m^2) of disappeared material</u>

	1966-7	1967-8
Ground Vegetation Litter	2210.84^a	1210.53^a
		(1350.37^b)
Tree Litter	<u>1924.21</u>^{c}	<u>1217.88</u>^{c}
	4134.65	2428.41$^{a + c}$
		(2568.25$^{b + c}$)

    a - paired plots

    b - paired plots with litter divided

    c - Litter fall + change in forest floor biocontent

	1966-7	1967-8
INPUT TO FOREST FLOOR =	2465.35	2624.61$^{a + c}$
		(2764.45)$^{b + c}$

tree litter (cf. Section VII). As expected from the biomass data

the disappearance in 1966-7 was much greater than in 1967-8. If

net increase in Forest Floor biocontent is subtracted from total

disappearance, an estimate of input to the Forest Floor is obtained.

In both years this was in the region of 2,500Kcal/m^2. In 1966-7,

985.44Kcal/m^2 or 40% of this came from the ground vegetation.

In 1967-8 1184.63Kcal/m^2 or 45% came from the ground vegetation

using method (A), or 1324.47Kcal/m^2 (48%) using method (B).

VIII. v. Discussion

The loss of trophic energy from the L - layer is the sum

of energy dissipated by heterotrophs in the litter and energy lost

to lower soil horizons, by leaching, commination or other means.

If there is no net accumulation or loss of energy from these horizons,

the loss of trophic energy from the L - layer (as calculated from

disappearance) equals the total dissipation of energy by the decomposer

component of the ecosystem, at least so far as detritus formed above

ground is concerned.

If a simple model of litter decay such as that proposed by

Jenny et al (1949) or Olson (1963) is adopted, ~~instantaneous~~ decay

rates may be calculated using the formula

$$k = \frac{L}{L+A} \text{ , where } \begin{array}{l} L = \text{annual litter fall} \\ A = \text{biomass of litter layers} \end{array}$$

If L+A is taken after the time of Tree litter fall (October) k is

calculated as

$$\frac{2465.35}{3264.00} \quad \text{in 1966-7} \quad = \quad 0.76$$

and
$$\frac{2624.61}{2652.30} \quad \text{in 1967-8} \quad = \quad 1.00$$

using estimate (a) of input. If estimate (b) is used, the value of k is given as 1.02. k may also be calculated for total Forest Floor organic matter. In February 1968 twenty-four 0.01m x 10cm soil cores were taken, three at random in each of the eight 20 x 20m^2 of the Grid. From subsamples after drying, the organic matter content was determined using a muffle furnace at 500°C for 24 hours, root material having been carefully removed. The volatile matter was 7761.12g/m^2; taking a calorific value of 4.5Kcal/g for this ash-free material (see Table XI) (Section III), the soil organic matter biocontent came to 34925.26 Kcal/m^2. Adding the litter layer to this, k is calculated as 0.068. If time necessary for 95% breakdown (3/k) is calculated from these values, it is three years for the litter layer, but 44 years in the whole Forest Floor system.

It is likely that k for the whole Forest Floor is an underestimate and 95% breakdown time an overestimate, because the estimate of input to the litter plus soil organic matter biocontent did not contain an estimate of root mortality. If the simple exponential model of litter decay does apply to this system, the data suggest that a period of the order of 74 years (5/12) with litter production and decay of approximately the same order as at present would be necessary for the soil organic matter and litter fall

to have reached equilibrium. It is possible (cf. Sections II & IV) that such conditions have existed.

Along with biomass and biocontent data for the Forest Floor, it is possible, using the paired plots data, to calculate input to the Forest Floor by the ground vegetation, that is, its litter production. Bray & Gorham (1964) summarised much of the data available for ground vegetation litter production but they cite no case where this litter contributed more than 28% of total litter; this maximum figure was for a very young stand of <u>Robinia</u> (Auten 1941). Also quoted was a figure of 25% of total litter for an old open stand of <u>Eucalyptus</u> (Ashton 1964). The other figures cited average 9% of total litter.

Table LVIII shows data (Ashton 1964; Auten 1941; Ovington 1959; P'Yavchenko 1961; Scott 1955; Witkamp & van der Drift 1961) from several woodlands.

It should be noted that the <u>Eucalyptus</u> data may contain litter fall from lower storey trees. The data from P'Yavchenko contain an estimate of die-back of roots.

Where known, the method of measuring ground vegetation litter production has been shown. The method commonly used has been to harvest the ground vegetation at some more or less appropriate time of year. The standing crop of ground vegetation calculated from this has been taken as an estimate of ground vegetation litter production. This is only a valid method if the amount of material harvested is the same as that falling into the litter. This will not be the case if :

TABLE LVIII

Ground Vegetation Litter in various woodlands

Source	Woodland	Age	Ground vegetation litter $(10g/m^2/yr)$	(% of total litter)	Method
	Young				
Auten 1941	Robinia Pseudoacacia	9	1.1	28	Mid-summer green clip
	Sassafras albidum	12	0.2	7	Mid-summer green clip
Ashton 1964	Eucalyptus regnans	25	0.8	11	———
	Mature				
Ovington 1959	Pinus sylvaticus	33-55	2.4	31	October green clip
P'Yavchenko 1961	Bog and grass Spruce forest	100-200	1.4	30	September green clip
	Low shrub and sphagnum pine forest	120	1.31	53	September green clip
Ashton 1964	Eucalyptus regnans	200	2.0	25	———
Scott 1955	Acer saccharum	-	0.3	15	Single clip
	Pinus strobus	-	0.3	16	Single clip
Witkamp & van der Drift 1961	Quercus robur	-	0.14	4	August green clip
	Mixed angiosperms	-	0.83	20	August green clip

(1) There is any net transfer of dry matter between the above
and below ground parts of the ground vegetation after
harvesting and before litter formation

(2) there is growth of ground vegetation in this time interval

(3) any ground vegetation dies back and forms litter before
harvesting. These situations may well be common.

In this study the estimate of ground vegetation litter
production was total annual disappearance of ground vegetation litter,
with a correction for the net change in its standing crop over the
year. This met the criticisms made above. If other methods had
been used, an underestimate would have resulted. For example, in
1966-7 the overall green ground vegetation dry matter increment was
$113.53 gms/m^2$ (a). The sum of species dry matter increments
(estimate b) was $178.94 gm/m^2$. The total annual disappearance,
with a correction for the net change in ground vegetation litter
standing crop (c), (the estimate used) was $269.88 g/m^2$.

Of these estimates, the lowest (a) was more accurate than
would be obtained if it were based on a single summer clipping.
(b) was markedly higher, as it took into account the spread of the
peak standing crops of the individual species through a large part
of the year. It did not, however, recognize the passage of materials
from the above ground to the below ground parts of plants that may
occur after peak standing crop. Nor did it account for pre-peak
mortality and post-peak growth in grasses. The highest estimate (c)

was based on the calculation by difference of the total input of dry matter to the litter by the ground vegetation. The estimate was dependent only on the instantaneous rate of disappearance and standing crop changes in the ground vegetation litter. It was not affected by the transfer of material between the above and below ground parts of plants. It accounted for mortality before peak green standing crop and disappearance of litter before peak mortality for the species concerned.

The work of Wiegert & Evans (1964) suggests that the peak standing crop of grasses represents at most 50% of the total litter production by the grasses. In this study grass litter disappearance in 1967-8 was calculated as $75.03g/m^2$. The net change in grass biomass in that year was $+24.37g/m^2$. Therefore grass litter production was $99.40g/m^2$. The sum of grass species increments was $45.62g/m^2$. The ratio of litter production to this was 1 : 0.45. If the grass contribution in estimate (b), 1966-7, is multiplied by 2.2, estimate (d), $232.94g/m^2$, results. If the 1967-8 data had not been used, but merely Wiegert & Evans' indication, a very similar estimate would have resulted. This would be completely independent of estimate (c), but close to it.

In this study evidence has been obtained for high ground vegetation litter production. If the method of summer clipping had been used a gross under-estimate would have resulted. The calculation of ground vegetation litter production from measurements of disappearance was adopted because :-

(a) it measures mortality that occurs before peak green standing

   crop and disappearance of litter before peak mortality for the species

   concerned.

(b) it is not rendered invalid by growth after peak green standing

   crop.

(c) the transfer of material between the above and below ground

   parts cannot affect it.

   This particular method may not be suitable for other woodlands,
but nevertheless attention should be paid to the three points mentioned
above.

   In summary, the data presented in this section indicate that
the annual addition of energy-rich material to the Forest Floor of the
Study Area was around 2500Kcal/m^2 with the study period. Of this 40
to 50% was contributed by the ground vegetation. Annual disappearance
equalled this, excepting in the first study year when an excess of
material from 1965 was broken down in the spring of 1966. As maximum
litter biocontent was around 2500Kcal/m^2, and total Forest Floor
organic matter (to 10cms depth) around 37,000Kcal/m^2, 95% breakdown
times of 3 and 4 years respectively were indicated.

   Thus the litter layer may be seen as a medium-term energy
store, the soil organic matter as a longer-term energy store.
What was not revealed in this investigation was what fraction of the
total decomposition actually took place in the L layer as distinct from
lower horizons. However, an indication of the size of energy flow
through the decomposer component of the ecosystem was obtained.

CHAPTER III

SECTION IX. Ground Vegetation Net Primary Production

IX. i. <u>Introduction</u>

The data presented in Sections VII and VIII suggest an important role for the ground vegetation in the biocontent structure, litter formation and breakdown of the system under study. In this section estimates of above-ground net primary production of ground vegetation will be presented.

Many authors give estimates of ground vegetation biomass (Auten 1941; Baskerville 1965; Frankland et al 1963; Scott 1955; Sviridova 1960; Tamm 1953; Traczyk 1967; Traczyk & Traczyk 1967; Ovington & Heitkamp 1960; Ovington, Heitkamp & Lawrence 1963; Whittaker 1961; Whittaker 1963). There have been rather fewer attempts to make detailed analyses of net primary production by this stratum. Of these, Tamm (1953) worked on carpets of forest moss, not directly comparable with the vegetation investigated here. In most other cases ground vegetation net primary production has been equated with the standing crop on one arbitrarily chosen occasion, or at best as the peak of a biomass curve based on infrequent samples. The criticisms levelled at this approach by Wiegert & Evans (1964) and in Section VIII of this thesis are relevant here, too.

A modified approach was used by Traczyk (1967) and Traczyk & Traczyk (1967), involving analysis of density and the calculation of an index of average individual increment for individuals

of each species. The individual increment was based on the separation of current from previous years increment at the time of fructification. This approach takes cognisance of the complex spatial distribution of individuals of a species, and bases the separation of current from previous years increment on reliable phenological and anatomical indicators. However, it assumes no death of new parts before fructification, and no net increment after it. For many of the forest herbs these are probably reasonable assumptions, but do not hold true for grasses (cf. Section VIII) and certain other perennial plants. Moreover, it is impossible to know what transfers between the above-ground parts and below ground parts have taken place and such transfers could well affect an estimate made in this way. Nevertheless, the work at Kampinos represents the most detailed consideration of ground vegetation primary production in the literature to date.

An important characteristic of the ground flora of forests in the cool temperate zone is that it contains few annual species, and few individuals of those that are present (Richards 1952; Traczyk & Traczyk 1967; Section II of this thesis). Thus we are concerned almost entirely with perennial plants, in which transfer between above and below ground parts must affect any but a perfectly timed production estimate. That is to say, a full knowledge of the timing, nature and magnitude of energy and material transfer between the various organs of each species concerned would be necessary before

it could be decided which apparent increment is to be taken as the estimate of net primary production. This matter is confused and the problem intensified further where only above ground net primary production is being measured. Where root studies are carried out, caloric phenology may help to define transfers between organs (Kieckhefer 1962; Hadley & Kieckhefer 1963). For reasons of labour shortage and the nature of the soil at Wynyard this was not possible in this study.

The apparently necessary division of net primary production into that taking place above ground and that below may lead to confusing simplifications. Where root studies are impracticable it is more profitable to distinguish between the products of net primary production that may be measured above or below the soil surface. Thus net primary production measurable above ground equals the sum of net above ground biomass change, losses to decomposers, losses to herbivores and losses in solution. Net primary production measurable below ground equals the sum of net transfer from above ground minus below ground respiration and this in turn equals biomass change plus a series of loss terms analogous to those for above ground parts.

In order to solve for net primary production (either total or for the above or below ground components) it is necessary to measure the net change in biomass for the period concerned plus the periodic integrals of the loss rates indicated. Thus even where only a partial

estimate is possible, it may be clearly defined in terms related to

the realities of dry-matter energy accumulation and trophic transfer.

This avoids the pitfall of abstraction about nature being over-

determined by inadequate observational techniques (e.g. the range

management research practice of taking total above ground dry

matter as an index of production). It does not, of course,

obviate inaccuracy due to technique or uncertainty due to the

heterogeneity of the material.

In this study net primary production of the ground vegetation

was only measured above the mineral soil surface, as for the tree

stratum. Losses to herbivores, and in solution, were not measured.

Thus net primary production was estimated as the sum of net change

in biomass and loss to decomposers. Both of these parameters were

measured above the mineral soil surface only.

IX. ii. Methods

The methods used in the collection of the data presented

in this section have been described in Sections VII and VIII.

Changes in biomass and biocontent are taken from Section VII,

whilst loss to decomposers is taken as the input to the Forest Floor

from the ground vegetation calculated in Section VIII.

IX. iii. <u>Results - biomass</u>

Table LIX shows details of the calculation of net primary production for 1966-7. The mortality term is the sum of disappearance and ground vegetation litter standing crop increase. The growth term is the sum of mortality and green ground vegetation standing crop increase. The two most comparable estimates, that is, those based on disappearance calculated for undivided litter, are within 1% of one another for the two years. The figure calculated from the disappearance of separated litter is higher, but less reliable (see Section VIII). Of this 43.0, 27.5 and 29.5% of the growth is attributed to the Ferns, <u>Rubus</u> and Grasses respectively. In the separation of ground vegetation litter it was not possible to identify those species with less persistent litter. In the case of undivided litter this was clearly not a problem. For this and other reasons (cf. Section VIII) the estimate based on the disappearance of undivided litter is accepted. Thus net primary production of the ground vegetation measured above ground was $277.86g/m^2$ in 1967-8.

These figures may be compared with data analogous to those on which other authors have based primary production estimates (Table LX). The peak standing crop of a largely perennial vegetation is not a measure of its net primary production, nor is the difference between the maximum and minimum biomass a good estimate of net primary production. The sum of species dry matter increments is more realistic, for not all species show peak or minimum biomass in

TABLE LIX   Calculation of Ground Vegetation Net Primary Production
(g/m^2)

	Mortality	Change in green biomass	Growth
1966-7 Total	269.90	+ 7.96	277.86
1967-8			
Ferns	142.67	- 1.93	140.74
Rubus	95.31	- 5.46	89.85
Grasses	99.40	- 2.97	96.37
Total of these	337.38	- 10.36	327.16
1967-8 Total	291.96	- 11.76	280.20

TABLE LX   Biomass   Various net primary production calculations (g/m^2) for ground vegetation

	1966-7	1967-8
Peak standing crop	137.70	106.23
Dry matter increment	113.53	89.87
Sum of spp. dry matter increments	178.94	143.17
Sum of spp. increments + grass	223.88	188.85
Estimate from Table LIX	277.86	280.20
Table LIX estimate by spp. groups	-	327.16

the same months. This estimate is made more realistic by the doubling of the grass contribution (cf. Section VIII). Even so, it is considerably less than the estimate based on disappearance and green biomass change (19.5% less in 1966-7, and 32.5% in 1967-8). This implies that there must be considerable loss to litter before peak biomass or growth after peak biomass in a species other than grasses. An examination of the 1967-8 biomass data suggest that this may be the case for <u>Rubus</u>, where there was an increase of litter biomass in the month after peak green biomass that was not fully accounted for by the decrease in living biomass. This suggests a dying off of overwintered material after the new year's shoots were well established but not fully grown. The total discrepancy for the months of May to July was $53.52 g/m^2$.

For the Ferns, the peak biomass of the main species, <u>Dryopteris filix-mas</u>, occurred at the end of the season, and was followed by an increase in litter biomass. Thus it seems likely that the major discrepancy between species increment and net primary production that one might expect, apart from the grasses, is the case of <u>Rubus</u>. The discrepancy here appeared to be of the order of the summer standing crop of the species, or greater. Thus it is reasonable to assume that the real net primary production of the vegetation in question was $30 - 40 g/m^2$ greater than the sum of species dry matter increments plus the grass contribution. This gave figures of the order of $250 - 260 g/m^2$ in 1966-7 and $220 - 230 g/m^2$ in 1967-8.

These data are not inconsistent with the net primary
production estimates based on disappearance and total biomass change,
although essentially independent of them.

IX. iv. Results - biocontent

Table LXI corresponds to Table LX and gives various
biocontent data for primary production of ground vegetation measured
above ground. Similar comments apply to the various biocontent data
as to the biomass data. In addition, it should be noted that there
is less difference between the species group disappearance based
estimate and the total disappearance based estimate than for biomass
(13.8% as against 16.8%). Thus it is reasonable to assume that the
net primary production of the ground vegetation that may be measured
above ground lay between 900 and $1300Kcal/m^2$ for the two study years.
In fact, the accepted estimates were $1016.2Kcal/m^2$ for 1966-7 and
$1142.4Kcal/m^2$ for 1967-8.

IX. v. Discussion

The net primary production of the ground vegetation measured
above ground (circa $1000Kcal/m^2/yr$) was not much smaller than the total
litter fall from the trees (circa $1450Kcal/m^2$). These two figures
are comparable in that they approximate to the production of photo-
synthetic parts, and their immediate support organs, by the strata
they represent. The difference between the two strata is the

TABLE LXI Biocontent Various net primary production calculations
$(Kcal/m^2)$ for ground vegetation

	1966-7	1967-8
Peak standing crop	581.3	445.6
Dry matter increment	516.3	380.6
Sum of spp. dry matter increments	678.9	534.0
Sum of spp. increments + grass	833.1	714.6
Estimate from Table LIX	1016.2	1142.4
Table LIX estimate by spp. groups	-	1280.8

production of large amounts of long-term storage by the tree stratum ($2000Kcal/m^2/year$ or more).

It is clear that the cost of maintaining a smaller photosynthetic machinery for a longer growth season was relatively greater than the cost of maintaining the tree canopy from early May to October. A major contributor to this energy cost must have been the replacement of old tillers of perennial grasses through a large part of the year. It is possible that the position would be reversed if fine root production and loss were also included as a running cost charged against dry matter accumulation.

The role of the ground vegetation in the woodland ecosystem is discussed further in the last Section of this thesis.

CHAPTER IV

Section X.   Insolation

X. i. Introduction

Ecologists see incident solar radiation, or more strictly
the sun, as the ecosystem's energy source.   Apart from the small
amounts of energy which are thought to be fixed chemically, the
ecosystem must gain all the energy dissipated in its life-processes
by fixing the energy of incident solar radiation.   Therefore, in
any study of ecosystem energetics this must be a key measurement.
Extra-terrestrial solar radiation has wavelengths from 0.2 to 3.0
microns (a very small fraction of its energy lies beyond 3.0 microns).
However, that which is of use in photosynthesis lies between 0.4 and
0.7 microns.   If the primary purpose of this study was to compare
the photosynthetic efficiency of different plants or vegetation
strata, radiation between these wavelengths would have to be measured.
However, a measure of total incident short wave radiation is required
so that net primary production and net ecosystem production may be
expressed as fractions of the total available energy.   In essence,
measurements in the waveband 0.4 to 0.7 microns allow for the present
state of evolution of the photosynthetic machinery, whereas total
short wave (SW) radiation measurements do not.

In this study SW radiation above the tree canopy was
measured over a period of one year.   So that SW radiation records

might be compared with those for growth, canopy closure etc., they were obtained in the form of integrated weekly totals. In addition, SW radiation at points in and beneath the canopy was measured. These latter measurements were carried out more in order to test the apparatus than to define irradiation incident on the lower vegetation strata. As will be seen below, much more extensive instrumentation would have been required for this purpose.

X. ii. Methods

To avoid compensation for the present state of evolution of the photosynthetic machinery, and because of our relative ignorance of its evolutionary characteristics, SW radiation should be measured by an instrument that does not have a differential spectral-sensitivity.

Tricket, Moulsley & Edwards (1957) were among the first to suggest that the most appropriate instruments for measuring total short wave radiation are those based on the principle of the thermopile. Reliable instruments of this kind are available commercially but are, in the main, expensive. However, several cheap but effective solarimeters have been developed (Monteith 1959; Szeicz, Monteith & dos Santos 1964; Szeicz 1966). In this study a commercial version of the Monteith 6cm Dome solarimeter (Monteith 1959) was used. For the measurement of irradiation within and beneath the canopy, the tube type of solarimeter (Szeicz, Monteith & dos Santos 1964) would have been most appropriate. These are not available commercially, and as time was limiting, the dome type of solarimeter was used in this

part of the study also. The glass dome acts as a filter which cuts off at 0.28 microns and 3.0 microns.

A method of integrating the solarimeter output was required. Of those described in the literature (Trickett et al 1957, Monteith & Szeicz 1962) the required components are not always readily available, or cheap. In this study, a simple inexpensive integrator for use with solarimeters and other devices with a similar output was developed.

The Integrator

Two main approaches have been adopted in the integration of solarimeter output; either it is integrated directly by means of a sensitive summation device such as an inverted burette (e.g. the Siemens meter) or ~~the~~ amplified ~~amplification~~ and then ~~subsequent~~ integration ~~of the output~~ (Trickett et al 1957; Monteith & Szeicz 1962). In this study the second course was adopted.

It was clear that transistorized amplifiers would be most convenient for field use but a serious problem was encountered in the temperature dependence of the transistor base-emitter bias voltage. The difficulty appears to have been overcome in a circuit described by Holford 1962 where a long-tailed pair circuit was used to measure small voltages over a number of ranges. In this system the signal is applied differentially between the base terminals of two similar transistors whose emitters are common. If the temperature

dependence of the two base-emitter bias voltages were identical there would be complete compensation for temperature change. In practice, using silicon P-N-P junction transistors BCZ11, Holford found this compensation to be usually better than 99% over a 20 degree centigrade range (op.cit.).

The multirange input and the output sections of Holford's circuit have been modified for simple input and output and the circuit adjusted to operate at 9V (Fig.56). The circuit values were calculated with reference to the output data for the type of solarimeter used (Monteith 1959) and the nature of the integrator (Tanner et al 1963). A shunt was inserted across the output so that it could be adjusted to a suitable range for the integrator at a given time of year.
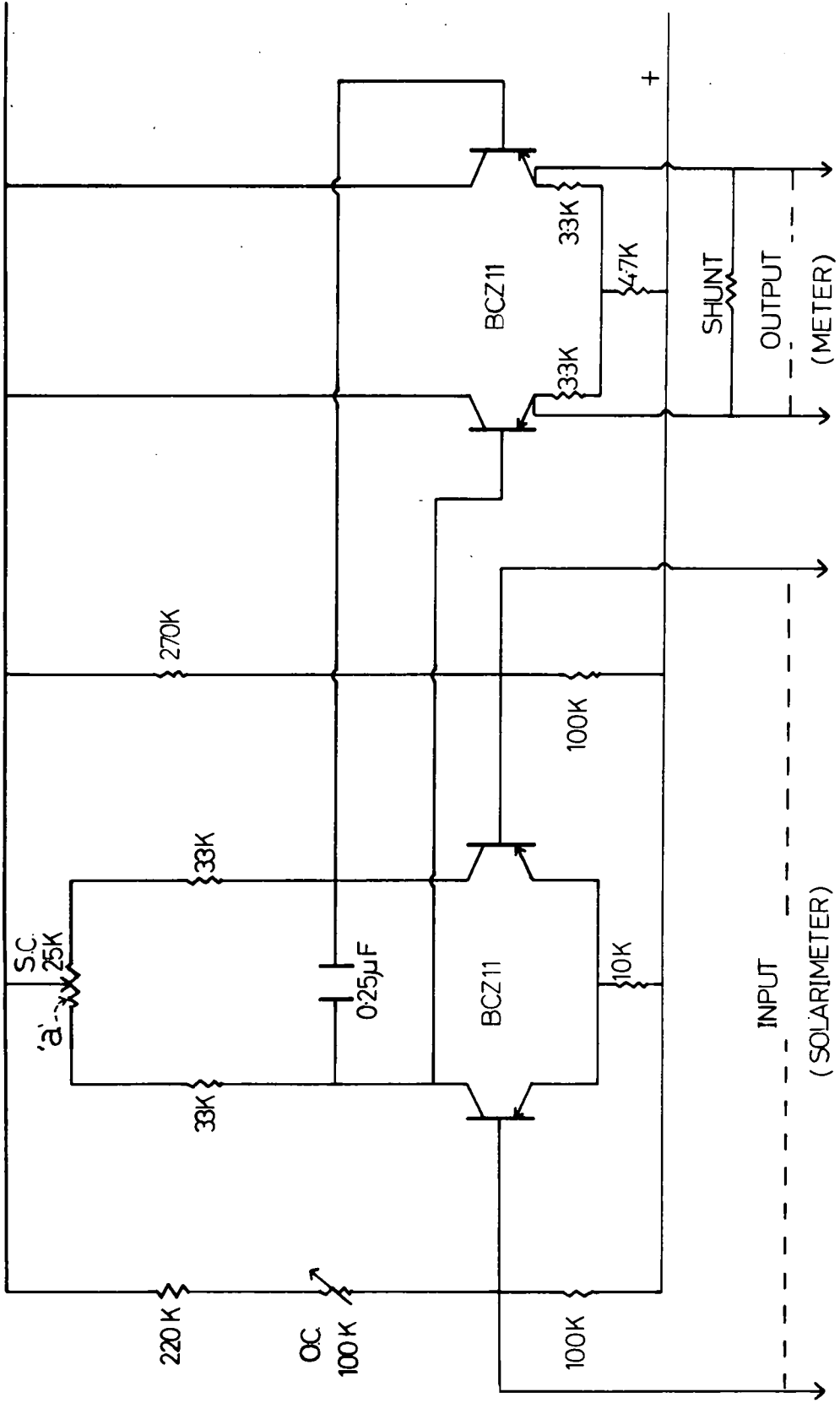
The output from the transistorized amplifier was integrated by a simple electrolytic coulometer (Tanner et al 1963; Macfadyen & Webb 1968). It consists of a glass capillary tube containing a mercury thread interrupted by a bubble of electrolyte. Terminals are sealed into the ends of the tube. As a small current (not greater than 150μ A)is passed, mercury electroplates from one side of the bubble to the other, so that the bubble is proportional to the integral of the current passed through the coulometer per unit time. This meter (available commercially as the 'Mercron' or the 'Curtis meter') is inexpensive. The movement of the meniscus of the mercury was measured accurately using a microscope with a calibrated mechanical stage. (A calliper micrometer could equally well have been used).

Figure 56.

The modified amplifier circuit. An explanation is given on pages 150-1.

FIELD AMPLIFIER CIRCUIT

-9V

S.C. 25K
'a'
33K
33K
0·25µF
270K
BCZ11
100K
BCZ11
33K
47K
33K
SHUNT
OUTPUT
(METER)
+

10K

220K
OC 100K
100K
INPUT
(SOLARIMETER)

X. iii. Performance of the Integrator

The transistorized amplifier produced a small current output when the input was zero; however, this was minimized by adjustment of the potentiometer shown as 'a' in Fig.56. Fig.57 shows that the present amplifier provided an effective linear amplification of the output of the Monteith solarimeter. The amplifier output was correlated with the irradiance measured by a Moll pile as follows in this case :

Coefficient of correlation, $r = 0.983$

Degrees of freedom $df = 59$

Probability of non-linearity, $P < 0.001$

The rate of movement of the coulometer mensicus was shown to bear a linear relationship to the current passing through it (Fig.58).

The whole assembly (Monteith solarimeter-amplifier-coulometer) was tested against a Moll pile for 12 days in March - April 1967. The total insolation (radiation in the wave-band 0.28μ to 3μ) recorded by this assembly is highly correlated with the integrated output of the Moll pile (Fig.59). The reading of the meter came within 3% of the integrated output of the Moll pile. More extensive trials than were possible would be necessary to assess adequately the percentage error of the solarimeter - integrator assembly with reference to the integrated output of the Moll pile. However, from Fig.57, the maximum deviation of the output of the solarimeter amplifier assembly from that of the Moll pile is 14.3%.

Figure 57.

Amplifier output (μA) against irradiance ($10'$ Kcal/m^2/min.) Solarimeter 1.

AMPLIFIER OUTPUT VS. OUTPUT OF MOLL PILE
SOLARIMETER I
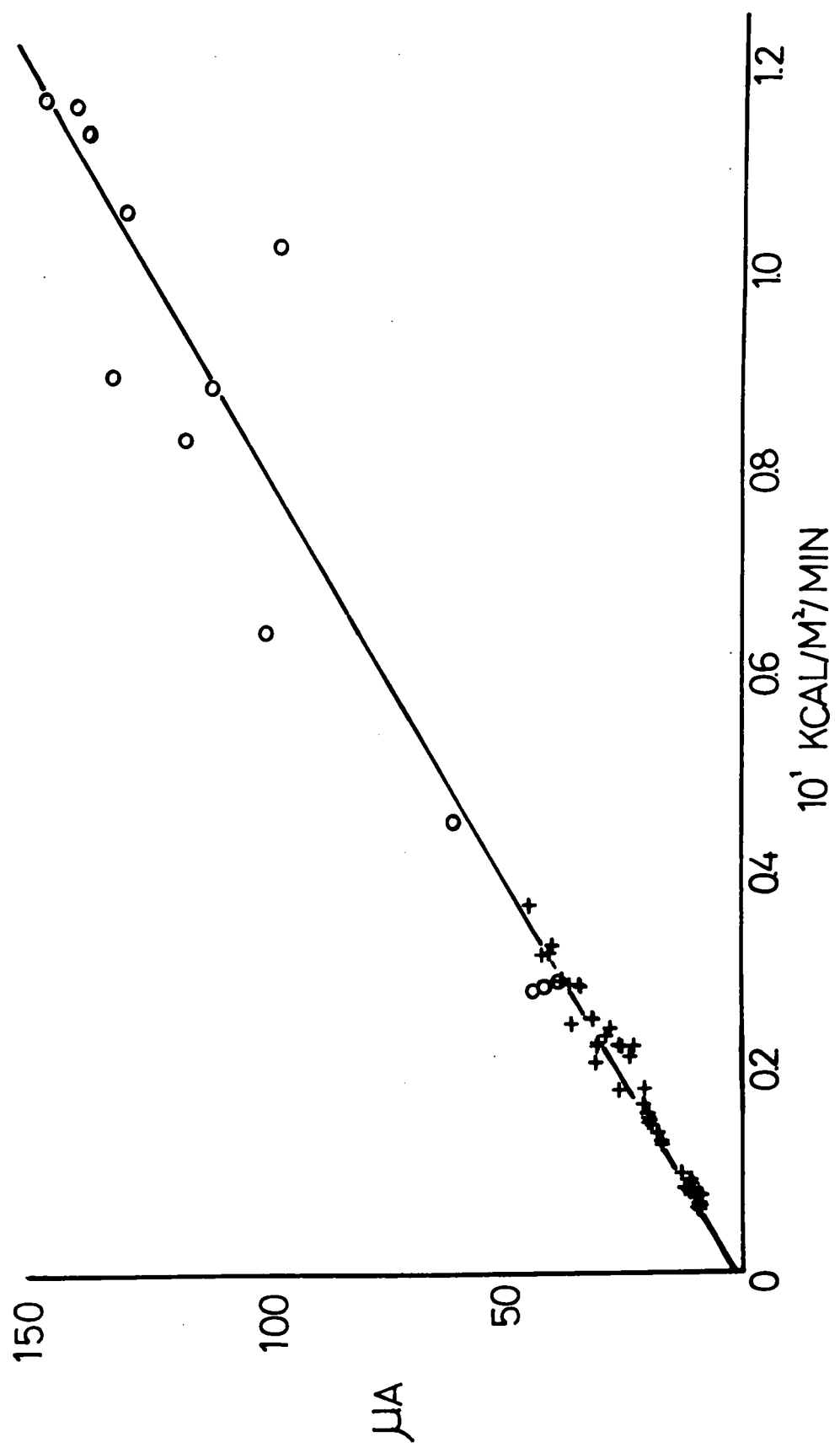
Figure 58.

Rate of meniscus movement (10^{-3} mm/hr) through Mercron 2 against current passed (μA).

RATE OF MENISCUS MOVEMENT VS. CURRENT
MERCRON 2

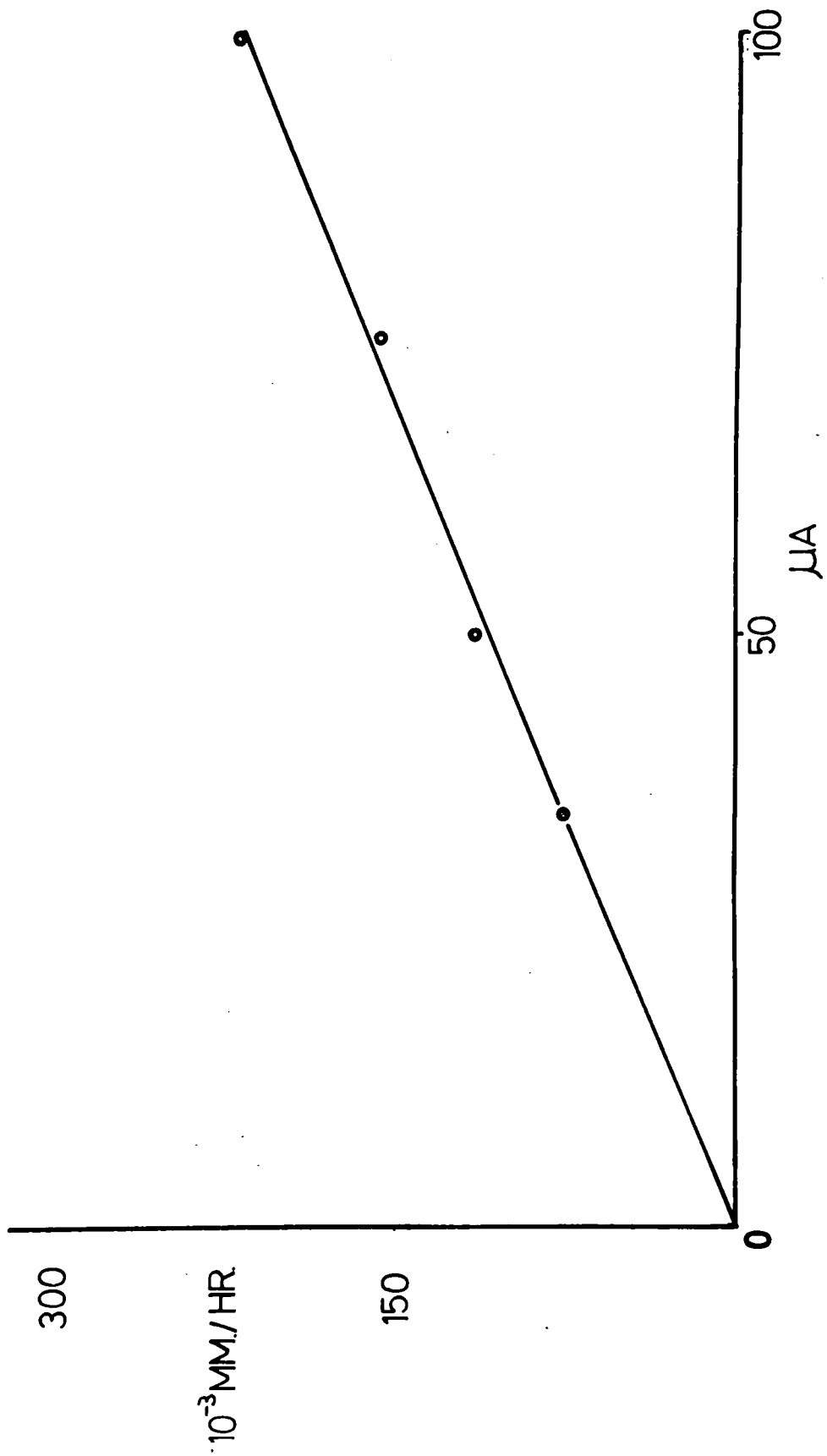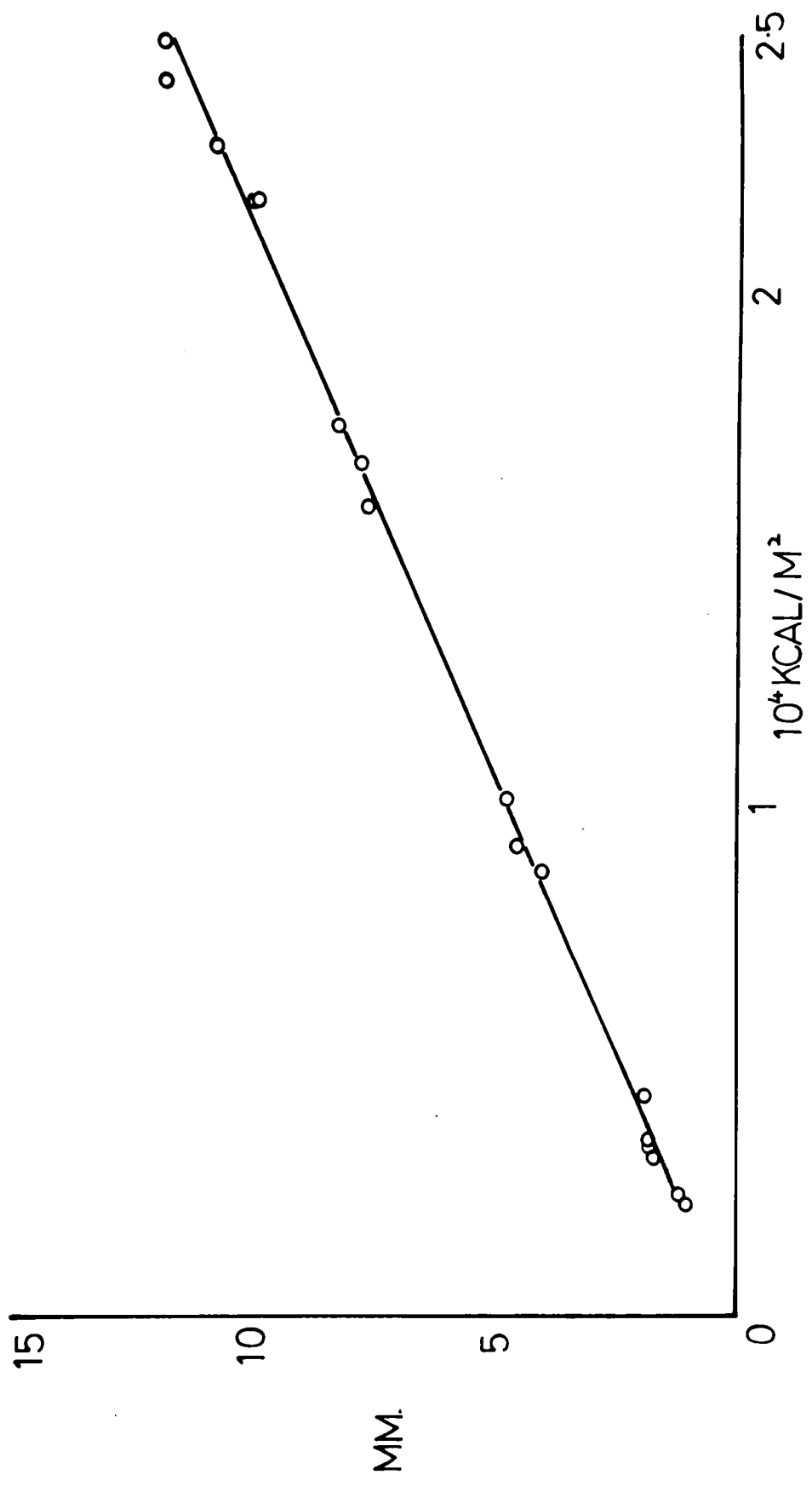300

$\cdot 10^{-3}$MM./HR

150

0   50   100

μA

Figure 59.

Meniscus movement (m.m.) in solarimeter-integrator against integrated irradiance (10^4 Kcal/m^2).

MENISCUS MOVEMENT VS. INTEGRATED OUTPUT OF MOLL PILE

Macfadyen & Webb (op.cit.) attribute an accuracy of $\pm$ 1% to the electrolytic coulometer and so it seems unlikely that percentage errors will exceed $\pm$ 15%. In fact, an examination of Fig.59 suggests that the actual errors are considerably less than this. Whole assemblies were tested under constant light conditions at 5, 15, 19, and 24 degrees centigrade air temperature for two weeks. There was no change in output with temperature.

X. iv. Calibration of the Solarimeter-Integrator Assemblies

Three alternative calibration procedures may be followed for these assemblies. Firstly, it is possible to disconnect the solarimeter and connect a calibration circuit in place of it. This is a device to provide a known small signal from a source of known impedence (Tricket et al 1957). This approach depends on accurate knowledge of the calibration of the solarimeter.

Secondly, the whole assembly may be run alongside a standard or sub-standard high quality instrument, such as a Moll pile. Then the movement of the meniscus may be plotted against the integrated output of the Moll pile so that a calibration factor can be derived. This method allows for calibration under field conditions if some means of integrating the output of the Moll pile is available.

Thirdly, known currents may be passed through the coulometers and a calibration factor for these derived. This may be done using a voltage regulator, decade resistor and high quality microammeter,

in series with the coulometer. Then the solarimeter-amplifier assembly may be calibrated by plotting the current output of the amplifier against the output of the Moll pile as measured by a portable potentiometer. Thus a series of spot readings under various conditions can be obtained. Hence the relationship between meniscus movement and total short wave radiation can be derived.

For the assemblies constructed, the third procedure was followed. Figs. 57, 60, 61 and 62 show the output of the amplifier vs short wave radiation measured by the Moll pile for Solarimeters 1, 2, 3, and 4 respectively. For each the regression of short wave radiation on current output provides a calibration equation as follows :-

Solarimeter 1.

$$x = 0.4716zd + 0.7630$$

where x = short wave radiation ($10Kcal/m^2/day$)

z = calibration factor for coulometer ($\mu Ahrs/mm$)

d = daily average of distance moved by meniscus (mm)

Solarimeter 2.

$$x = 0.4638zd + 12.41$$

Solarimeter 3.

$$x = 0.3078zd + 40.22$$

Solarimeter 4.

$$x = 0.2868zd - 56.86$$

Figure 60.

Amplifier output (µA) against irradiance ($10'$ Kcal/m^2/min).
Solarimeter 2.

AMPLIFIER OUTPUT VS. OUTPUT
OF MOLL PILE
SOLARIMETER 2

10^1 KCAL/M^2/MIN

μA
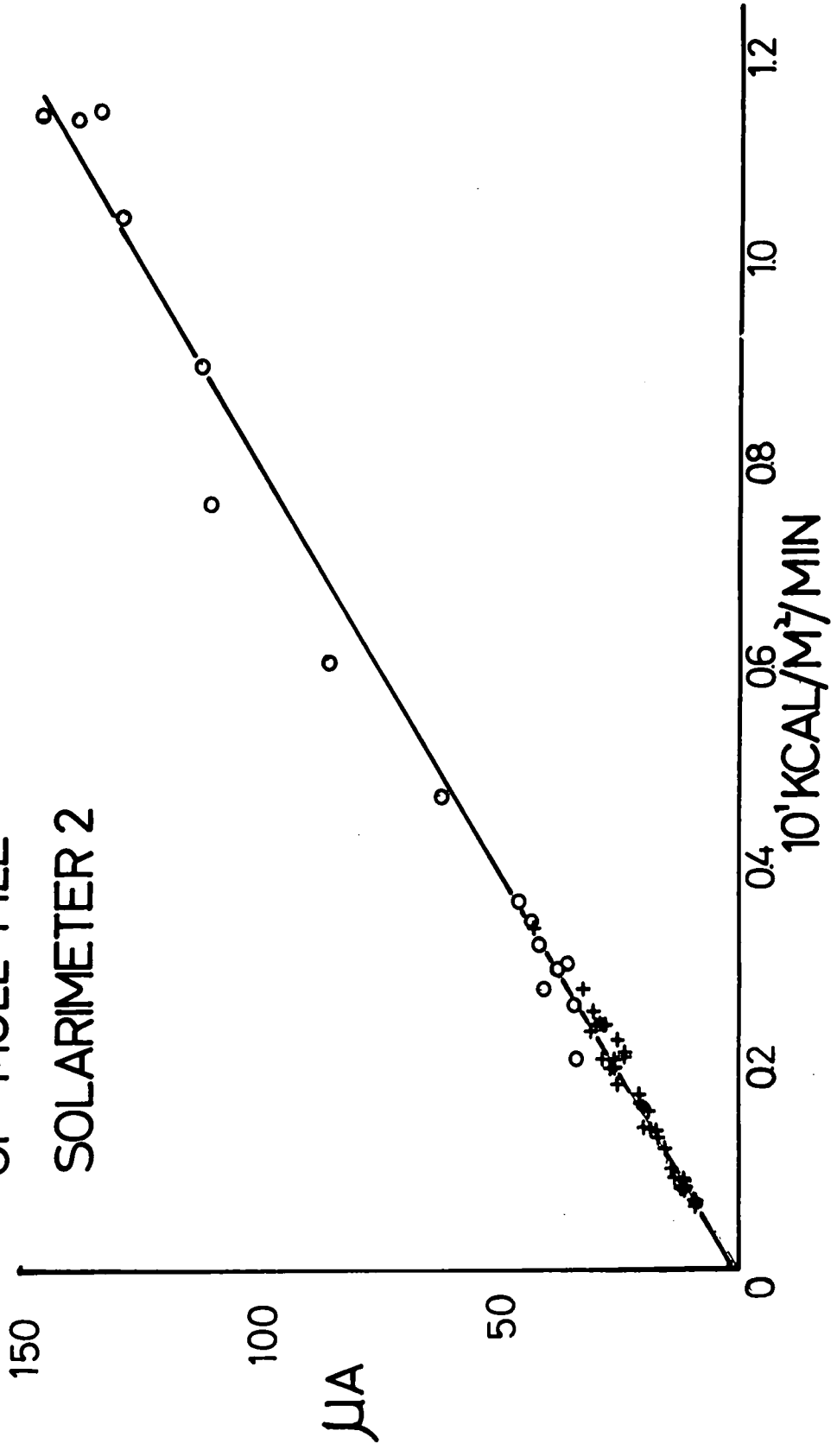
Figure 61.

Amplifier output (μA) against irradiance ($10'$ Kcal/m^2/min). Solarimeter 3.

AMPLIFIER OUTPUT VS. OUTPUT
OF MOLL PILE
SOLARIMETER 3
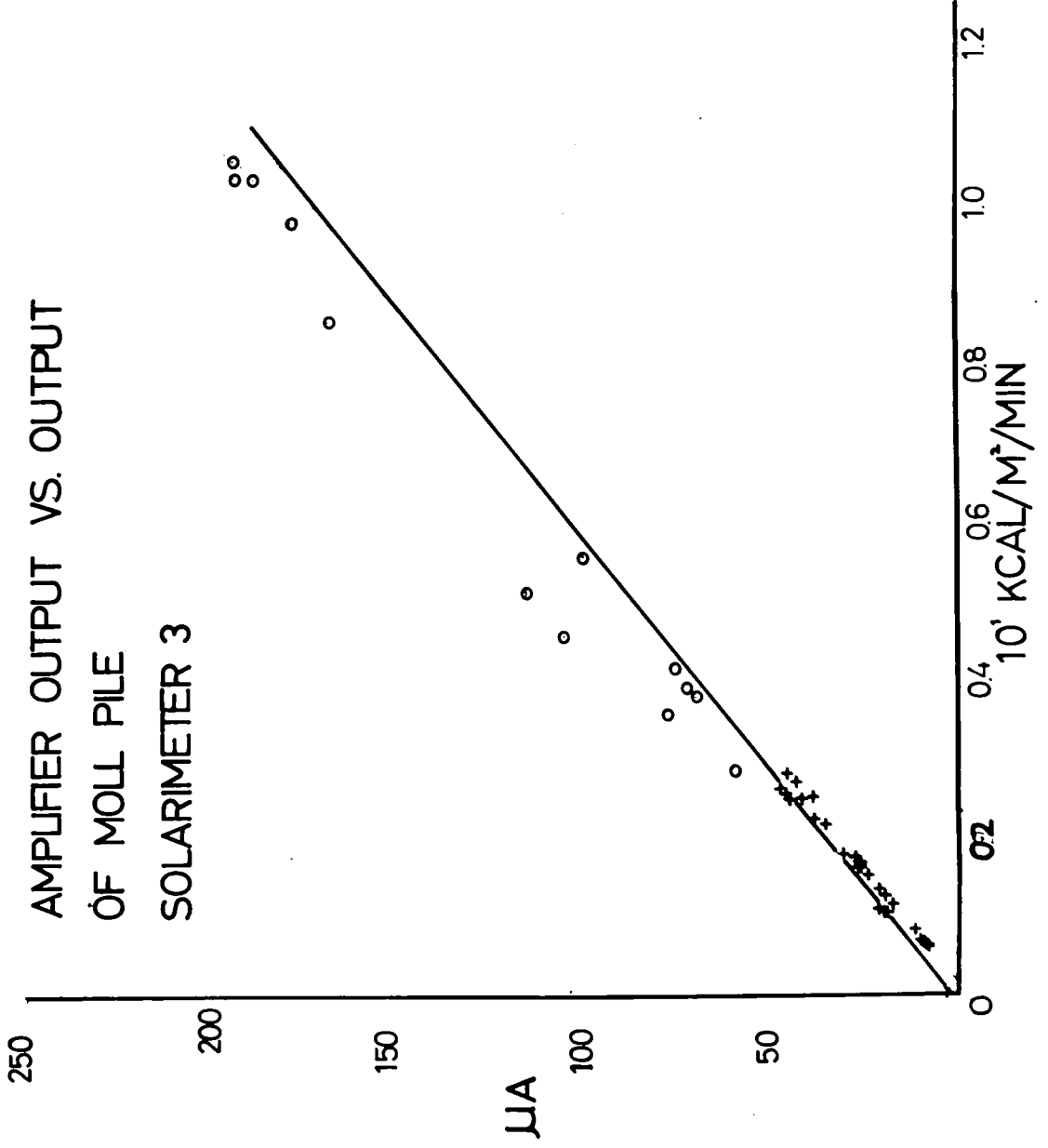
Figure 62.

Amplifier output (µA) against irradiance ($10'$ Kcal/m^2/min).
Solarimeter 4.

AMPLIFIER OUTPUT VS. OUTPUT
OF MOLL PILE
SOLARIMETER 4
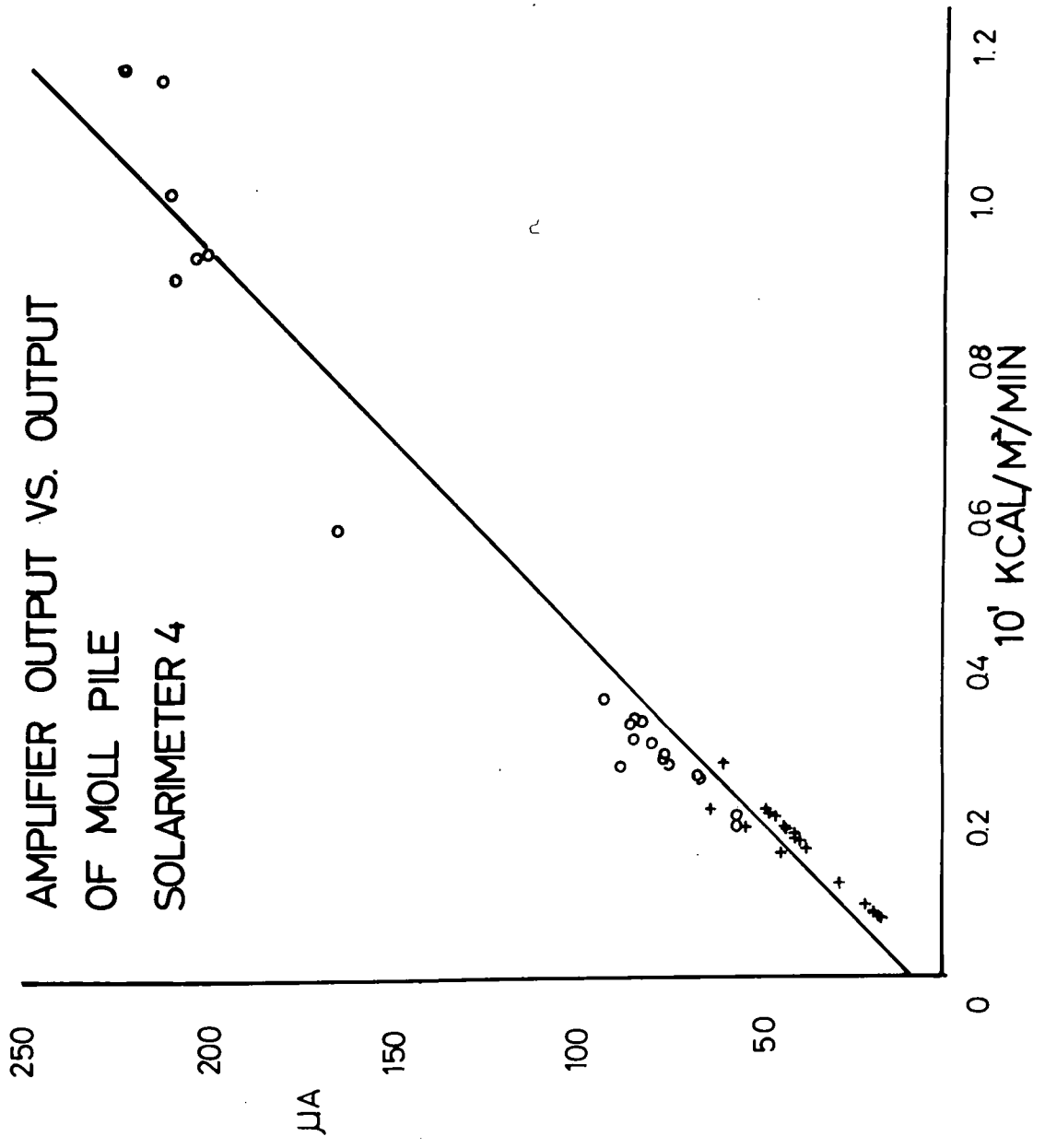
Coulometer calibration factors were as follows :-

$$1 = 419.8\mu A \text{ hrs } /m.m.$$

$$2 = 439.2\mu A \text{ hrs } /m.m.$$

$$3 = 426.1\mu A \text{ hrs } /m.m.$$

$$4 = 409.0\mu A \text{ hrs } /m.m.$$

X. v.   Field Use of the Solarimeter-Integrator Assemblies

The amplifier circuits were encased in a metal box, which also contained their power source and a quantity of silica gel. The power source was 9v cells that had been stabilized in the laboratory (Figs. 63a & b). The coulometer was mounted in a Perspex casing of identical length and width to a microscope slide. The connection with the amplifier was made through a pair of pin sockets. So that the output of the amplifier might be monitored without removing the coulometer, a jack-socket was inserted so that when it was in use the coulometer was removed from the circuit.

The box containing the circuit was enclosed in an air-tight polyethylene container. Around the metal box and coulometer was a 2.5cm thick layer of polystyrene foam. This was further wrapped in aluminium foil within the polyethylene container. Thus, in effect, the integrator was encased in a white box. A scaffolding tower (Fig.64) was erected in the Study Area (see Section II). Solarimeter 1 was exposed above the canopy on a vertical extension of this 13m above ground. Solarimeter 2 was initially exposed 10m above ground,

Figure 63.

The solarimeter-integrator assembly.
a. closed.
b. open.

solarimeter

mercron

circuit box

circuit board

mercron mount

battery points

S/C

OUT

IN

SHUNT   METER
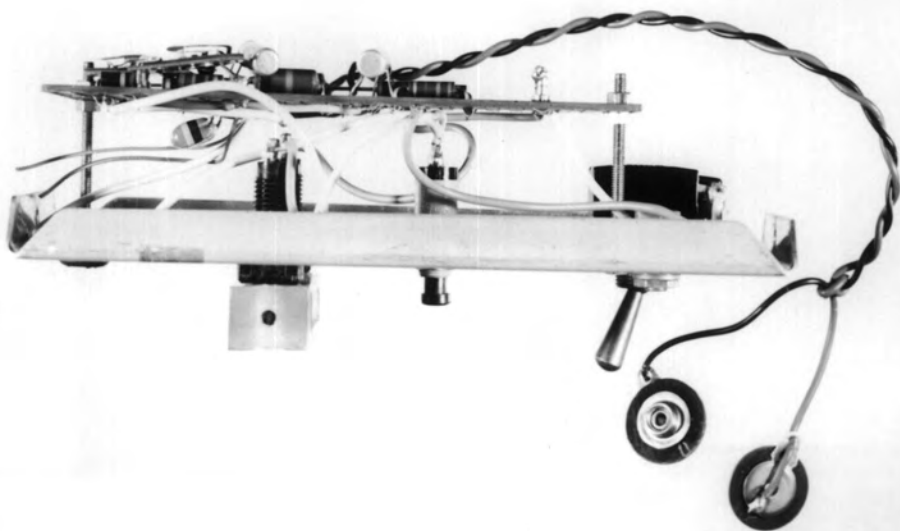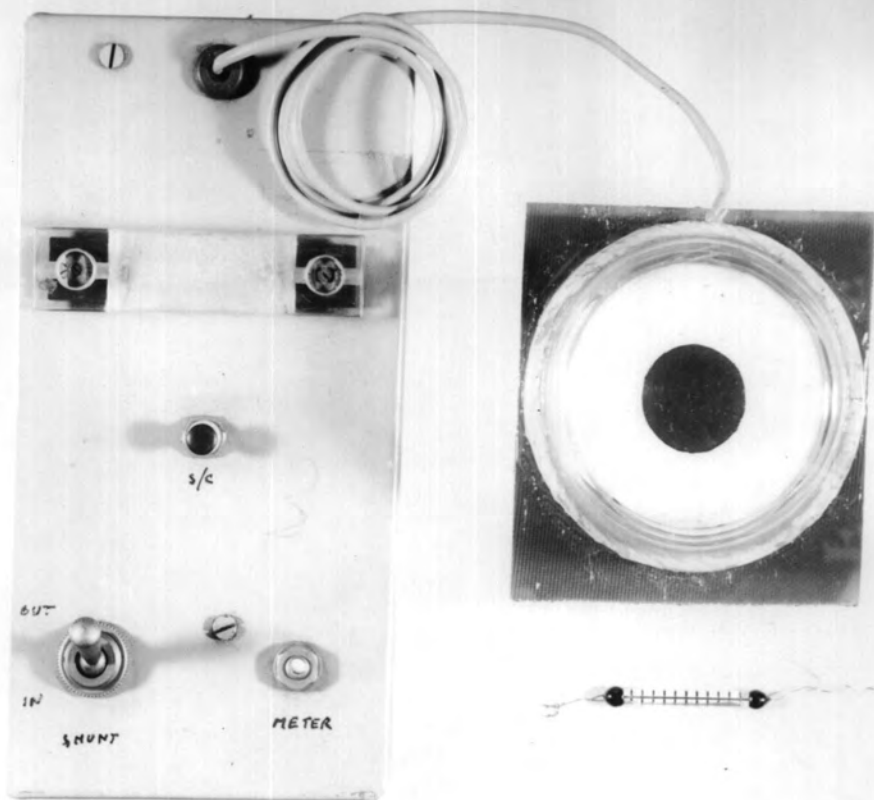
Figure 64.

The scaffolding tower (position shown in Fig.1).

The positions (1,2,3) of three solarimeters are shown.

DIAGRAM OF TOWER

⌊1M⌋

EAST ELEVATION   SOUTH ELEVATION
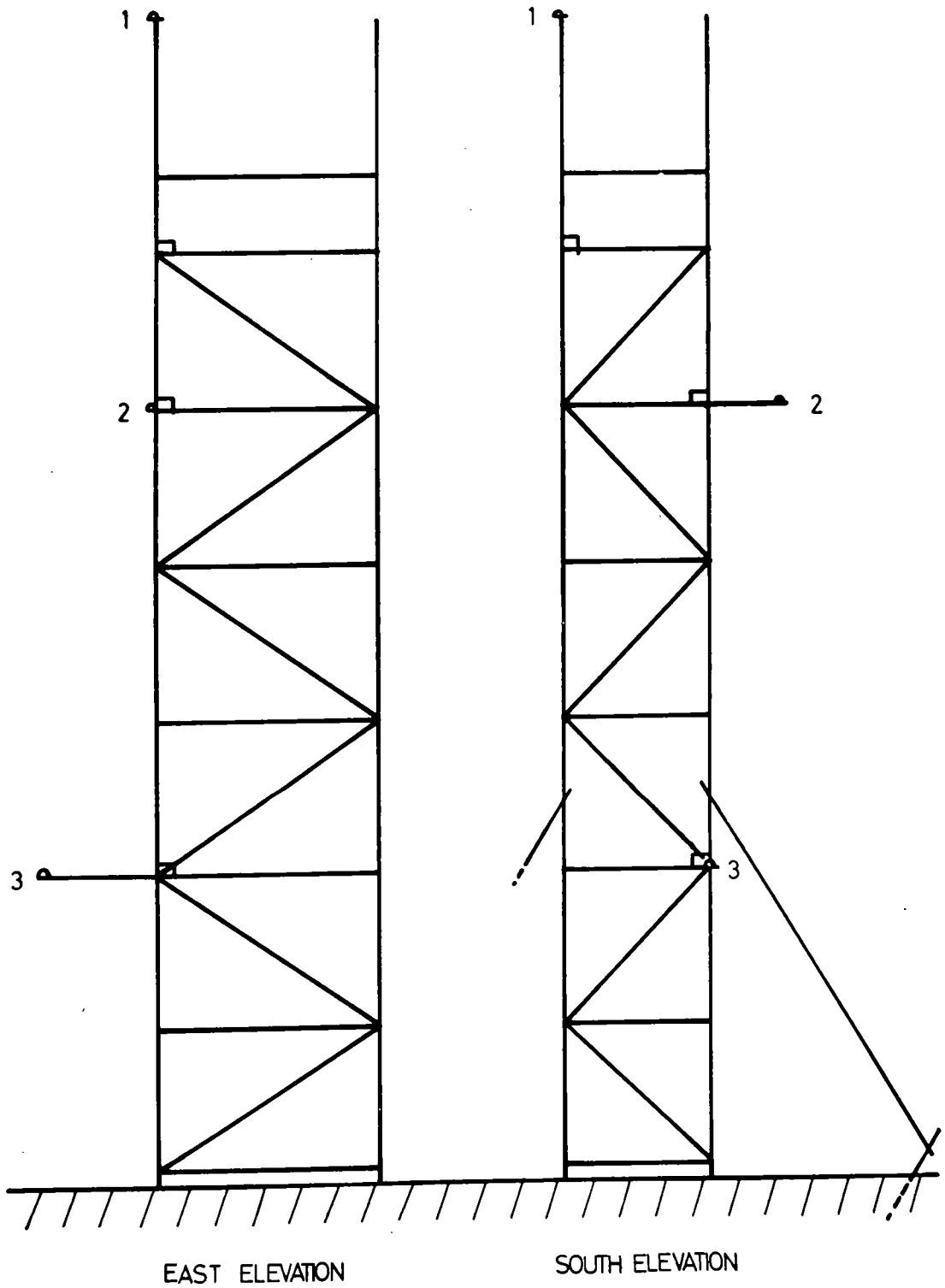
solarimeter 3 at 4m as in Fig.64. Solarimeter 4 was exposed at 30cms above ground some metres in from the tower.

The disposition of solarimeters below solarimeter 1 was clearly inadequate for a survey of short wave radiations at various levels bearing in mind the complexities of the woodland light climate (Evans 1939, 1956; Evans & Coombe 1957, 1965, 1966; Anderson 1964a,b,c, 1966a & b; etc.). However, in order to test the effectiveness of the solarimeter-integrator assemblies under a variety of field conditions they were placed as described. Although crude, this instrumentation yielded some useful information on energy input to the various woodland strata.

The procedure adopted was as follows. The assemblies were normally visited at weekly intervals. Each solarimeter was examined for alignment, misting over and obstructions. The coulometer was removed, the meniscus position determined and recorded, and then replaced. The current output of the assembly was checked, and the condition and output of the battery noted. Batteries were replaced at least every six weeks. In the event of any assembly being faulty, it was either immediately repaired or replaced by the spare. A substandard was kept against which each assembly was check-calibrated every three months.

X. vi. Results

Table LXII gives daily rates and periodic totals of short wave radiation as measured by each solarimeter from 1st May 1967 to

TABLE LXII

Daily + Periodic Totals of Short-wave Radiation (10 Kcal/m²)

DATE	DAYS	DAILY			PERIODIC		
		SOL 1	SOL 3	SOL 4	SOL 1	SOL 3	SOL 4
1/5 - 8/5	7	375	265	279	2625	1860	1950
8/5 - 15/5	7	215	137	172	1505	959	1204
15/5 - 22/5	7	560	105	348	3920	735	2436
22/5 - 29/5	7	570	75	242	3990	525	1694
29/5 - 5/6	7	667	350	203	4669	2450	1421
5/6 - 12/6	7	596	212	175	4172	1484	1225
12/6 - 19/6	7	571	211	113	3997	1477	791
19/6 - 26/6	7	369	133	74	2583	931	518
26/6 - 3/7	7	449	171	49	3143	1197	343
3/7 - 10/7	7	427	145	46	2989	1015	322
10/7 - 17/7	7	371	127	43	2597	889	301
17/7 - 24/7	7	396	142	27	2772	994	189
24/7 - 31/7	7	336	77	18	2352	539	126
31/7 - 7/8	7	347	116	15	2429	812	105
7/8 - 14/8	7	154	96	10	1078	672	70
14/8 - 21/8	7	84	40	8	588	280	56
21/8 - 28/8	7	168	67	15	1176	469	105
28/8 - 4/9	7	415	158	33	2905	1106	231
4/9 - 11/9	7	407	155	27	2849	1085	189
11/9 - 18/9	7	238	92	15	1666	644	105
18/9 - 25/9	7	205	80	13	1435	560	91
25/9 - 2/10	7	225	84	24	1575	588	168
2/10 - 9/10	7	207	87	71	1449	609	497
9/10 - 16/10	7	153	69	49	1071	483	343
16/10 - 23/10	7	163	85	61	1141	595	427
23/10 - 30/10	7	278	99	90	1946	693	630
30/10 - 6/11	7	179	81	88	1253	567	616
6/11 - 13/11	7	104	67	87	728	469	609
13/11 - 20/11	7	80	56	65	560	392	459
20/11 - 27/11	7	32	31	29	224	217	203
27/11 - 4/12	7	38	37	36	266	259	252
4/12 - 11/12	7	55	53	50	385	371	350
11/12 - 18/12	7	53	50	49	371	350	343
18/12 - 8/1	21	50	46	48	1050	966	1008
8/1 - 15/1	7	52	50	47	364	350	329
15/1 - 22/1	7	51	50	45	357	350	315
22/1 - 29/1	7	55	52	50	383	364	350
29/1 - 12/2	14	57	55	49	798	770	686
12/2 - 19/2	7	59	56	45	413	392	315
19/2 - 26/2	7	59	54	58	413	378	406
26/2 - 4/3	7	58	52	52	406	364	364
4/3 - 11/3	7	59	56	55	413	392	385
11/3 - 18/3	7	71	69	62	497	483	434
18/3 - 25/3	7	80	78	72	560	546	504

TABLE LXII (Contd.)

| | | DAILY | | | | PERIODIC | | |
DATE	DAYS	SOL 1	SOL 3	SOL 4	SOL 1	SOL 3	SOL 4
25/3 - 1/4	7	80	79	75	560	553	525
1/4 - 8/4	7	147	132	130	1029	924	910
8/4 - 22/4	14	280	274	275	3920	3836	3850
22/4 - 29/4	7	461	424	418	3227	2968	2926
29/4 - 1/5	3	350	322	320	1050	966	960

1st May 1968. These can be more readily seen in Figs. 65, 66 and 67.

Solarimeter 2 was damaged early in the season and no results were obtained. Table LXIII shows the annual totals for solarimeters 1, 3 and 4. The total for solarimeter 1 was more than twice that for solarimeter 3, just below the canopy, and 2.1/8th times that for solarimeter 4, near ground level. The seasonal march of radiation above the canopy was much as expected, but that beneath the canopy and near the ground was, as expected, quite different. For example, 48% of the short wave radiation received by solarimeter 4 came in April and May.

Figs. 68 & 69 show radiation received by solarimeters 3 and 4 as a percentage of that received by solarimeter 1. This is a measure of penetration which is a function of solar elevation, atmospheric conditions, canopy structure and depth, leaf inclination, reflectivity, transmissivity and so on. Although controlled by many complex factors, the seasonal pattern of penetration is fairly simple and shows a direct relationship to canopy development and leaf fall. In particular, the SW fraction penetrating to near the ground (solarimeter 4) decreased sharply during May and June as the Alder buds opened and the leaves grew. For part of July and most of August and September it was less than 10%. In October and November, as leaf fall progressed, the fraction penetrating rose again towards 100%. Throughout the winter and spring until the end of April it stayed just short of 100%. The simplicity of this pattern can be accounted for by the Alder Zone's nearly closed

<u>TABLE LXIII</u>   <u>Annual Totals of Short-Wave Radiation</u> (Kcal/m^2)

Solarimeter	Position	Total
1	15m above ground - above canopy	818,490
3	4m above ground - just below canopy	408,450
4	30cms above ground - at top of ground vegetation	339,120

Figure 65.

Weekly totals (10^4 Kcals/m^2) of short-wave radiation at
solarimeter 1 (above tree canopy).

WEEKLY TOTALS OF SHORT-WAVE
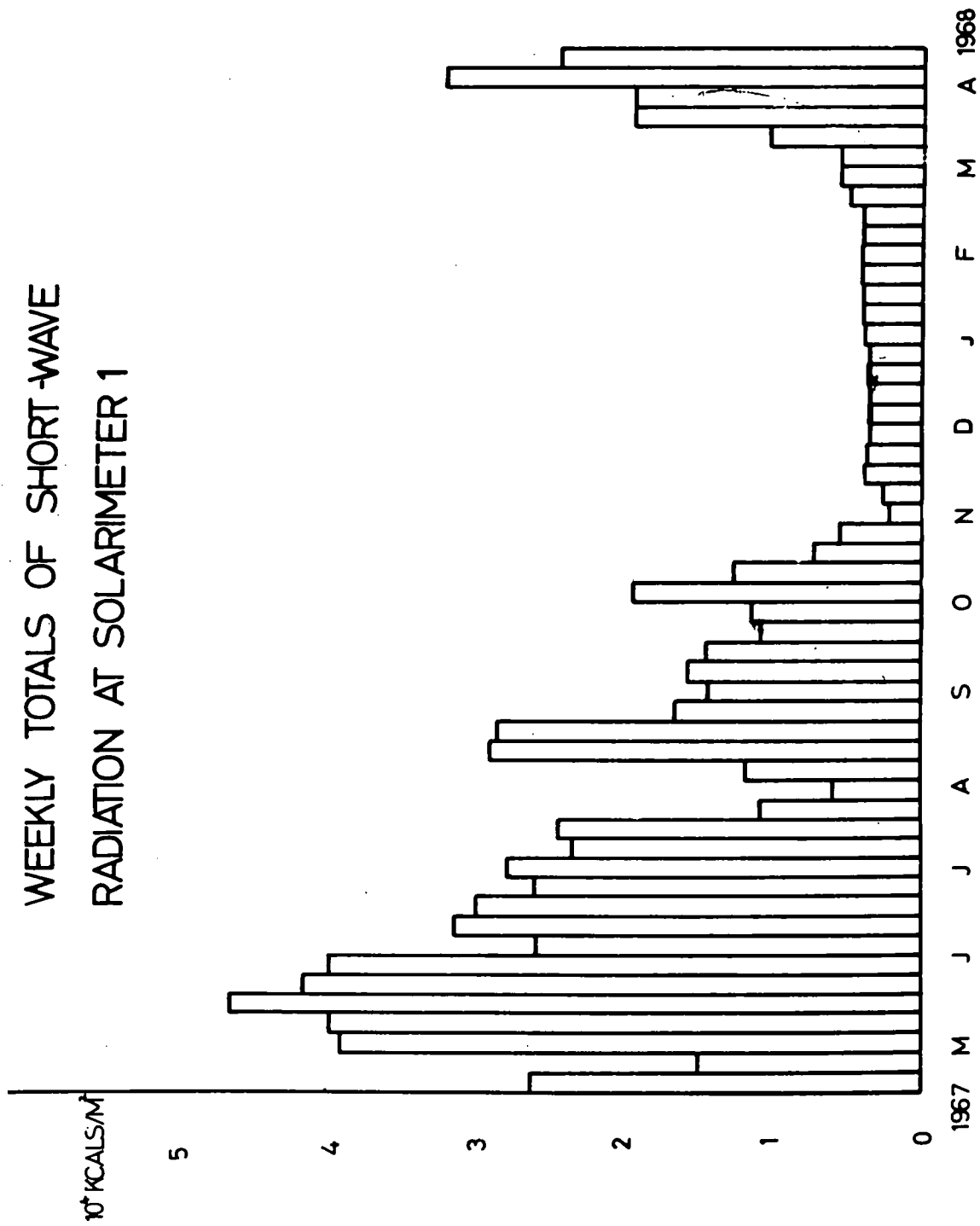RADIATION AT SOLARIMETER 1

Figure 66.

Weekly totals (10^4 Kcals/m^2) of short-wave radiation at solarimeter 3 (just below canopy).

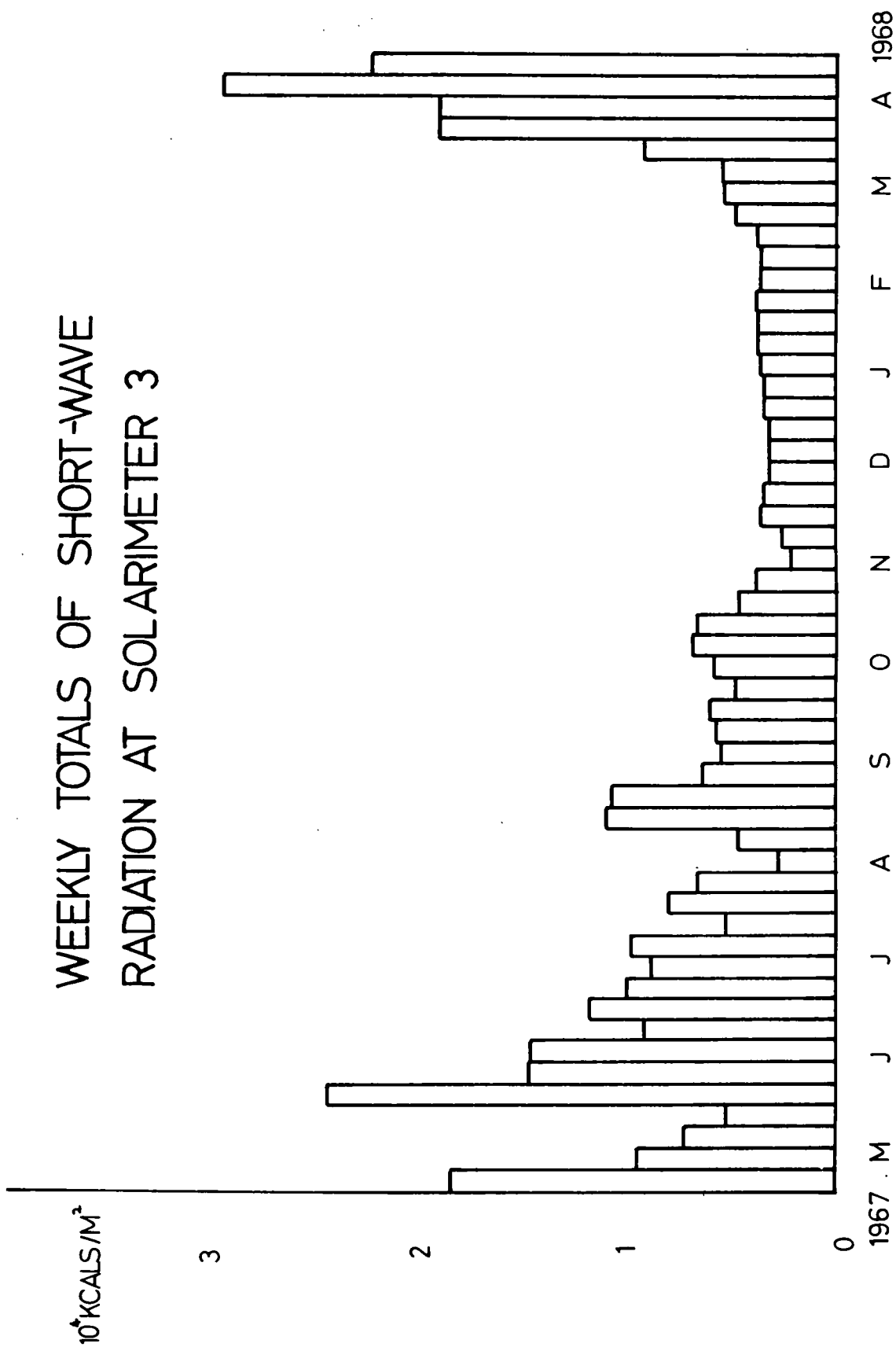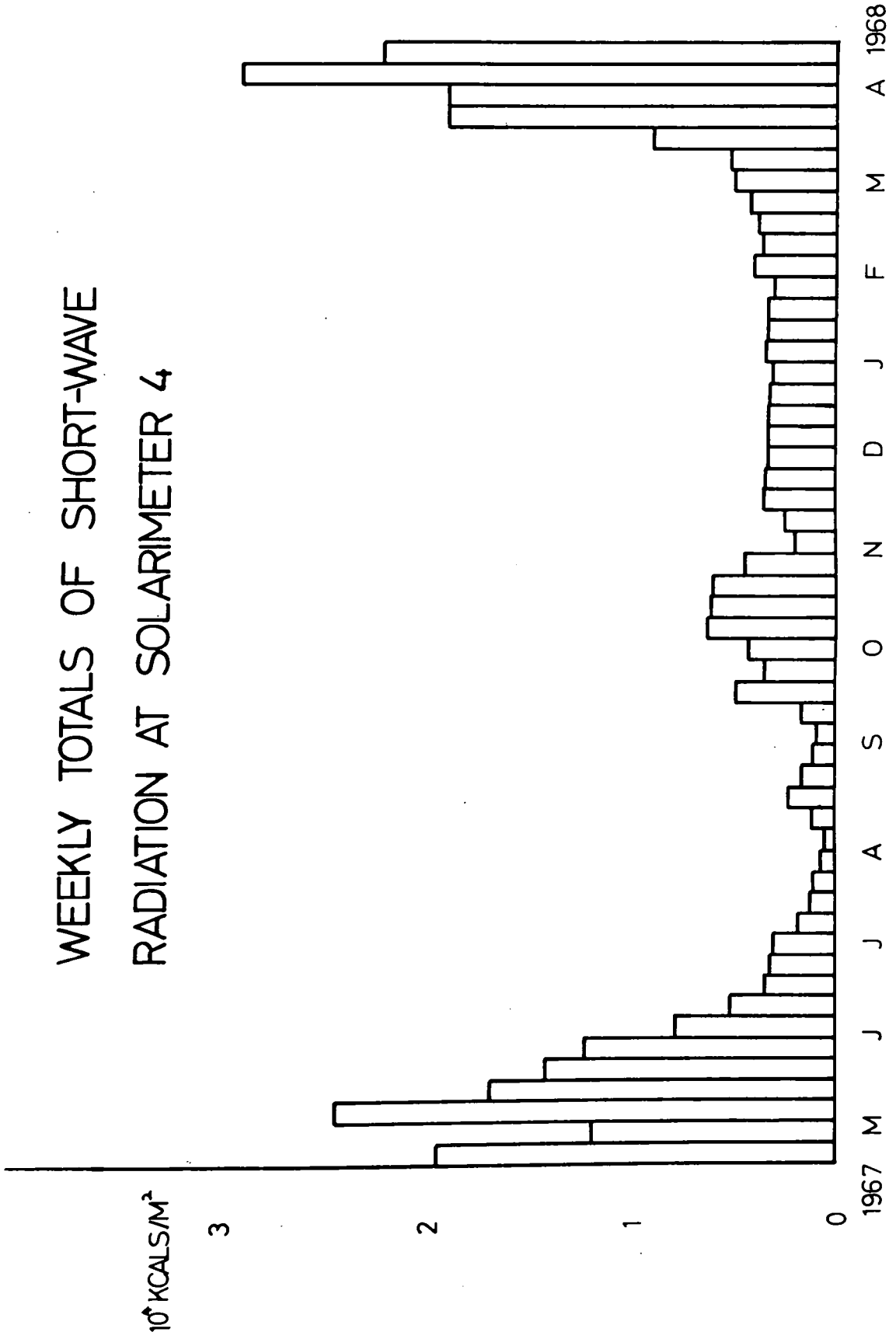WEEKLY TOTALS OF SHORT-WAVE
RADIATION AT SOLARIMETER 3

Figure 67.

Weekly totals (10^4 Kcals/m^2) of short-wave radiation at solarimeter 4 (just above ground).

WEEKLY TOTALS OF SHORT-WAVE
RADIATION AT SOLARIMETER 4

canopy, its opaque leaves, their large area and horizontal inclination. It is reasonable to expect that a more complex pattern would be found in the Birch Zone.

The seasonal pattern of penetration is less marked just under the canopy (Sol.3). In May, less radiation was reaching this solarimeter than solarimeter 4. This was probably due to its being directly obscured by a leafy twig for part of this month. For most of the summer, 30-40% of the short wave radiation penetrated to this solarimeter. Some higher values were recorded in August. These coincided with periods of very low short wave radiation above the canopy. The fraction penetrating to this level began to increase in October at the time of leaf-fall. Through the winter and spring it was very similar to that reaching solarimeter 4.

If the values obtained for solarimeters 1 and 4 are in any sense representative of the vegetation strata above which they are placed, it may be of interest to calculate the totals of short wave radiation reaching them in certain growth seasons. If, for the tree stratum, the growth season is taken as 1st May to 30th September, the total short wave radiation incident at solarimeter 1 was 560,562Kcal/m^2. If the ground vegetation growth season is taken as 1st April to 16th October, total SW radiation incident on solarimeter 4 was 230,126Kcal/m^2. Of this latter, 200,081Kcal/m^2 came in the months of April, May and June.

Figure 68.

Radiation at solarimeter 3 (just below canopy) as a % of
that at solarimeter 1 (above canopy).

% PENETRATION OF SHORT-WAVE RADIATION TO SOLARIMETER 3
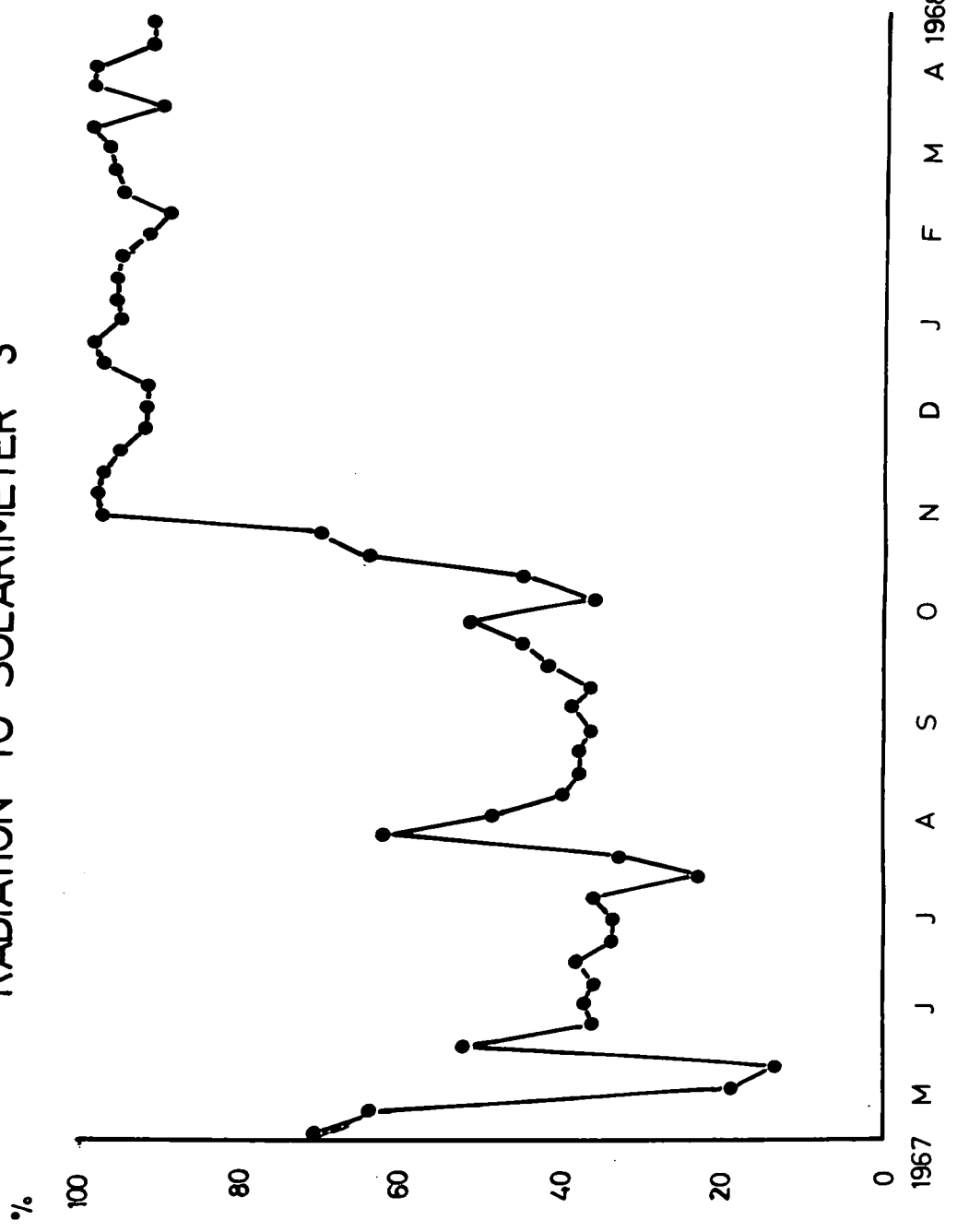
Figure 69.

Radiation at solarimeter 4 (just above ground) as a % of
that at solarimeter 1 (above tree canopy).

% PENETRATION OF SHORT-WAVE
RADIATION TO SOLARIMETER 4
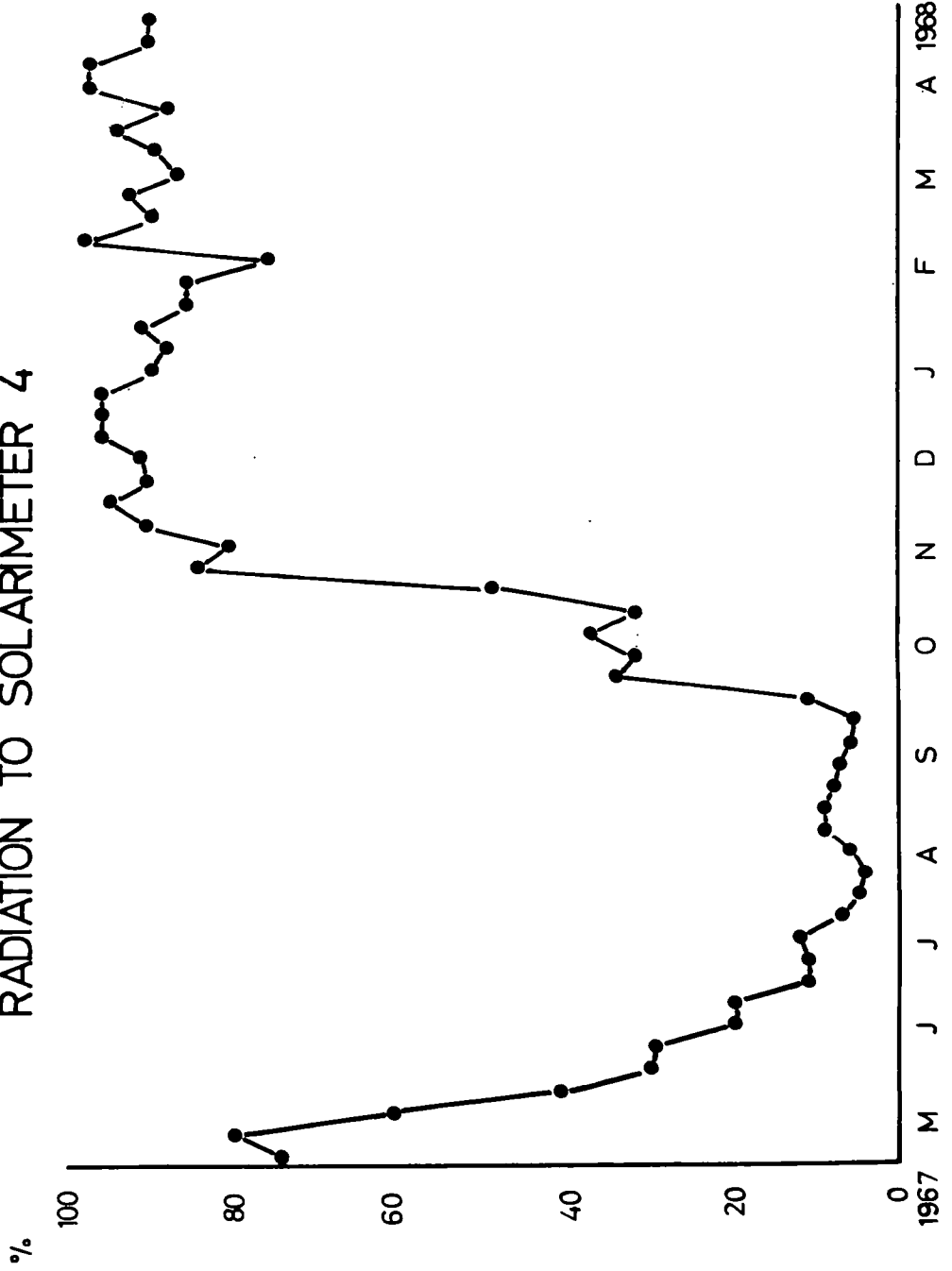
X. vii. Discussion

Ovington (1961), Blackman & Black (1959) and Penman (1948) calculated annual totals of short-wave (Rc) from Angot's calculated values of radiation received through a perfectly transparent atmosphere (Ra). They used an equation of the form :-

$$Rc/Ra = a + b\, {}^n/N$$

where ${}^n/N$ is the ratio actual/possible hours of sunshine, and a and b are constants.

Day (1961) has calculated values of a and b for various stations in the British Isles where both SW radiation and sunshine records are kept. Using a = 0.14 and b = 0.68, with the sunshine records from Durham University Observatory, the annual total of short wave radiation at Durham (from 1st May 1967 to 1st May 1968) was calculated as 847,900Kcal/m^2, and approximated the figure obtained at Wynyard by direct measurement -818,490Kcal/m^2.

Addition to Section X.

This calculation supports the direct measurement for total short wave radiation above the canopy. There is less reason to take the estimates at lower levels as representative for those levels. One small sensor is hardly an adequate sampling of woodland light climate. Nevertheless, the results obtained are consistent with changes in tree leaf area index and changes in total insolation above the canopy (compare Fig.69 with Fig.30). This concurrence may have

been partly fortuitious. The data for lower levels must be viewed with considerable caution.

The data do justify the conclusion that during the earlier part of the ground vegetation's growth season, i.e. April - May, levels of incident radiation were not very different from those in the open and there is little reason to suppose that its spectral composition differed markedly, either. Of the growth season total of $230,126 Kcal/m^2$, $87,050 Kcal/m^2$ or 26% was received in April and May.

Section XI.   Energy Flow and Accumulation

XI. i. <u>Ecosystem biomass and biocontent</u>

Tables LXIV and LXV are summaries of ecosystem biomass and biocontent data respectively.   Unfortunately it is necessary for comparative purposes to give biomass data because many authors have not given biocontent data.   The biomass and biocontent columns in these two tables give extreme ranges of biomass or biocontent each year for the components listed.   The net change columns were calculated from April to April.   All dead material has been included in the litter category.

Total ecosystem plant biomass or biocontent (without roots) in 1966-7 was close to $18,500g/m^2$ or $86,000Kcal/m^2$.   Of this approximately 55% was included in the living matter.   For most of the year the vast bulk of the living matter was made up of tree branches and boles.   Of the total ecosystem biocontent (without roots) almost 54% was stored as wood and approximately 42% as litter and soil organic matter.

Although ecosystem biomass and biocontent were a little higher in 1967-8, the pattern of their distribution was very similar.

Comparable figures for total ecosystem biocontent (without roots) are difficult to find, but figures for above-ground biomass are more easily available.   Table LXVI gives some of these, all for allegedly natural systems or the unmanaged products of secondary

Biomass + Biomass changes (g/m^2)

TABLE LXIV

	1966-7		1967-8	
	Biomass	Net Change	Biomass	Net Change
Trees Branch + Bole Wood	9856.2- 10291.1	+ 434.9	10291.1- 10727.3	+ 436.2
Canopy leaves	0 - 168.1	-	0 - 142.9	-
Other	0 - 70.4	-	0 - 94.9	-
Ground Vegetation	16.0 - 137.7	+ 7.9	16.5 - 106.3	- 11.8
Bryophytes	9.9 - 49.4	- 1.6	3.8 - 18.1	- 8.4
Total Living matter (AG)	9882.1- 10716.7	+ 441.2	10311.4- 11089.5	+ 416.0
Litter	401.5- 795.6	- 385.6	461.9- 471.2	+ 42.6
Soil Organic Matter	7761.2	?	7761.2	?
Ecosystem Total	18044.8- 19273.5	+ 56.0 (+)	18534.5- 19324.9	+ 458.6

TABLE LXV

Biocontent and Biocontent Changes (Kcal/m^2)

	1966-7		1967-8	
	Biocontent	Net Change	Biocontent	Net Change
Trees Wood	46,922.6 - 49,016.1	+ 2093.5	49016.1 - 51102.9	+ 2086.8
Canopy leaves	0 - 828.1	-	0 - 732.2	-
Other (new parts)	0 - 507.6	-	0 - 552.5	-
Ground Vegetation	82.7 - 581.3	+ 30.8	68.5 - 445.6	- 42.2
Bryophytes	34.8 - 173.3	- 5.5	13.2 - 63.4	- 29.5
Total Living material	47,040.1 - 51,106.4	+ 2118.8	49,097.8 - 52,896.6	-
Litter	1,847.6 - 3,516.9	- 1666.3	1,617.2 - 2,652.3	+ 196.2
Soil Organic Matter	34,925.3	?	34,925.3	?
Ecosystem Total (without roots)	83,813.0 - 89,548.6	+ 452.5	85,640.3 - 90,474.2	+ 2211.3

TABLE LXVI   Living above ground biomass of various ecosystems
(g/m^2)

Plant Community	Stage	Biomass	Author
Tall grass prairie	-	3 - 100	Ovington et al (1963)
Old - Field	Broomsedge	circa 300	Golley (1965)
Savannah		3400	Ovington et al (1963)
Oak - Pine Forest	-	6561	Whittaker & Woodwell (1969)
Birch Wood	Young	7590	Smirnova & Gorodentseva (1958)
Birch Wood	Young	7640	Ovington & Madgwick (1959)
Populus davidiana	Middle stage	12880	Satoo et al (1956)
Oakwood	Middle	16500	Ovington et al (1963)
Birchwood	Mature	18490	Smirnova & Gorodentseva (1958)
Birchwood	Mature	19350	Ovington & Madgwick (1959)
Birchwood	Mature	22270	Smirnova & Gorodentseva (1958)
Oakwood	Mature	27500	(Mina (1955) & Remezov et al (1959))
Cove forest	Mature	50065	Whittaker & Woodwell (1969)

successions. There is a clear increase in biomass (of living matter) from a few hundred grams/m^2 for grassland to tens of thousands for older woodlands. The grassland figures are not strictly comparable with those for woodland, because their major above ground storage may well be as standing dead (Golley 1965; Ovington et al 1963). Moreover, their below ground parts are probably of greater importance as storage organs (Dahlman 1968; Kucera & Dahlman 1967) than is the case for woodlands (Whittaker & Woodwell 1969). It is clear that the above ground living biomass on the Study Area (circa 10,000g/m^2) lies in the range observed for other comparable woodlands.

Organic matter accumulated in the litter and upper horizons of the soil almost doubles the ecosystem biomass when added to the living material. This is hardly surprising in an ecosystem which has been woodland for over 100 years and before that was probably a wet grassland with a large accumulation of soil organic matter.

The low value for total ecosystem biomass net change in 1966-7 was the result of the high accumulation of litter in spring 1966. It is reasonable to assume that this was an unusual state of affairs and that the annual net change in biomass or biocontent for the ecosystem is close to that for tree branches and boles. If so, the figure will be around +460g/m^2 or +2,200Kcal/m^2.

XII. <u>Net Primary Production, Heterotroph Respiration and Net Ecosystem Production</u>

Tables LXVII and LXVIII summarise Net Primary Production, Decomposition and Litter Production data for the Alder-Birch woodland at Wynyard in biomass and biocontent terms respectively.

TABLE LXVII   Net primary production $(g/m^2/yr)$

		1966-7	1967-8
Trees	Wood	434.9	436.2
	Litter	273.5	282.7
	Total	708.4	718.9
Ground Vegetation		277.9	280.2
Bryophytes		39.5	14.3
Total Net Primary Production		1025.8	1013.4
Litter production		545.7	574.6
Decomposition		918.7	512.3

TABLE LXVIII   Net Primary Production ($Kcal/m^2/yr$)

			1966-7	1967-8
Trees	Wood		2093.5	2086.8
	Litter fall		1479.9	1440.1
	Herbivory (minimum)		23.6	23.6
		Total	3598.0	3550.5
Ground Vegetation			1016.2	1142.4
Bryophytes			138.5	50.2
Total Net Primary Production			4752.7	4743.1
Litter Production			2465.3	2624.6
Decomposition			4134.6	2428.4

The data for ground vegetation were given in Section IX,
for the tree stratum in Section VI and for decomposition in
Section VIII. Net primary production of bryophytes was calculated
as the maximum increment of bryophyte material for the year in question.
In both years NPP was close to $1kg/m^2$ or $4750Kcal/m^2$. This is to the
lower end of the range for above ground net production for woodlands,
which is overlapped by the range for grassland (Table LXIX). If
the assumptions outlined in Section VIII are valid, decomposition or
decomposition plus respiration by herbivores equals Rs_H. Therefore

$$\text{Net Ecosystem Production} = NPP - Rs_H = 4752.7 - 4142.6$$
$$= 610.1 Kcal/m^2$$
$$\text{or } 107.1 g/m^2 \text{ in } \underline{1966\text{-}7}$$
$$\text{and} \qquad 4743.1 - 2436.4$$
$$= 2306.7 Kcal/m^2$$
$$\text{or } 501.1 g/m^2 \text{ in } \underline{1967\text{-}8}$$

both on an above ground basis.

For reasons given above, the 1967-8 figures are considered
more representative of this development stage of this woodland.

Net Ecosystem Production as a percentage of Net Primary
Production (biocontent) was 12.8% in 1966-7 and 48.9% in 1967-8.
That is, under normal conditions this woodland was storing almost
half its yearly net above ground primary production. For purposes
of comparison figures of biomass net primary production and decomposition
are more readily available. Table LXIX summarises some of the available

data. Where authors have not specifically measured decomposition,
litter production has been taken as a measure of this so long as it
seemed reasonable to assume no net annual accumulation of litter or
soil organic matter. Decomposition as a percentage of net primary
production is an indicator of whether or not accumulation of dry
matter is taking place. Thus the ratio tends to 100% when the
ecosystem is at a stable stage. The series runs from a **Sphagnum**
hummock, where decomposition is negligible, through old-fields (where
it tends to 100% as age increases) to tall-grass praire where
decomposition is almost 100% of net primary production. These are
f ollowed by a group of three woodlands (the Brookhaven Forest,
Meathop Wood and Wynyard) where decomposition is around half of
net primary production. Meathop and Wynyard have been managed by
coppicing - a practice which removes the above ground parts of trees
whilst leaving much of the root system intact. Brookhaven is a fire
forest and fire is thought to have had a similar effect here to
coppicing.

Thus each of these three woodlands had a root system older
than the above ground parts and probably much better developed than if
it had been the same age as the above ground parts. Thus it is possible
that the ratio decomposition/NPP calculated on an above ground basis for
these ecosystems might wrongly estimate the importance of decomposition.
The data from Brookhaven, which are for the whole ecosystem, suggest
that this need not be the case. Thus these three ecosystems, all the

TABLE LXIX

Net Primary Production and Decomposition ($g/m^2/annum$)

Plant Community	Location	Net Primary Production A/G	Net Primary Production Total	Decomposition A/G	Decomposition Total	Decomposition as a % of Net Primary Production A/G	Decomposition as a % of Net Primary Production Total
1. Sphagnum fuscum hummock	Westmorland, England	269	-	0	-	0	-
2. Old field (broomsedge)	S. Carolina, U.S.A.	493	650	296	?	60.0	?
3. Old field (grass-forb) Upland (a)	Michigan, U.S.A.	320	463	297	440	92.8	95.0
Swale (b)	U.S.A.	1064	1422	874	1232	82.1	86.6
4. Tall grass Prairie	Missouri, U.S.A.	500	950	500	950	100	100
5. Oak-Pine Forest	Long Island, U.S.A.	859	1195	?	571	?	47.8
6. Alder-Birch Wood	Wynyard, England	1013	?	512	?	50.5	?
7. Mixed deciduous wood	Meathop, England	8613	?	5122	?	59.5	?
8. Beech forest	Poland	1017	?	307	?	30.2	?
9. Beech forest	Denmark	990	1130	370	390	37.4	34.5
10. Oak forest	U.S.S.R.	-	900	-	650	-	72.2
11. Deciduous cove forest	Tennessee, U.S.A.	1911	?	1911	?	100	?
12. Tulip Tree forest	"	2408	?	2408	?	100	?
13. Rain Forest	Thailand	-	2444	-	2322	-	85.5

A/G – above ground

Authors

1. Bellamy & Rieley 1967
2. Golley 1965
3. Wiegert & Evans 1964
4. Dahlman 1968, Kučera & Dahlman 1967
5. Whittaker & Woodwell 1969
6. This work
7. Pers. comm. – data as Kcal/m²/annum

8. Medwecka – Kornas 1967
9. Möller, Müller & Nielsen 1954
10. Mina (1955)
11. Whittaker 1966
12. Whittaker 1966
13. Kira, Ogawa, Yeda & Ogira 1967

subject of recent events of catastrophic scale, are now going through a period of very rapid energy accumulation. The Beech forests in Poland and Denmark (8 & 9) have been managed for the same purpose. The older forests of the U.S.S.R. and U.S.A. have presumably reached or closely approached the size where energy storage is maximal and if the rate of energy dissipation is to increase, a breakdown of the existing storage will be necessary.

It is clear from the work at the Savanna River Project (Odum 1960; Golley 1965; Golley & Gentry 1967) that a state of low or no net accumulation of energy does not necessarily imply that the maximal rate of energy storage for the site has been reached, but rather that a further increase awaits the completion of changes in the biotic and physical environment being effected by the currently existing biota. Alternatively, catastrophe (e.g. fire), or management, or indirect human effects, may prevent the further development of the ecosystem. In marginal environments a combination of these factors and the availability of ecologically variable species may hold up ecosystem development (Bellamy et al 1969).

XIII. The Utilisation of Insolation

All the trophic energy of the ecosystem is derived from fixation by autotrophic organisms. Therefore a consideration of photosynthetic efficiencies is of relevance to a study of ecosystem energetics. Table LXX summarises the data obtained.

TABLE LXX   The utilization of insolation

Net Photosynthetic Efficiency		1966-7	1967-8

$$\frac{NPP \times 100}{Insolation} \%$$

	NPP	Insolation	1966-7	1967-8
1.	Total A/G	Annual total above canopy	0.58	0.58
2.	Tree A/G	" " " "	0.44	0.43
3.	Tree A/G	Total non-transmitted	0.56	0.56
4.	GV + Bryophytes A/G	Total transmitted	0.34	0.35
5.	Tree A/G	Total above canopy in growing season	0.64	0.64
6.	GV + Bryophytes A/G	Total below canopy in growing season	0.51	0.52
7.	Tree A/G	Growing season PAR (43% of total)	1.02	1.01
8.	GV + Bryophytes A/G	Growing season PAR (25% of transmitted)	2.04	2.08
9.	Ecosystem net accumulation	Annual total above canopy	0.06	0.27
10.	Decomposition	" " " "	0.50	0.29

GV   =   ground vegetation

A/G =   above ground

PAR =   photosynthetically active radiation

The most relevant and generally comparable efficiency for the whole ecosystem is Net Photosynthetic Efficiency as total above ground Net Primary Production over total shortwave radiation incident on the top of the canopy in one year (1). The value of 0.58% obtained does not differ greatly from those of 0.65% for pine plantation (Minderman 1967), 0.26% for a small oak wood (Bray 1962) and 1.3% for pine (Ovington 1962). The data for pine included root production. Similarly, Wassink (1948) reported a range of 0.23 - 1.10% for well-cultivated field crops in the temperate zone. The Wynyard value is markedly higher than the 0.16 - 0.20% reported by Golley (1965) for the old-field stage.

The most remarkable fact about all these systems is the extremely small fraction of incident energy that they are able to fix. It should be pointed out that they do utilize rather more but in this case we are concerned with net rather than gross primary production.

An examination of other net photosynthetic efficiencies is informative. Of the total of 0.58% of the total annual insolation that made up net above ground primary production, 0.43% may be attributed to the tree stratum and 0.15% to the ground vegetation and bryophytes. The tree stratum fixed 0.56% of the energy that did not reach the ground vegetation (3), whereas the ground vegetation and bryophytes fixed 0.35% of that reaching a level 30cms above ground (4). In their respective growing seasons (cf. Section IX) the tree and

lower strata fixed 0.64% and 0.52% respectively of the energy available to them (5 and 6). This narrowing of the efficiency gap between the two strata is largely a result of the lower stratum's longer growth season.

It is difficult to make meaningful comparisons between the NPEs of vegetation strata unless allowance is made for the differing spectral composition of energy incident at differing levels. If the total short wave energy contains 43% Photosynthetically Active Radiation (Szeicz 1966) and it is assumed that the energy reaching the ground vegetation contains 25% PAR in the growth season, NPEs for the growth seasons of the trees and lower strata were 1.01 and 2.08 respectively. Whilst no data are available to support the assumption about the quality of light below the canopy, it seems a reasonable assumption to make if the tree canopy intercepts around 70 - 80% of the PAR at that level. If these assumptions are at all reliable, it is clear that the ground vegetation was very much more efficient as an energy-fixing system than the tree stratum. If this is the case it might be explained in terms of nutrient availability and perhaps carbon dioxide levels near the Forest Floor as well as in terms of high climate. However, before any such conclusions may be drawn, investigations of incident PAR at the ground vegetation must be made along with measurements of the nutrient and CO_2 parameters. Only then will suitable experiments be designed to examine the basis, if any, of differing NPEs for different vegetation strata.

In order to place trophic energetics in the perspective of radiation energetics it should be pointed out that the net annual above ground accumulation of energy by the alder/birch woodland was only 0.27% of total insolation, and the total above ground decomposition 0.29% of total short wave insolation.

X. iv. Ecosystem Energy Flow and Accumulation

For the purposes of energetics analysis the alder/birch wood ecosystem at Wynyard will be considered to have comprised the following components :-

1. Photosynthetic Machinery

    (a) Tree Canopy

    (b) Ground Vegetation

    (c) Bryophytes

2. Living Energy Stores

    (a) Tree Boles and Branches

    (b) Tree roots

    (c) Ground Vegetation Roots

3. Dead Energy Stores

    (a) Litter layer

    (b) Soil Organic Matter

4. Consumers

    (a) Consumers in the Herbivore component

    (b) Consumers in the Decomposer component

Figure 70.

Ecosystem components and transfers. Components are as
listed on page 168. Suitable data were not obtained for
the transfers and components shown as broken lines.
Certain transfers (eg.1a to 2a, 1a to 2b, 1b to 2c) may
be two-directional.

ECOSYSTEM COMPONENTS AND TRANSFERS
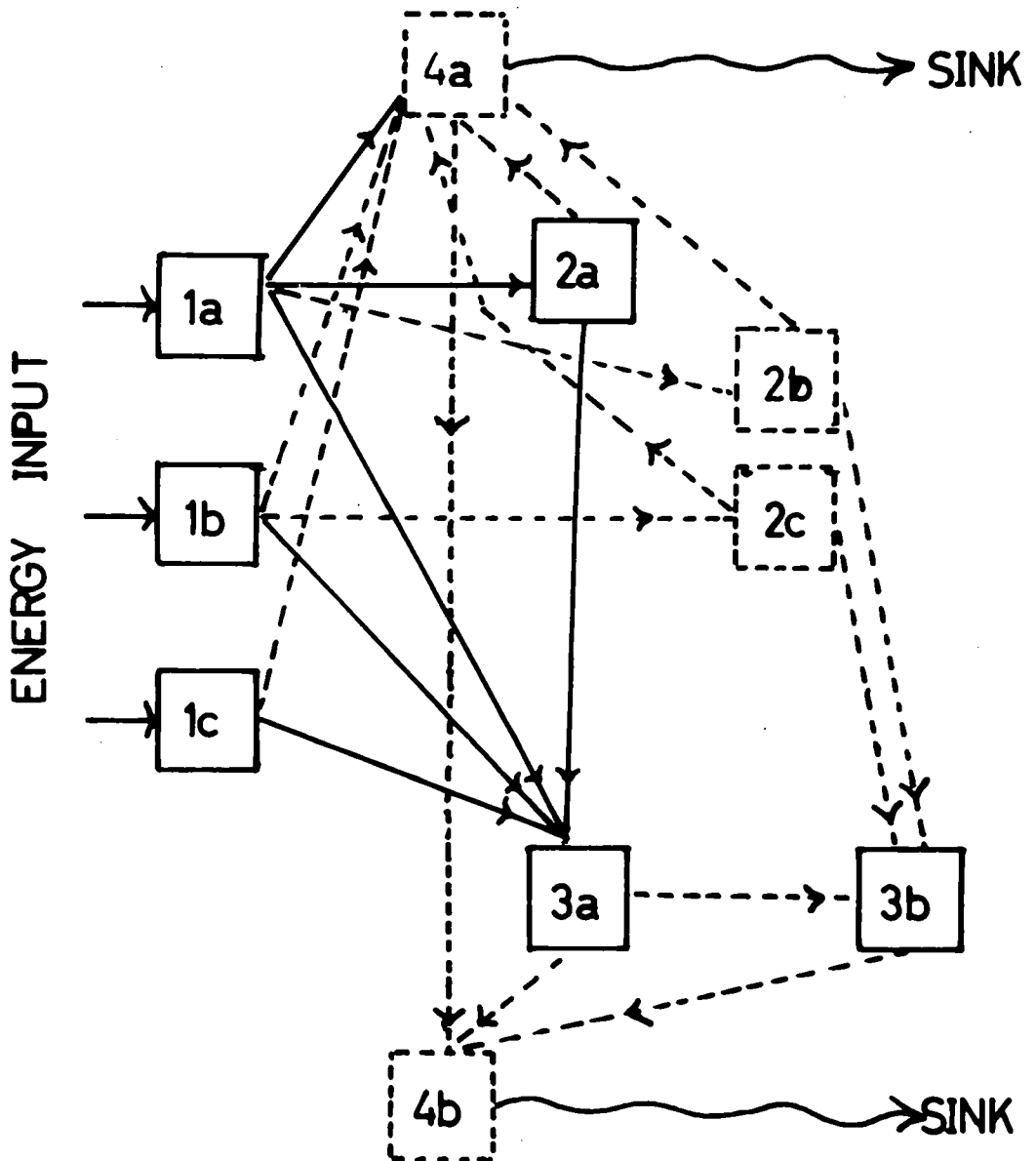(OR THE PARTITION OF NPP)

Fig.70 is a block diagram showing these components and the main possible directions of transfer between them. The model represented by this block diagram is concerned only with net primary production and dissipation by consumers. It assumes that the only input to tree roots is directly from the canopy.

It is clear that the major gap in this study (as in many others) was the lack of data for biomass net production and mortality of below ground parts of the vegetation. Without this data transfer functions for the photosynthetic machinery (output/input) can only be minimal estimates (see photosynthetic efficiencies, this section). Similarly, for the relationship between decomposer respiration and plant death (i.e. the transfer function for the dead energy stores). It would be possible to construct a complete energy-flow model if certain assumptions commonly found in the ecological literature were made; for example, that the relationship between net primary production and biomass below ground is the same as that above ground, or that biomass below ground approximates to a fixed fraction (e.g. 20%) of above ground biomass. Even if these assumptions are in some cases correct, it is less likely that this is the case for coppiced or fire woodlands. Although the data available are not complete for the alder/birch woodland, it seems better to present them as they are than to detract from what validity they may have by erecting a superstructure of dubious assumptions on them. Thus it can be said that the net photosynthetic efficiencies given in this Section are underestimates (without doubt) and that a transfer function for the dead energy store

derived merely from litter disappearance and fall may not be reliable.

What is possible with the data available for the alder/birch woodland is a characterisation of the predominantly above ground components in ecosystem energy flow and accumulation. In Table LXXI Net Primary Production, net biocontent accumulation overwinter biocontent and summer biocontent (peaks) are given for the measured components as a percentage of the total above ground (living biocontent and litter layer). The last column represents maximum residence time for the component concerned. For photosynthetic components this corresponds to the time from commencement of growth to litter fall; similarly, for the living energy stores. For tree boles and branches this must correspond to the longevity of that part of the species concerned on the Study Area. For the dead energy stores, maximum residence time was taken as 98% breakdown time according to the exponential model (cf. Section VIII). In the case of consumer organisms, maximum residence time must correspond to longevity of the species concerned.

An examination of Table LXXI supports the division of the alder/birch woodland into the components chosen. Basically three sub-systems may be discerned. Firstly, the photosynthetic machinery, comprising only a small fraction of the biocontent. However, the whole ecosystem energy flow passes through this and energy rich compounds rarely reside in it longer than a year, usually for much less.

TABLE LXXI

Ecosystem Parameters

Component	as % of total above ground				Maximum residence (yrs)
	NPP	Net accumulation	Overwinter storage	Summer Biocontent	
1. Photosynthetic Machinery	100.0	-	- 0.1	2.3	Circa 1
(a) Tree Canopy	74.8	-	-	1.4	0.6
(b) Ground Vegetation	24.1	-	0.1	0.8	- 1
(c) Bryophytes	1.1	?	0	0.1	?
2. Living Energy Stores					
(a) Tree boles & branches	-	94.6	94.8	92.7	50 - 100
3. Dead Energy Stores					
(a) Litter layer	-	5.4	5.1	3.7	5
(b) Soil Organic Matter	-	? -0	68.0	66.0	74
4. Consumers					
(a) Herbivore	-	-	- 0	- 0	days - 1 - ?
(b) Decomposer	-	-	- 0	- 0	mins - 7 - ?

Secondly, there are the energy stores. The vast bulk of the measured biocontent is in these, and apart from the small fraction represented by the litter layer, the maximum residence time for this subsystem is of the order of several decades. All incorporated energy passes through these stores, but annual input and output represents only a small fraction of them so that only particularly violent changes in the operation of other components will change their state.

Thirdly, the whole consumer component may be seen as having a common role; that is, the release of stored materials for recycling at the cost of a very rapid dissipation of stored energy. Both herbivores and decomposers operate in this way for energy stored as invertebrate tissue, for example, may be considered more available to decomposers than that stored as woody tissue. The biocontent of the consumers may be negligible, but a major proportion of the net primary production of the ecosystem passes through them (more than half on an above ground basis for the alder/birch wood). Generally speaking, the maximum residence time for fixed energy in consumer organisms is of the order of hours (microflora) days and months rather than years.

It is possible to argue that the ecosystem will tend to store as much of its fixed energy as possible in the least assailable form. Hence it will store in the form which will bring with it least increase in heterotroph respiration as well as least

autotroph maintenance respiration.   Whilst grassland may have a large and persistent energy-store in the soil (Kucera 1968 etc.) woodland has in addition to this the woody materials.   The large and persistent lignaceous component of the woody parts of trees may hold fixed energy for 50-100 years, and it may well be a further 70-80 years after death and fall before this energy is all dissipated by decomposers.

The present study would have been enhanced in value considerably if the following data had been collected :-

(1)   Chemical composition (e.g. hemicelluloses, celluloses, lignins)of newly produced material.

(2)   Chemical composition of live and dead storage materials.

(3)   The energy content of each type of material, according to chemical composition, and

(4)   The rate of decomposition of the various chemical constituents.

Were these data available for this and other systems, it might be possible to further the critical examination of various theories of ecosystem energetics.   Clearly any analysis of energy flow and accumulation should include knowledge of the nature (chemical) of transfer agents and storage forms, in addition to their taxonomic and morphological identities.

X.   .v.   Conclusion

In this thesis data for net annual above-ground primary production, litter fall and decomposition, energy accumulation and

insolation have been presented for an alder-birch woodland at Wynyard, Co. Durham. These data have been compared with those available from other studies throughout this thesis. In particular, a basic framework of ecosystem energetics is presented (cf. Tables LXV, LXVIII, LXX and LXXII, this section). Such a study would need to have been wider, more intensive and longer if it were to test adequately any ecological theory. However, it has added to the small pool of relevant data available.

This study has also made basic data available to workers investigating other aspects of the alder/birch woodland at Wynyard, particularly litter-dwelling invertebrates.

The fact remains that few complete ecosystem energetics studies have been carried out to date. A number are now in progress under the auspices of the International Biological Programme and it is to be hoped that they will avoid the pitfalls into which their predecessors have fallen. The most striking lesson the author has learnt in this study has been that a vast, perhaps inappropriate, amount of time and effort is required to produce relatively few data. Moreover, these data, whilst illuminating, are neither as precise nor as reliable as one might hope. These shortcomings, which have been discussed at length in almost every section of this thesis, and by many others, notably Trazcyk (1968), are characteristic of the dry-matter production and accumulation approach to the measurement of energy flow in ecosystems.

Whether or not this approach can be improved, or the difficulties it presents circumvented by new methods is difficult to see. As the technology of gas exchange measurement advances (Eckhardt 1968; Woodwell & Dykeman 1966), the dry matter approach may become obsolete. Even so, the major problem of investigating below ground processes remains. Furthermore, it is increasingly clear that if causal relationships between soil components of the ecosystem are to be established, the functions of each group of organisms must be investigated separately, and soil metabolism partitioned in detail.

Whilst these approaches may yield more and better data than the dry-matter production approach, they will necessarily involve a rapidly increasing expenditure of money and labour. Therefore it is of prime importance that their theoretical objectives be clearly stated and well based. Rather than study the so-called 'regional climax' or most 'productive' ecosystems, it would be most valuable to apply these approaches to ecosystems at various times after major stresses have been applied. In this way predictive models of ecosystem function may be built so as to guide future manipulation on scientific lines.

Despite their shortcomings, studies such as this one, based on the dry-matter production approach to ecosystem energetics, do provide a firm basis for general statements above ecosystems, when considered together. They may also provide basic descriptive data necessary to more advanced investigations of ecosystem function. Finally, in their own right, they have brought the ecologist to look

very closely and carefully at the ecosystem and to consider what

and how it is.

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APPENDIX II

The programme MEANWTS

(a) Programme print-out enclosed.

(b) Punch-card input was thus:-

First card

Month	Zone	Plotsize	Setno	Catno
(1-30)	(Alder or Birch)	(2 or 6)	(11 or 13)	(up to 18)

where Month = date of sample

Zone = Alder or birch zone

Plotsize = Quadrat size

Setno = Number of sample units taken in that zone

Catno = Number of categories of material harvested.

Subsequent cards

Weights were typed in to the nearest
10 mg thus:- 0.12   0.35   0.72   etc.

For the sake of clarity a new card was started for each category.

DATA FOR THE HARVESTED TREES

ALDER

Age (years)	D(t) (cms)	D(t-5) (uncorrected) (cms)	D(t-5) (corrected) (cms)	Fresh wts (Kg)			Dry Weights (Kg)		
				Bole	Branches	Whole shoot	Bole	Branches	Whole shoot
6	1.75	-	-	-	1.01	1.01	-	0.45	0.45
14	4.27	-	-	7.40	1.01	8.41	3.30	0.45	3.75
14	5.65	3.75	4.04	6.80	0.90	7.70	3.03	0.61	3.64
20	6.90	5.25	5.65	19.00	+	19.00	9.10	+	9.10
23	9.45	7.35	7.92	28.30	9.10	37.40	14.60	6.10	20.70
29	10.95	9.15	9.85	51.20	10.20	61.40	29.50	6.80	36.30
33	11.85	9.65	10.39	62.50	4.70	67.20	33.90	3.20	37.10
49	14.45	12.25	13.19	60.30	29.90	90.20	32.20	20.00	52.30
62	17.05	14.70	15.83	138.30	23.10	161.10	79.60	15.20	94.80
64	21.10	17.20	18.52	271.70	52.20	323.90	162.30	34.40	196.70
75	26.45	23.15	24.92	311.20	64.40	375.60	164.50	42.50	207.00
79	29.35	26.00	27.99	424.00	153.00	577.00	213.00	96.40	309.14

APPENDIX I (cont.)

BIRCH

Age (years)	D(t) (cms)	D(t-5) (Uncorrected) (cms)	D(t-5) (corrected) (cms)	Fresh wts (Kg)			Dry Weights (Kg)		
				Bole	Branches	Whole shoot	Bole	Branches	Whole shoot
8	2.73	1.30	1.46	1.93	0.85	2.78	1.48	0.68	2.16
9	2.95	—	—	2.84	1.47	4.31	2.30	1.18	3.48
15	4.87	—	—	9.33	3.04	12.37	7.58	2.43	10.01
23	5.75	4.50	4.82	13.04	8.84	21.88	10.60	7.07	17.67
24	8.00	6.65	7.05	26.76	9.52	36.28	21.74	7.61	29.35
28	6.65	5.25	5.59	24.15	5.44	29.59	19.62	4.35	23.97
29	15.35	13.70	14.45	100.24	34.47	134.47	81.45	27.55	109.00
31	11.45	—	—	42.10	18.27	60.37	34.21	14.60	48.81
34	10.80	9.60	10.12	51.82	15.76	67.58	42.11	12.60	54.71
37	10.55	9.05	9.55	52.16	15.65	67.81	42.38	12.51	54.89
47	20.00	17.15	18.01	223.62	82.10	305.72	181.69	65.61	247.31
49	18.50	16.30	17.16	190.06	99.11	289.17	154.42	79.21	233.63
50	26.30	22.65	23.75	335.21	141.07	476.28	272.35	112.74	385.09

Key   D(t) outside diameter (dbh) at time of sampling.

D(t-5) (uncorrected) inside diameter 5 years before sampling.

D(t-5) (corrected) outside diameter 5 years before sampling.

MEANWTS   PROC OPTIONS (MAIN)

```
          38            IF MEAN(A,B) = 0 THEN
          39               PUT EDIT (B, 'THIS CATEGORY IS ABSENT.')
                              (SKIP(2), F(4), COLUMN(25), A)
          40            ELSE
          40               PUT EDIT (B, MEAN(A,B), VAR(A,B), SEM(A,B))
                              (SKIP(2), F(4), COLUMN(27), F(9,2), COLUMN(60),
                               F(9,2), COLUMN(94), F(9,2))
          41            END
          42         FREE X
          43         END
          44         PUT PAGE EDIT('COMBINED PLCTS, LCADEC MEANS ETC.',
                         'TOTAL MEAN', 'TOTAL STANCARD ERRCR')
                         (SKIP(3), A, SKIP(3), COLUMN(30), A, COLUMN(55), A)
                      DO B = 1 TO CATNO
          45            A = 1
          46            IF MEAN(A,B) = 0 THEN
          47               DO
          48                  PUT EDIT (B, 'ONE OR BOTH SAMPLES LACK ANY VALUES',
          49                     'THEREFORE THIS CATEGORY IS IGNORED.')
                                 (SKIP(2), F(4), COLUMN(25), A, X(1), A)
                              GOTO FIN
                           END
          50            ELSE
          51               DO
          52                  MARK1 = MEAN(A,B)
          52                  MARK2 = VAR(A,B)
          53                  MARK3 = CHEK(A)
          54                  A = 2
          55                  IF MEAN(A,B) = 0 THEN
          56                     DO
          57                        PUT EDIT (B, 'CNE CR BOTH SAMPLES LACK ANY VALUES',
          58                           'THEREFORE THIS CATEGORY IS IGNORED.')
          59                           (SKIP(2), F(4), COLUMN(25), A, X(1), A)
                                    GO TO FIN
                                 END
          60            ELSE
          61               DO
          62                  SIGMEAN(B) = ((MARK1 * 0.49) + (MEAN(A,B)
          62                     * 0.51))
          63                  SIGMERR(B) = SQRT((((0.49 ** 2) * VAR(A,B)) / CHEK(A)))
                                 + (((0.51 ** 2) * VAR(A,B)) / CHEK(A)))
                                 * (((0.51 ** 2) * VAR(A,B)) / MARK3)
          64                  PUT EDIT (B, SIGMEAN(B), SIGMERR(B))(SKIP(2), F(4),
                                 COLUMN(25), F(9,4), COLUMN(60), F(9,4))
          65               END
          66            END
          67         FIN  END
          68         FREE MEAN, SEM, VAR, SIGMEAN, SIGMERR, SUBAR
          69         GO TO S
          70         END
          71
```

```
       MEANWTS   PROC OPTIONS (MAIN)
       /* PROGRAMME TC CALCULATE MEANS AND STANCARD ERRCRS CF SAMPLES
       FRCM DIFFERENT ZONES AND CIFFERENT AREA MAGNITUCES*/
  1    DECLARE (MCNTH, PLCTSIZE, SETNC, CATNC, B, A, C, D)FIXEC BIN,
       ZONE CHAR(5),
  2    (CHECK , MARK1, MARK2, MARK3, CHEK(2)) FLCAT,
       (MEAN(2,CATNC), SEM(2,CATNC), VAR(2,CATNO), SIGMEAN(CATNC),
       SIGMERR(CATNC), SUBAR(SETNC), X(CATNC,SETNC))FLCAT CCNTRCLLED
  3  S DC A = 1 TO 2
       /* ITERATES THIS BLCCK TWICE*/
  4    GET LIST (MCNTH)
  5    GET EDIT ( ZONE, PLCTSIZE, SETNC, CATNC)
       (A(5), X(1), F(1), X(1), F(2), X(1), F(2))
  6    PUT PAGE EDIT (A, MONTH, ZCNE, 'PLCT SIZE = ', PLCTSIZE,
       'NO OF SETS = ', SETNC, 'NO OF CATEGCRIES = ', CATNC,
       'MEAN', 'VARIANCE', 'STANDARC ERRCR')
       (SKIP(2), COLUMN(25), F(2), COLUMN(50), A(5),
       SKIP(2), A, COLUMN(25),
       F(4), SKIP(2), A, CCLUMN(25), F(4), SKIP(2), A,
       COLUMN(25), F(4), SKIP(3), COLUMN(30), A, CCLUMN(60), A,
       CCLUMN(90), A)
  7    CHEK(A) = SETNC
  8    ALLCCATE X
  9    IF A = 1 THEN ALLCCATE MEAN, SEM, VAR, SIGMEAN,
       SIGMERR, SUBAR
 11    GET LIST (X)
 12    DO B = 1 TO CATNC
 13    SUBAR = X(B,*)
 14    CHECK = SUM(SUBAR)
       /*CHECK ALLOWS A CHECK TO BE MADE CN THE CONTENTS CF
       THE ARRAY IN QUESTICN.*/
 15    IF CHECK = O THEN
 16    DO
 17      MEAN(A,B) = O
 18      SEM(A,B) = O
 19      VAR(A,B) = O
 20    END
 21    ELSE
 22    DO
 23      MEAN(A,B) = CHECK / SETNC
         VAR(A,B) = (SUM((SUBAR - MEAN(A,B)) **2))
         /(SETNC - 1)
         SEM(A,B) = SGRT(VAR(A,B) / SETNC)
 24    END
 25    IF PLCTSIZE = 2 & MEAN(A,B) = O THEN
 26    DO
 27      MEAN(A,B) = MEAN(A,B) * 32
 28      VAR(A,B) = VAR(A,B) * 1024
 29      SEM(A,B) = SEM(A,B) ** 32
 30    END
 31    ELSE
 32    IF PLCTSIZE = 6 & MEAN(A,B) = O THEN
 33    DO
 34      MEAN(A,B) = MEAN(A,B) * 1C.4
 35      VAR(A,B) = VAR(A,B) * 1C8.1
 36      SEM(A,B) = SEM(A,B) * 1C.4
 37    END
```