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AMOUNT AND DISTRIBUTION OF DRY MATTER IN A MATURE BEECH/PODOCARP COMMUNITY

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The total plant dry matter in a mature beech/podocarp community was estimated at 703 t/ha. The principal species and their above-ground dry matter (d.m.) content (in t/ha) were: **Nothofagus truncata** (145), **N. fusca** (36), **Podocarpus ferrugineus** (25), and **Weinmannia racemosa** (63); d.m. was distributed among the major components as follows: stem wood (201), stem bark (23), branch wood (50), branch bark (19), dead branches (6.5), and foliage (5.7). Dead standing trees contributed a further 22 t/ha. Together, these above-ground components comprise 47% of the forest d.m. content. The forest floor detrital matter was estimated at 226 t/ha and, when roots were included, 373 t/ha or 53% of the forest d.m. content. Commercial logging extracted 27% of the dry matter as utilisable logs; and of the residual 73%, 36% comprised material already dead and in various stages of decomposition.

Regression analysis was used for the trees and shrubs, and unit area harvesting methods for the remaining forest components.

INTRODUCTION

Information on the amount of dry matter and its disposition among the forest components is essential for developing models of forest structure and function, both in the natural and perturbed state. Worldwide, mature natural forests are declining at an alarming rate (Myers 1979). New Zealand is fortunate in still having relatively extensive areas of unmodified forest suitable for providing the requisite dry matter data for natural forest communities.

Beech/podocarp forests are currently being investigated to provide information on the influence of logging methods and subsequent management practices on the soil and nutrient reserves of sites potentially suitable for forest production and utilisation (Pearse *et al.* 1976; Neary *et al.* 1978). Estimates of the dry matter content were required for six experimental catchments (Fig. 1) to which various management practices would later be applied. The dry matter content of an additional catchment, designated 7, was also desired. This latter catchment was set up to test the adequacy of the weirs and sediment traps in the experimental catchments to be logged.

The primary objective of this study was to provide estimates of the amount of dry matter and its distribution among the components and species in a mature beech/podocarp forest at Tawhai State Forest, Maimai, Nelson Conservancy. Preliminary results

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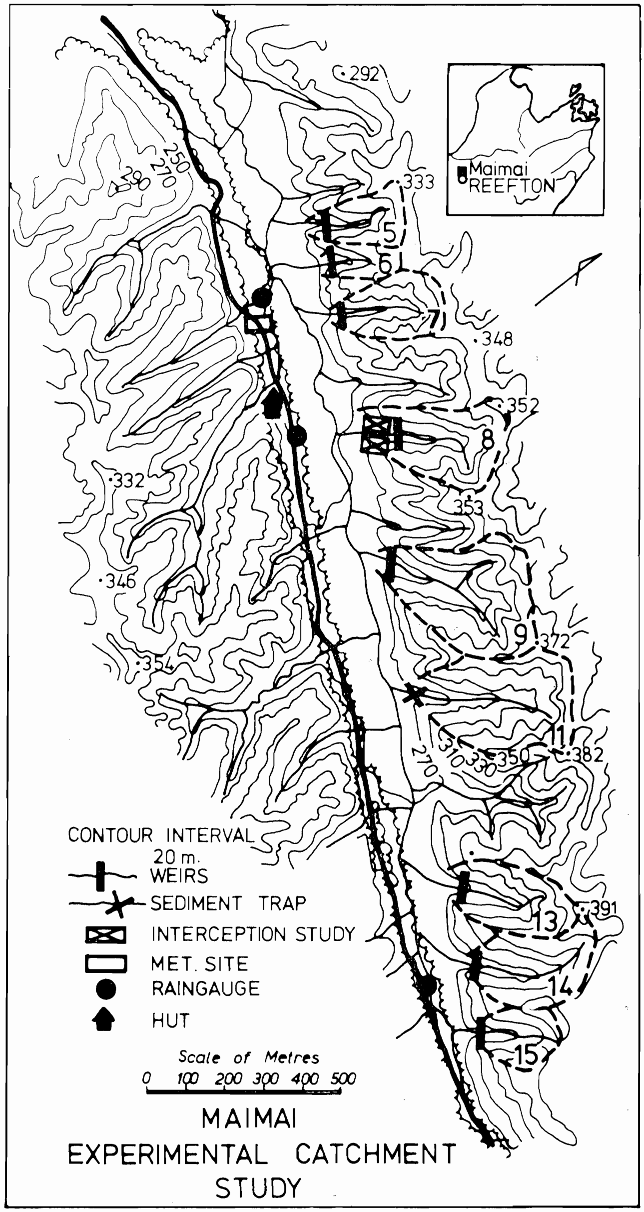

FIG. 1—Locality map: Pylon Gully, Maimai, Tawhai State Forest, showing disposition of the six experimental catchments to be compared in the logging study and catchments and 11 from which sample data were selected for this dry matter study. Catchment 8a lies between 8 and 9.

to meet this objective are based on the stand inventory data for catchment 7, which was considered sufficiently large (4.14 ha) for this purpose. Dry matter estimates for 7 were also required as objective 2. Estimates for the experimental catchments will be presented in a later paper along with updated estimates for the forest as a whole, based on the extensive inventory of the six experimental catchments and 7.

Dry-matter data for indigenous New Zealand forests are scanty. Litter fall has been measured in beech forest (Miller & Hurst 1957; Wardle 1970; Bagnall 1972; Levett 1978) and in podocarp/hardwood forest (Daniel 1975; Levett 1978), and accumulated litter in beech/podocarp (Webster, unpubl. data) and podocarp/hardwood forest (Levett 1978). Dry matter in live trees of an even-aged hard beech stand was determined by Miller (1963). The most comprehensive study of dry-matter content was made by Levett (1978) who estimated, from the logs harvested and the residue after logging, the accumulated litter and the total above-ground component weight of vegetation. A breakdown by species was not given, nor were roots estimated. Numerous overseas studies dealing with the dry-matter content of a range of forest types have been published (Rodin *et al.* 1975; Levett 1978). Few studies include the accumulated dead matter component provided in Lang & Forman (1978) and Grier & Logan (1977). This is difficult to measure in mature forests.

Site description

The forest occurs on the dissected gravel country of the South Island of New Zealand. Pylon Gully, Maimai, was selected as a study site because it is subdivided into a number of adjacent catchments in an area otherwise uniform in forest type and climate, and this permitted comparisons of treatment effects to be made at the catchment level.

At Maimai slopes are steep (average 36°), less than 300 m in length, with local relief ranging between 100 and 150 m (Neary *et al.* 1978). Soils are shallow (approx. 25 cm deep), strongly weathered yellow brown earths of low fertility, formed over compacted Pleistocene Old Man Gravels of fluvial origin (Mew *et al.* 1975). The organic layer on the forest floor averages 17 cm in depth (Webster, unpubl. data) and supports the bulk of the root mass. Precipitation is evenly distributed and averages 2600 mm each year (Neary *et al.* 1978). Monthly temperatures one mile distant at Reefton average 10.9°C, ranging from 4.8°C in July to 16.4°C in February (Mew *et al.* 1975).

Beech/podocarp forest, the natural vegetation of the area (classified as NZFS type PB 5) is largely unlogged mature forest with a 3-tiered structure and is rich in species. Despite this diversity only two species, one each from the canopy and subcanopy, contribute substantially to the basal area (cf. Fig. 2).

The canopy ranges from 20 to 36 m in height and is rather open (Fig. 3). *Nothofagus truncata* (Col.) Ckn. is the dominant canopy species, and occurs in association with scattered *Podocarpus ferrugineus* G. Benn. ex D. Don, co-emergent *Dacrydium cupressinum* Lamb., and very occasional *P. hallii* Kirk, the latter two species being confined to the ridge crests. At gully-heads and along stream margins *N. truncata* is displaced by *N. fusca* (Hook. f.) Oerst and *N. menziesii* (Hook. f.) Oerst. Although most canopy trees are less than 50 cm dbh some attain diameters of 1 and occasionally 2 metres at breast height (Table 1), and some trees are more than 300 years old.

The well developed subcanopy ranges from 7 to 19 m in height, with *Weinmannia racemosa* Linn. f., which attains a diameter of 40 cm or more, by far the commonest tree (Table 1, Fig. 4). *Fuchsia excorticata* (J.R. et G. Forst) Linn. f., *Griselinia littoralis* Raikym, *Elaeocarpus hookerianus* Raoul, *Carpodetus serratus* J.R. et G. Forst., and tree ferns (mostly *Cyathea smithii* Hook. f.) occur along stream margins; on slopes and ridges

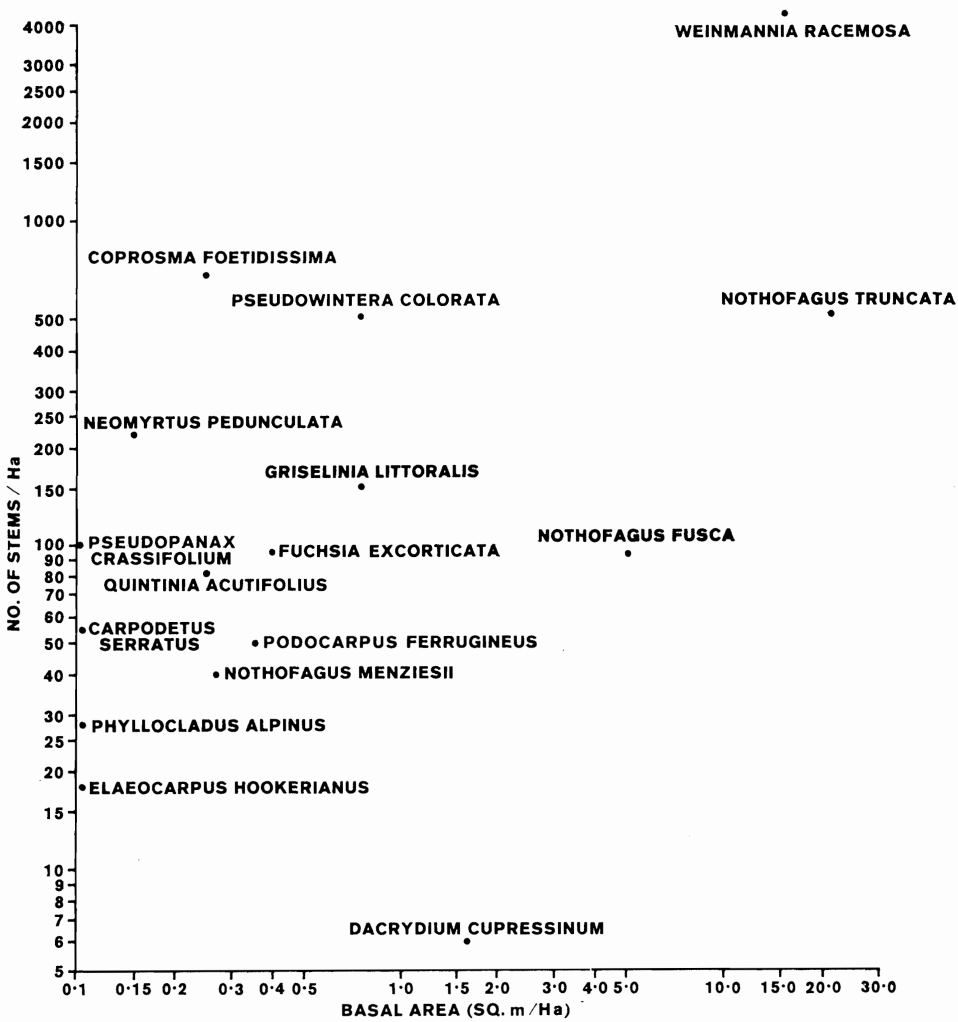

FIG. 2—Frequency and basal area of the principal tree and shrub species in catchment 7, Maimai. Trees equal to and exceeding 25 cm dbh are based on a 100% inventory of 7; those less than 25 cm occur on 20 random plots considered applicable.

Quintinia acutifolia Kirk forms locally dense thickets along with more scattered *Metrosideros umbellata* Cav., *Phyllocladus alpinus* Hook. f., *Neopanax simplex* (Forst. f.) Allan, and *Pseudopanax crassifolium* (Sol. ex A. Cunn.) C. Koch.

The shrub tier, which rarely exceeds 5 m in height, comprises dense groves of *Pseudowintera colorata* (Raoul) Dandy along stream margins and of *Neomyrtus pedunculata* (Hook. f.) Allan along ridge crests but is otherwise rather open. *Coprosma foetidissima* J.R. et G. Forst., along with scattered *C. parviflora* Hook. f., *Schefflera digitata* J.R. et G. Forst., *Cyathodes fasciculata* (Forst. f.) Allan, and *Neopanax colensoi* (Hook. f.) Allan occur throughout.

FIG. 3—Beech/podocarp forest canopy, catchment 9, Maimai. **Nothofagus truncata** is the dominant canopy species. The large tree in the foreground is **Nothofagus fusca**. Two emergent **Dacrydium cupressinum** at centre background.

The ground cover is dominated by locally dense patches of *Blechnum discolor* (Forst. f.) Keys, *Dicksonia lanata* Col., and filmy ferns (*Hymenophyllum* spp.) (Fig. 5). Cryptograms lavishly clothe the decaying logs and occur as dense mats scattered throughout the forest floor and on the stems of *P. ferrugineus* and *N. menziesii* especially. The succulent fern *Histiopteris incisa* (Thunb.) J. Smith and the scramblers *Lycopodium volubile* Forst. f. and *Rubus cissoides* A. Cunn. grow profusely in canopy gaps, the latter species frequently extending into the adjacent overstorey tree-crowns.

The forest floor is of the Mor type and averages 17 cm in depth (Webster, unpubl. data). The preponderance of large logs in the litter reflects the maturity of the forest. A thick humus layer has developed which exhibits a distinct boundary with the soil A horizon. The superficial root mass is largely confined to this humus layer (Fig. 5).

TABLE 1—Frequency distribution (stems/ha) of canopy and subcanopy species (catchment 7)

	Size class (cm)											
Species	<10	-25	-40	-55	-70	-85	-100	-115	-130	-145	-250	Total
Nothofagus truncata	364	55.0	50.0	27.5	13.5	6.5	3.2	1.4	0.5	0	0.2	521
Nothofagus fusca	69	8.0	2.6	6.6	2.5	2.8	0.7	0.2	0.4			96
Dacrydium cupressinum	0	0	0.9	2.4	1.2	0	0.7	0	0.2			6
Nothofagus menziesii	13	15.0	6.0	3.8	1.4	0.5						40
Podocarpus ferrugineus	11	15.0	15.7	8.2	1.9	0.2						50
Weinmannia racemosa	3773	402.0	49.4	5.8	0	0	0.2					4421
Metrosideros umbellata	2	0	1.2	0.2	0.2							4
Griselinia littoralis	127	26.0	0.7	0.2								154
Quintinia acutifolia	73	0.7	0.2									82
Phyllocladus alpinus	23	5.0	0.2									28
Elaeocarpus hookerianus	14	4.0										18
Fuchsia excorticata	75	21.0										96
Carpodetus serratus	52	3.0										55

METHODS

Definition of forest components

The plant biomass was categorised into the following forest components:

(1) Live trees and shrubs more than 2 m high.

(a) Trees equal to or greater than 25 cm dbh.

(b) Trees and shrubs less than 25 cm dbh.

As most species were too infrequent to warrant individual species regression equations the trees and shrubs were grouped into canopy species, subcanopy species, and shrub species.

(2) Standing dead trees.

(3) Fallen logs (> 25 cm diameter) and attached moss.

(4) Ground vegetation less than 2 m high.

(5) Ground moss, accumulated litter (< 25 cm diameter), humus, and roots.

Sample data were further categorised into plant components and size classes useful to ecologists, and which provided a basis for estimating the dry matter removed from or left on the site after logging to a chipwood standard. This has a lower utilisation limit of 10 cm diameter.

All plant samples were dried to constant weight at 65°C. Dry matter estimates were expressed on a horizontal area basis.

Sampling design

A sampling design that would provide estimates of the dry matter in a mature beech/podocarp forest and on individual experimental catchments was based on the following considerations, which led to a spatial and temporal separation of the sampling and inventory phases.

Sampling from within the six experimental catchments was not possible as these were being calibrated, requiring that all pre-logging disturbances be kept to a minimum.

FIG. 4—Mature ridge crest stand, catchment 7, Maimai. Large stem is **Nothofagus truncata**, with small **Weinmannia racemosa** understorey trees in foreground and centre. Several large standing dead trees in centre background.

Also, the physical effort entailed in collecting separate allometric and unit area data by catchment would have been prohibitive.

It was therefore intended that forest data collected in one area should be applied to another. The validity of this approach depends both on the uniformity of the particular forest component and on the catchment size. Webster's (unpubl.) earlier survey results of forest floor depth down to the mineral soil demonstrated the uniformity of this component in the six experimental catchments. The only other component of major size, the large trees, is generally variable in mature forests, when observed at the scale of the smallest experimental catchment. These ranged in area between 1.63 and 4.62 ha.

Because it was possible to inventory each experimental catchment immediately before it was logged the problem just observed could be eliminated, within the constraint

FIG. 5—Lower slope access road cutting, catchment 9, Maimai. Dense **Dicksonia lanata** is the typical fern cover of the lower slopes. The 18 cm thick humus layer, to which most of the root mass is confined, overlays nutrient-poor soil and Old Man Gravels.

that no sampling was permitted. A 100% inventory of trees equal to or exceeding 25 cm dbh was therefore conducted in each catchment for which dry matter estimates were required. The inventory was conducted immediately before logging.

Measurement and estimation of plant biomass

Allometric and unit area harvest data were collected from catchments 7, 8a (between 8 and 9 in Fig. 1), and 11 (total area *c.* 16 ha). These latter catchments are additional to the *six* of the main study and no sampling restrictions applied. However, to avoid damage due to destructive sampling already underway, selected aspects of the study programme were allocated to specific catchments. The areas were sufficiently extensive to permit this.

One difference in sampling design between 7 and the other six experimental catchments is noteworthy. Whereas part of the harvest data derives from 7, no sampling was conducted in the other six catchments. The 100% inventory of trees ≧ 25 cm dbh was universal in all the catchments for which dry matter estimates were later required.

Catchment-level measurements and sampling

Catchment inventory

A 100% inventory of trees ≧ 25 cm dbh (for component 1a) in catchment 7 was carried out during February 1976. Tree species and dbh were recorded.

This measurement phase was unique to the catchment. All subsequent sample and inventory data were common to all the catchments.

(1a) Sample tree selection for component 1a

Fourteen sample trees ≧ 25 cm dbh were selected from within catchment 11 during December 1975. A stratified random sample with proportional representation of the species and size classes was determined from the prior survey and inventory of 11. Tree height and dbh were measured.

Twenty-six additional trees were selected from 7 before it was logged, to provide data on log recovery. A random sample of trees with proportional representation of the species and size classes exceeding 10 cm dbh was determined from the inventory of 7.

Plot-based estimates

The sampling and inventory of all vegetation other than live trees ≧ 25 cm dbh were confined to 20 (20 × 20 m) plots, allocated proportionally by catchment area: 12 in 7 and 8 in 8a. The plots were measured and sampled during January and February 1976.

(1b) Small trees and shrubs inventory and sampling for component 1b

The diameter of all plot trees less than 25 cm at breast height, or at ground level for shrubs, was recorded by species for vegetation over 2 m high. A random sample of small trees and shrubs with proportional representation of the species and size classes was selected. Height and dbh for tree species or diameter at ground level for shrubs were recorded.

Breakdown of sample trees and shrubs (components 1a and 1b)

The following crown components were separated:

Diameter (cm)

Live branches: 0–2; 2–10; 10–25; > 25

Dead branches: all sizes combined

The total fresh weight of each component and the fresh weight of a sample therefrom were obtained in the field. Live-branch samples were separated in the laboratory into wood and bark before oven drying. The 0–2 cm component (foliage-bearing twigs) was first defoliated; the foliage was bagged and the twigs were then further subsampled for separation into wood and bark. Dead branches were not debarked.

Stems less than 5 cm dbh for trees (or at base for shrubs) were separated entirely into wood and bark, and oven dried. For stems between 5 and 25 cm dbh, the fresh weight of each stem and its disc samples (8 cm thick) was measured in the field immediately after felling. Discs were separated in the laboratory into wood and bark, and were oven dried. Stem weight was calculated by multiplying disc weight by the stem sampling fraction by fresh weight. Stems of 25 cm dbh or larger in the unlogged catchment 11 were not weighed in the field. Stem weight was calculated by multiplying disc sample weight by the sampling fraction by volume. The 26 additional tree stems, that had been extracted as part of the normal logging operation of catchment 7, were sorted and identified after extraction, the logs were weighed individually on a weigh-bridge during November 1976, and disc samples were cut, weighed, and later oven dried for determining moisture content.

Regression analysis (components 1a and 1b)

Regressions relating component weight to dbh were calculated separately for the three major species groups: canopy trees, subcanopy trees, and shrubs (Appendix 1). Several types of regression model were fitted. This was necessary since there was no single constant-coefficient model and fitting method that could deal with the wide range of tree size encountered in this forest

For some components linear regressions of logarithmically transformed data provided good fits for all values of the independent variable, X. This power model, fitted to data after logarithmic transformation, is the model most commonly postulated in forest biomass mensuration (Madgwick 1976).

Generally, however, the power model did not fit all tree sizes equally well, which can be expected when X has a wide range. Excellent fits to the small trees could always be achieved after transforming the data to logarithmic units. Unfortunately, fits to the large trees departed by up to 20% from the sample data using this transformation. Untransformed data proved the best for large trees; the greater variance associated with large trees providing a natural weighting which ensured good least squares fits using non-linear regression methods. The improvement in fit to the large tree sizes occurred at the expense of that for the small sizes. Estimates for the latter departed by a factor of 2–4 times from the sample data. Transforming the data so they had equal weighting would result in a better fit to the intermediate sized trees, but to the detriment of the extreme sizes. These are unfortunate aspects of working with a model that is not entirely appropriate.

Since the larger trees comprise the bulk of the dry matter, it seemed reasonable to apply the non-linear regression equations to the large trees (those with dbh's $\geqq$ 25 cm). Linear equations fitted to logarithmically transformed data were applied to trees $<$ 25 cm dbh. This excepted extractable stem matter, shrubs, and dead branch matter in the crowns of live trees, for which non-linearly fitted regressions were used, regardless of size. For these particularly variable components the relatively small sample size resulted in unstable solutions to the logarithmic equations (Mountford & Bunce 1973).

The equations used in this study are detailed below:

(i) *Logarithmic regression equations*

The power function:

$$Y = aX^b \quad \text{......} \quad (1)$$

was fitted using simple linear regression after logarithmic transformation of the data. In this case, individual predictions, $\hat{Y}_i$ at X_i were obtained in natural units using the expression:

$$\hat{Y}_i = (e^{s^2})^{\frac{1}{2}} e^{a + b \ln X} \qquad (2)$$

with variance:

$$RMS_i = e^{s^2} (e^{s^2} - 1) e^{2 (a + b \ln X)} \qquad (3)$$

The RMS_i replaces the residual mean square of the usual standard error formula as given in Sokal & Rohlf (1969), which in this modified form accommodates changes in variance with respect to the independent variable, X. That is:

$$SE_{\hat{Y}_i} = \left[RMS_i \left(\frac{1}{k} + \frac{1}{n} + \frac{(X_i - \bar{X})^2}{\Sigma x^2} \right) \right]^{\frac{1}{2}} \qquad (4)$$

where:

- Y = component to be estimated
- X = independent variable measured at the inventory (dbh), with mean $\bar{X}$
- Σx^2 = corrected sum of squares of X
- s^2 = variance about the linear fit
- a, b = equation coefficients estimated using regression analysis
- k = number of trees on which the prediction is based
- n = number of sample trees in the regression equation.

(ii) *Non-linear regression equations*

The power equation (1) or, when solutions to this were unstable, the quadratic equation (7) were fitted to the natural data using non-linear regression. An individual prediction, $\hat{Y}_i$, was obtained directly from equation (1) or (7). The increasing variance with tree size was accounted for by using the modified standard error formula (4), in which the variance was

$$RMS_i = \frac{n}{n - 4} (\hat{d}_i)^2 \qquad (5)$$

where $\hat{d}_i$ is the estimated absolute deviation of the sample data from the preferred equation (1 or 7) at X_i, predicted using the relationship between the absolute of the residuals and X. The latter relationship was fitted either by the ratio of means estimator when the relationship was linear, or by the power function when it was non-linear. The degrees of freedom of the RMS_i were reduced by an extra two, with the $\hat{d}_i$ given by:

$$\hat{d}_i = \hat{Y}_i - cX^f_i \qquad (6)$$

where c and f are equation coefficients estimated by regression, and the other variables are as defined previously.

Confidence intervals based on the above formulae were graphed on the raw data as a check. The approach provided good approximations of standard errors.

The quadratic equation is given by:

$$Y = a_0 + a_1X^{b1} + a_2X^2 \quad (7)$$

where a_0, a_1, a_2, and b_1 are equation coefficients. In Tables 2, 3, and 4, $b_1 = 1$ when the quadratic equation was fitted, or $b_1 = b$ of equation (1) when the power equation was fitted.

Each prediction, $\hat{Y}_i$, and its associated error were separately accumulated for all k trees of the inventory for which a prediction was required. Although valid for the 100% assessment, this procedure leads to a systematic underestimation of standard error for the plot trees, since formula (7) does not include a term for between-plot variance. This underestimation will be of only minor significance, however, since the plot trees, of which only those less than 25 cm are relevant, contributed negligibly to the total weight and error.

Tree ferns

A random sample of tree ferns was separated into fronds and stems for oven drying. The frond and stem average weights were multiplied by the number of ferns per hectare, recorded at the 100% inventory of 7.

Standing dead trees

The stem height and dbh of all dead standing trees $\geqq$ 25 cm dbh on the 20 plots were measured, and stem volumes calculated using taper data for the live trees. Stem weight, $\hat{Y}$, and error, $SE_{\hat{Y}}$, per hectare were estimated using formulae (8) and (9).

$$\hat{Y} = N a + b \bar{\bar{X}} \quad (8)$$

$$SE_{\hat{Y}} = \left[N^2 \, RMS \left(\frac{1}{n} + \frac{(\bar{\bar{X}} - \bar{X})^2}{\Sigma x^2} \right) + b^2 s^2_{\bar{\bar{x}}} \right]^{\frac{1}{2}} \quad (9)$$

where N is the number of dead stems per hectare in the plots, $\bar{\bar{X}}$ and $s_{\bar{\bar{x}}}$ are the dead stem volume and variance per hectare respectively, and a and b are regression constants. The constants were derived from disc samples cut from recently fallen logs since dead standing trees proved impracticable to sample. The resulting bias associated with this substitution was not determined but is unlikely to be excessive. The standard error formula is based on that given in Schumacher & Chapman (1954), and is expressed on an area rather than on individual tree basis. RMS is the variance about the linear regression and Σx^2 and $\bar{X}$ are the corrected sum of squares and mean of X respectively.

Dead trees less than 25 cm dbh were estimated from the average weight of a random sample of dead trees in the plots multiplied by the number of dead trees per hectare on the plots.

Branch matter of dead standing trees proved impossible to measure adequately. This component is not large since most limbs detach rapidly, and only the unbranched spar remains. The ratio of branch to stem for live trees was calculated to give an indication of the upper limit of branch weight.

Fallen logs ($\geqq$ 25 cm diameter) and attached moss

The diameter and sectional length of all fallen logs within the 20 plots were measured at marked intervals and individual log volumes calculated using Simpson's rule. Disc samples (8 cm thick) were obtained for a random sample of these logs at points measured for diameter, thus ensuring an unbiased sampling fraction based on volume. The moss was removed from the discs before oven drying. Log dry weight and error per hectare were estimated using formulae (8) and (9) where the coefficients a and b were based on the full set of fallen logs and disc samples.

Ground vegetation < 2 m high

Standing live and dead matter on 5 randomly-located strips, each 20 × 1 m, was harvested during January and February 1976 from within each of the 20 sample plots. The fresh weight of the harvested matter and a weighed sample therefrom were obtained immediately in the field. The sample was oven dried in the laboratory without regard to species or plant component. (Ground ferns were processed separately where these formed a predominant element of the ground vegetation.)

Ground moss, accumulated litter (< 25 cm diameter), humus, and roots

A typical forest floor profile at Maimai includes litter, fermenting (F) and humus (H) layers (Webster, unpubl. data), the latter exhibiting a clearly defined boundary with the soil mineral horizon.

Five pits (30 × 30 cm) were located randomly within each of 10 plots in catchment 7. The following forest floor components were separated after oven drying, which facilitated the separation of the roots from the humus:

(a) Moss.

(b) Accumulated litter (< 25 cm) including some F.

(c) Humus including any remaining F.

(d) Root size classes: < 10; 10–20; > 20 live; > 20 dead (diameters in mm).

The roots, which at Maimai are confined largely to the F and H layers, include both live and dead roots for components less than 20 mm. The largest class of dead roots included buried branch and stem litter, indistinguishable from dead roots. Sampling was carried out during February 1976.

RESULTS

Biomass estimates

(1) *Trees and shrubs > 2 m high*

Regression equations

Coefficients of regression equations relating various plant components to stem size for the canopy, subcanopy, and shrub species groups are presented in Tables 2, 3, and 4 respectively. The fits are good for live components with r^2 values ranging between 0.75 and 0.98 for stem components and 0.58 and 0.95 for crown components (r^2 for non-linear fit). Dead branch matter was the component estimated with least precision.

TABLE 2—Estimating equations for component weights* of canopy species

Component (Y)	n	r^2	Coefficients of Eqn (7)				Coefficients of Eqn (6)		Coefficients of Eqn (2)		
			a_0	a_1	b_1	a_2	c_1	f_1	a	b	s^2
Total Fwt	14	0.93	0.0	1.300×10^{-2}	1.9645	0.0	4.562×10^{-3}	1.8731	—5.8360	2.1954	5.859×10^{-2}
Crown Fwt	14	0.79	0.0	5.022×10^{-3}	1.8950	0.0	5.586×10^{-4}	2.0290	—6.5737	2.0732	1.899×10^{-1}
Branch — wood	14	0.82	0.0	3.655×10^{-4}	2.1432	0.0	8.518×10^{-5}	2.1997	—8.3885	2.1873	2.577×10^{-1}
Branch — bark	14	0.93	—10.5002	5.423×10^{-2}	1.0	3.073×10^{-4}	5.641×10^{-2}	1.0	—11.397	2.5342	1.032×10^{-1}
Twigs — wood	14	0.58	0.0	1.499×10^{-3}	1.6624	0.0	5.075×10^{-5}	2.0618	—7.1365	1.7142	4.034×10^{-1}
Twigs — bark	14	0.89	—6.645	5.791×10^{-2}	1.0	3.769×10^{-5}	1.880×10^{-2}	1.0	—10.478	2.2155	1.461×10^{-1}
Dead branches	14	0.55	8.187	3.481×10^{-2}	1.0	6.636×10^{-5}	1.991×10^{-2}	1.0	—10.031	1.9452	1.1743
Foliage	14	0.77	0.0	6.742×10^{-4}	1.5824	0.0	6.198×10^{-4}	1.4402	—6.1149	1.3896	2.687×10^{-1}
Stem — volume (T)	31	0.94	0.0	3.430×10^{-6}	2.1402	0.0	8.366×10^{-4}	1.0	—13.399	2.2676	4.86×10^{-2}
Stem — Fwt (T)	32	0.93	0.0	1.045×10^{-2}	1.9566	0.0	5.982×10^{-2}	1.4259	—6.6315	2.2782	6.304×10^{-2}
Stem — wood (T)	32	0.93	0.0	1.092×10^{-2}	1.8305	0.0	4.039×10^{-1}	0.9897	—7.1095	2.2313	6.272×10^{-2}
Stem — bark (T)	32	0.89	0.0	4.601×10^{-5}	2.3426	0.0	6.374×10^{-2}	1.0	—8.7582	2.1503	1.652×10^{-1}
Stem — volume (U)	29	0.93	0.0	9.088×10^{-7}	2.3179	0.0	9.221×10^{-4}	1.0	—	—	—
Stem — Fwt (U)	29	0.93	0.0	3.104×10^{-3}	2.1166	0.0	7.863×10^{-1}	1.0	—	—	—
Stem — wood (U)	29	0.93	0.0	3.505×10^{-3}	1.9784	0.0	3.224×10^{-1}	1.0	—	—	—
Stem — bark (U)	29	0.88	0.0	1.825×10^{-5}	2.4685	0.0	6.921×10^{-2}	1.0	—	—	—
Branches <10 cm											
Wood	13	0.91	—64.644	4.393×10^{-1}	1.0	7.560×10^{-6}	7.496×10^{-2}	1.0	—	—	—
Bark	13	0.93	—23.518	1.619×10^{-1}	1.0	5.065×10^{-5}	2.928×10^{-2}	1.0	—	—	—
Tree height (cm)	14	0.81	0.0	2.879×10^{2}	0.3481	0.0	5.804×10^{-1}	1.0	—	—	—

* Weights are all oven-dry (o.d.) wts, in kg, except where indicated by Fwt (fresh wt, also in kg); X = dbh (mm); volumes in m^3; T = total components; U = utilisab'e (extracted) portion only.

TABLE 3—Estimating equations for component weights* of subcanopy species

Component (Y)	n	r^2	Coefficients of Eqn (7)				Coefficients of Eqn (6)		Coefficients of Eqn (2)		
			a_0	a_1	b_1	a_2	c_1	f_1	a	b	s^2
Total Fwt	36	0.98	0.0	4.586×10^{-4}	2.4897	0.0	2.082×10^{-1}	1.0	—6.8197	2.3431	0.0465
Crown Fwt	36	0.95	0.0	1.723×10^{-4}	1.4556	0.0	9.770×10^{-2}	1.0	—7.5236	2.2198	0.1458
Branch — wood	36	0.93	0.0	6.828×10^{-5}	2.4242	0.0	3.896×10^{-2}	1.0	—9.6210	2.3827	0.2218
Branch — bark	36	0.94	2.1491	—0.07305	1.0	4.677×10^{-4}	1.726×10^{-2}	1.0	—9.6440	2.1665	0.1837
Twigs — wood	36	0.85	0.0	9.264×10^{-4}	1.6226	0.0	8.421×10^{-3}	1.0	—7.1977	1.6654	0.3666
Twigs — bark	36	0.84	0.0	2.194×10^{-5}	2.1817	0.0	5.462×10^{-3}	1.0	—8.1156	1.7159	0.2467
Dead branches	36	0.57	0.0	1.450×10^{-4}	1.7437	0.0	5.309×10^{-3}	1.0	—10.943	1.7764	9.4235
Foliage	36	0.93	0.0	1.303×10^{-4}	1.9634	0.0	5.954×10^{-3}	1.0	—7.3288	1.6662	0.1717
Stem — volume (T)	22	0.94	0.0	5.022×10^{-7}	2.4159	0.0	3.148×10^{-5}	1.3318	—13.093	2.1541	0.0686
Stem — Fwt (T)	44	0.96	0.0	2.219×10^{-4}	2.5559	0.0	2.085×10^{-1}	1.0	—7.3544	2.3694	0.0731
Stem — wood (T)	44	0.96	0.0	1.361×10^{-4}	2.5012	0.0	9.147×10^{-2}	1.0	—8.0478	2.3512	0.0682
Stem — bark (T)	44	0.92	3.5408	—0.1098	1.0	6.506×10^{-4}	2.454×10^{-2}	1.0	—9.6250	2.2372	0.1718
Stem — volume (U)	22	0.89	0.0	3.199×10^{-7}	2.4766	0.0	6.110×10^{-5}	1.2652	—	—	—
Stem — Fwt (U)	22	0.91	74.746	—1.3996	1.0	8.699×10^{-3}	3.081×10^{-1}	1.0	—	—	—
Stem — wood (U)	22	0.91	27.993	—0.5507	1.0	3.690×10^{-3}	1.408×10^{-1}	1.0	—	—	—
Stem — bark (U)	22	0.91	12.958	—0.1962	1.0	7.934×10^{-4}	1.956×10^{-2}	1.0	—	—	—
Branches <10 cm											
Wood	14	0.87	0.0	1.429×10^{-3}	1.7982	0.0	3.052×10^{-2}	1.0	—9.4937	2.3202	0.1928
Bark	14	0.85	0.0	4.104×10^{-6}	2.6330	0.0	1.238×10^{-2}	1.0	—9.2233	2.0587	0.1955
Tree height (cm)	36	0.87	0.0	101.916	0.4845	0.0	1.3160	1.0	—	—	—

* Weights are all o.d. wts (in kg), except where indicated by Fwt (fresh wt, also in kg);
X = dbh (mm); volumes in m^3; T = total components; U = utilisable portion only.

TABLE 4—Estimating equations for component weights* of shrubby species

Component (Y)	n	r^2	Coefficients of Eqn (7) a_0	a_1	b_1	a_2	Coefficients of Eqn (6) c_1	f_1
Total Fwt	10	0.97	0.0	2.515×10^{-3}	1.9633	0.0	1.847×10^{-1}	0.2789
"Stem fresh"	10	0.97	0.0	6.209×10^{-4}	2.1508	0.0	7.476×10^{-3}	1.0
Crown Fwt	10	0.90	0.0	2.342×10^{-3}	1.7936	0.0	3.279×10^{-2}	0.6848
Stem — wood	10	0.90	0.0	2.441×10^{-4}	2.1678	0.0	2.459×10^{-2}	0.5504
Stem — bark	10	0.98	0.0	2.297×10^{-5}	2.2443	0.0	3.312×10^{-4}	1.0
Branch — wood	10	0.87	0.0	6.705×10^{-4}	1.6322	0.0	5.731×10^{-3}	0.6795
Branch — bark	10	0.86	0.0	3.430×10^{-4}	1.6560	0.0	1.323×10^{-3}	1.0
Dead branches	10	0.13	0.0	6.117×10^{-4}	0.7998	0.0	4.620×10^{-4}	0.8663
Foliage	10	0.92	0.0	3.952×10^{-4}	1.8022	0.0	2.133×10^{-2}	0.3509

* Weights are all o.d. wts (in kg) except where indicated by Fwt (fresh wt, also in kg); X = diameter (in mm) at ground level.

Since most published results are based on equations fitted to logarithmically transformed data, the difference in the dry-matter estimates had logarithms been used in this study is indicated for comparison. The oven-dry (o.d.) weight per hectare for all species combined changes by —1.0, 5.0, 5.9, 3.8, and —4.4% for the stem, crown, branch wood, branch bark, and foliage, respectively. The closeness of the estimates was gratifying, though surprising in view of the frequently poor fits obtained for the large trees using the logarithmic equations. The far larger differences obtained for species group (8, —20, 16, 36, and 15% for the same components) indicated a fortuitous compensation of the differences between the models. Standard errors were even more divergent. Graphs of the sample data with the weight and error estimates superimposed indicated a systematic underestimation of the standard errors by the non-linear method but a correspondingly far greater overestimation by the logarithmic method for the larger trees. The converse was true for the smaller tree sizes.

Overall, the weight estimates obtained using the combined non-linear/logarithmic approach employed in the study are expected to be reasonably accurate. The standard errors will, however, be marginally underestimated.

Distribution of dry matter within individual trees

The relative distribution of weight among components to above ground tree weight changes markedly with tree size (Table 5). In general, the relative weight of foliage decreases and stem and branch weight increases with size. The shorter subcanopy species have relatively more weight apportioned to the branches, foliage, and stem bark compared with the canopy species which have relatively more stem wood. Because shrub size was measured at ground level no comparison with the tree species was attempted.

Amount and distribution of dry matter/ha in the trees and shrubs

The amount of dry matter above ground in the trees and shrubs is summarised by species and plant component in Table 6. *Nothofagus truncata* and *Weinmannia racemosa* together comprise two-thirds of the above-ground dry matter in the trees and shrubs. Shrubs comprise less than 1% of this component.

TABLE 5—Component weight as a percentage of above ground tree weight

Species group	dbh (mm)	Foliage	Branch wood	Branch bark	Dead branches	Stem wood	Stem bark
Canopy species	10	22.0	14	1.4	2.5	51	8.5
	40	8.3	16	2.6	2.0	62	9.3
	100	4.0	16	3.7	1.6	65	9.1
	260	1.1	14	6.2	0.91	73	5.3
	400	0.98	15	6.7	0.54	70	6.4
	800	0.77	18	6.7	0.66	66	8.5
	1000	0.41	19	6.6	0.75	64	9.3
Subcanopy species	10	21.0	12	6.5	5.3	48	7.7
	40	10.0	15	6.3	2.7	58	8.3
	100	5.8	16	5.7	1.7	63	8.1
	260	3.0	20	6.1	0.8	62	7.9
	400	2.4	20	6.7	0.7	62	9.0
Shrubs*	10	22	25	14.0	3.5	32	3.5
	20	21	22	12.0	1.7	39	4.6
	40	20	18	9.9	0.77	46	5.8
	80	17	13	7.4	0.33	55	7.4
	100	17	13	7.4	0.25	55	7.4

* Diameter (in mm) at ground level.

TABLE 6—Above-ground dry-matter (t/ha) distribution by major species and components

Species	Component: Stem wood	Stem bark	Branch wood	Branch bark	Dead branches	Foliage	Species total	%
Nothofagus truncata	96.3	10.7	23.5	9.3	3.50	1.43	144.7	47.3
Nothofagus fusca	23.0	2.8	5.9	2.3	1.37	0.31	35.7	11.7
Nothofagus menziesii	10.2	1.1	2.4	1.0	0.26	0.17	15.1	4.9
Podocarpus ferrugineus	17.3	1.7	3.9	1.6	0.30	0.27	25.1	8.2
Dacrydium cupressinum	7.6	0.9	2.0	0.8	0.01	0.09	11.4	3.7
Weinmannia racemosa	39.6	5.2	11.2	3.7	0.90	2.63	63.2	20.7
Minor tree spp.	4.6	0.6	1.3	0.4	0.10	0.33	7.3	2.4
Shrubs	0.7	0.1	0.3	0.1	0.11	0.41	1.7	0.6
Component total	200.9	23.0	50.4	19.2	6.53	5.65	306.0	
± SE	10.1	1.8	6.7	2.1	1.21	0.71	22.5	

The distribution of dry matter with respect to tree size is presented in Fig. 6. Whereas stem dry matter occurs mostly in the large trees, a relatively greater proportion of foliage is distributed on the smaller sizes.

Not apparent from the Figs and Tables is that, of the total branch matter, 26% is less than 2 cm in diameter, 41% is between 2 and 10 cm, and the remaining 33% exceeds 10 cm diameter.

Removal of plant mass during logging

Dry matter removed during logging of catchment 7 was estimated at 158 ± 12.2 t/ha of stem wood, 18 ± 2.3 t/ha of stem bark, and 8.9 ± 1.4 and 2.5 ± 0.3 t/ha of branch wood and branch bark, respectively. The fresh weight of extracted stem and branch matter estimated at 358 ± 40 t/ha compares surprisingly closely with the 360 t/ha extracted fresh weight recorded at the weighbridge (Cline, pers. comm.). Seventy-nine percent of stem matter exceeding 10 cm dbh was extracted. In the absence of measurement data, 50% recovery of branch matter exceeding 10 cm diameter was assumed.

(2) *Dead standing trees*

Of trees exceeding 25 cm dbh, 18% were dead. Dead trees numbered from 0 to 4 stems on the 20 × 20 m plots, with an estimated weight of 18.5 ± 4.8 t/ha (Table 7). Dead trees less than 25 cm diameter numbered 261 stems/ha with a weight of 2.03 ± 1.45 t/ha.

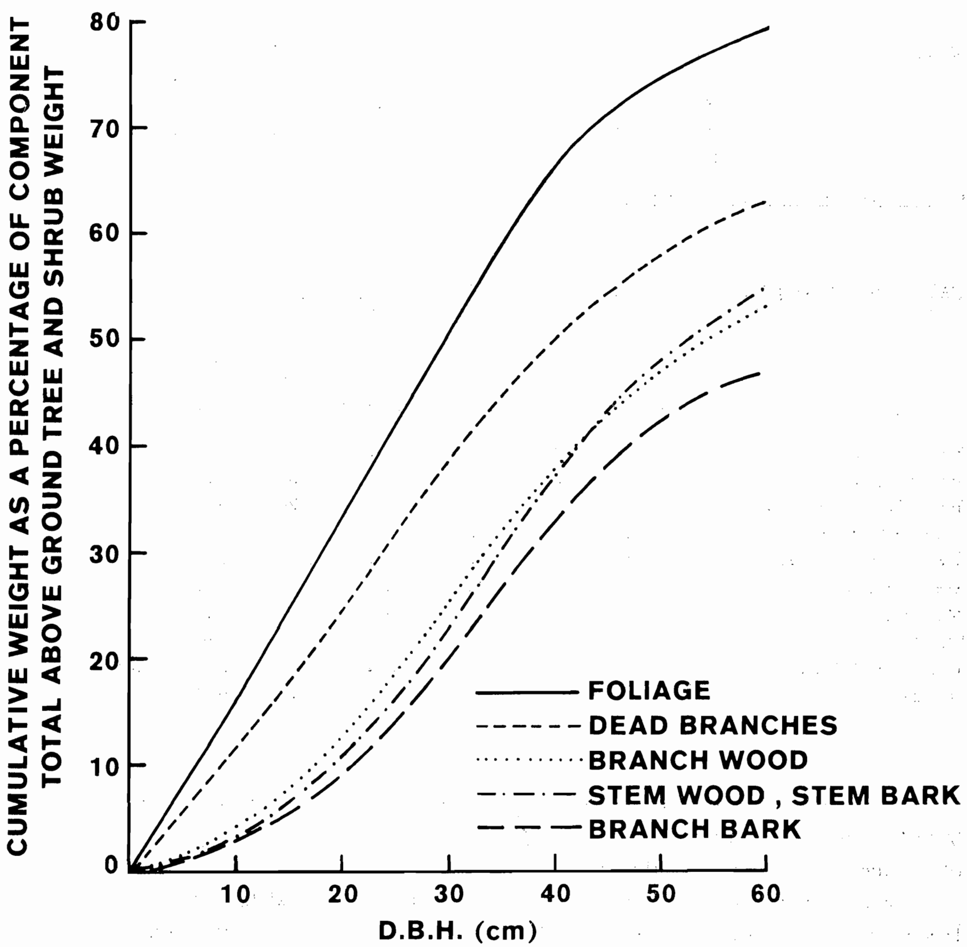

FIG. 6—Distribution of dry matter with respect to size for major components.

The amount of attached dead branch matter proved too difficult to measure accurately. The proportion of weight of live branch greater than 10 cm diameter to stem weight, calculated at 10%, provides a useful indication of the maximum branch weight that could occur on dead standing trees. More than 1–2 t/ha attached dead branch matter is unlikely.

Extraction of standing dead trees was assumed to be nil. Cline (pers. comm.) estimated that 1% of the extracted logs' weight comprised dead standing trees. Assuming a figure of 80% recovery of dead *Nothofagus fusca* trees over 20 m high, their maximum contribution to the extracted logs' weight could attain 5%, so that the maximum error incurred by assuming nil extraction will be relatively small. Dead individuals of the other species at Maimai are unlikely to be extracted.

(3) *Fallen logs (> 25 cm diameter)*

The average number of fallen logs either partially or totally within the 20 × 20 m plots was 5.95, ranging from 0 to 13, with an estimated weight of 33.0 ± 6.58 t/ha (Table 7).

State of decay was not recorded for these logs. Decay was related to log age and species, partially buried *N. fusca* logs supporting advanced regeneration commonly still possessed sound heartwood; *Weinmannia racemosa* and *N. truncata* were rarely sound even as standing dead trees.

Moss growing on fallen logs was estimated at 0.17 ± 0.06 t/ha.

Extraction of fallen logs was assumed to be nil.

TABLE 7—Linear regression of stem weight ($\bar{Y}$ in kg) on volume ($\bar{x}$ in m³) for dead trees ≥ 25 cm diameter

	n	$\bar{X}$	$\bar{Y}$	Σx^2	a	b	RMS
Fallen logs	31	0.944	0.169	29.304	0.0365	0.1408	0.0141
Standing dead	52	1.207	0.291	10.354	0.224	0.0551	0.0129

(4) *Ground vegetation (< 2 m high)*

All vegetation less than 2 m high, including both live and dead standing matter (excluding dead stumps greater than 25 cm dbh), was estimated at 2.87 ± 0.248 t/ha; of this, 17% was composed of ground-fern fronds. Dead matter contributed negligibly to this total.

(5) *Moss, litter (< 25 cm diameter), humus, and roots*

The average depth and weight of accumulated litter and root components are summarised in Table 8. The forest floor organic matter is of the Mor type and forms a distinct layer ranging from 1 to 67 cm (average 18 cm) deep, with little incorporation of humus into the mineral soil.

Roots comprise 33% of the forest live plant dry matter. Most of the root mass (Table 8) occurs in the large size class that includes buttress roots. These latter are characteristic of both *Nothofagus fusca* and *N. truncata* and may explain the relatively high proportion of dry matter in the roots.

TABLE 8—Dry weights (t/ha) and SE of organic components of the forest floor

	Moss		Surface litter (<25 cm diam.)		Humus		Roots by diameter class (cm)					
	Depth	Weight	Depth	Weight	Depth	Weight	<10	10–20	>20	>20 dead	Live roots	Total organic matter excluding moss
Dry weight	0.88	0.05	3.18	15.07	14.78	155.04	11.38	5.90	129.55	23.13	146.83	340
SE	0.23	0.01	0.28	1.29	2.70	35.37	2.03	1.10	32.08	10.02	33.04	66

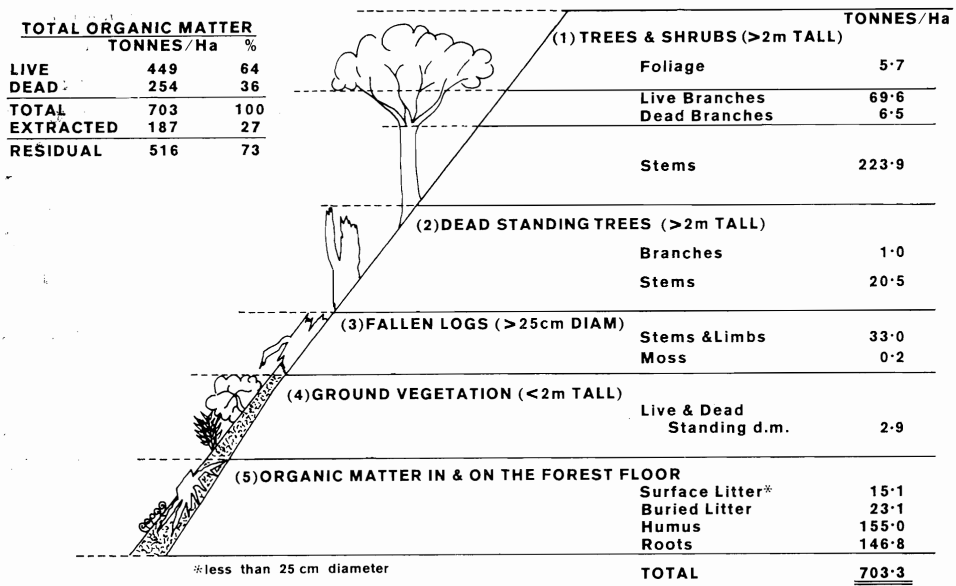

FIG. 7—Dry matter distribution in a mature beech/podocarp forest community, catchment 7, Maimai, Tawhai State Forest.

Disposition of dry matter among the major forest components

The total dry matter content of a mature beech/podocarp community was estimated at 703.3 t/ha. Almost two-thirds (449 t/ha) was live. The residual one-third (254 t/ha) comprised material already dead and in various stages of decomposition (Fig. 7).

The forest floor dead matter, including logs lying on its surface, was estimated at 226 t/ha. If roots were included, the forest floor weight becomes 373 t/ha, or 53% of the forest dry-matter content. More dry matter occurs, therefore, in and on the forest floor than in the above-ground standing crop.

Of the above-ground dry matter 90% was live. The 10% that was non-living occurred mostly as large dead stems of *N. fusca.*

Harvesting to a chipwood standard removed 187 t of dry matter/ha, or 27% of the forest dry matter content. Harvesting removed mostly live tree-stems. Of the 516 t/ha dry matter remaining on the site after logging, 72% comprised forest floor matter.

DISCUSSION

Plant communities have been characterised, with respect to their overall structure, into broad vegetation types (Rodin & Bazilevich 1968). In terms of its live dry-matter content, beech/podocarp forest bears closest affinity with the beech type of Rodin & Bazilevich. However, its detrital component is most uncharacteristic of this type.

Christensen (1977) in his analysis of temperate oak and beech stands concluded that soil surface dead branch and bole matter levels off at 4–6 t/ha by age 200 years, and standing dead dry-matter values of 2–5 t/ha are representative. The corresponding values for beech/podocarp forest exceed these plateau values by a factor of 5.

Of the several interpretations accounting for structural differences between communities of similar type, the most cogent is a concept of forest maturity (Odum 1969). During the early stages of stand development detrital matter comprises mostly small-sized fractions. As the stand ages, suppressed trees become less important as the source of detrital matter, which is derived increasingly from moribund canopy dominants.

It is anticipated that the relatively young deciduous forests dealt with by Christensen (1977) could attain a second higher plateau comparable to that found for the mature beech/podocarp forest. This is supported by the high detrital matter content found in New Jersey (U.S.A.) for a mature oak forest that had been unmodified for at least 250 years (Lang & Forman 1978).

Biological, geological, and climatic variables could be expected to determine the ultimate size of the detrital pools. Rates of decomposition differ markedly between species, as was noted for *N. fusca* and *N. truncata;* the availability of heterotrophs is an important unstudied factor in the beech/podocarp forest. The importance of size and longevity of the predominant canopy species is exemplified by dry matter data for a Douglas fir community in Oregon. This community attains 215 t/ha in the standing dead trees and fallen logs greater than 15 cm dbh (Grier & Logan 1977); this exceeds the corresponding values for the beech/podocarp forest by a factor of 4. Rodin & Bazilevich (1968) indicate the influence exerted by climatic factors on dry-matter accumulation by presenting the major vegetation types of the world with respect to latitude.

Removal of dry matter during logging

With regard to its capacity to provide nutrients, the amount and distribution of dry matter remaining on the site after harvesting influences the development of future crops.

At Maimai most of the residual dry matter occurred on the forest floor, and remained largely intact after extraction. Growth of future crops will be determined by the further effects of managerial practices on the humus layer, particularly the use of fire.

The effects of logging on stream water quality are dealt with by Neary *et al.* (1978). Accumulations in the stream channels of tree crown material and forest floor matter scalped off spur crests during the extraction of logs were considered important sources of nutrients with regard to stream quality.

CONCLUSIONS

Dry matter in the live components of the beech/podocarp forest was similar both in amount and distribution to the beech type of the northern hemisphere. However, root matter, which comprised 33% of the 449 t/ha of live matter at Maimai, was exceptionally high. Detrital matter in the standing dead trees and fallen logs exceeded that found for the European beech type by a factor of 5. It is considered that the concept of forest maturity provides a satisfactory explanation for the accumulation of large amounts of detrital matter.

Emphasis was placed in this study on the reliability of estimates based on regression methods. The use of non-linear regression for the large trees and logarithm-based linear regressions for estimating the weight and standard error for small trees provided adequate, although compromise, solutions. Graphing the sample data with the weight and error estimates superimposed was necessary to verify the adequacy of the approach.

A more complete picture will be presented when the results of the nutrient analyses become available and when assessment data are collected for more catchments at Maimai. The wider data base should obviate the major drawback of the present study of catchment 7 which, being of limited area, may not adequately characterise this very variable forest type.

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APPENDIX 1

Number of sample trees and shrubs by species available for inclusion in regression equations

	Crown components		Stem components	
Canopy spp.	11	**N. truncata**	17	**N. truncata**
	2	**N. fusca**	7	**N. fusca**
	1	**P. ferrugineus**	4	**N. menziesii**
			4	**P. ferrugineus**
Subcanopy spp.	33	**W. racemosa**	44	**W. racemosa**
Shrub spp.	6	**Coprosma foetidissima**	6	**Coprosma foetidissima**
	3	**Pseudowintera colorata**	3	**Pseudowintera colorata**
	1	**Neomyrtus pedunculata**	1	**Neomyrtus pendunculata**