

WEIGHT AND NUTRIENT CONTENT OF ABOVE-GROUND BIOMASS AND LITTER OF A PODOCARP-HARDWOOD FOREST IN WESTLAND, NEW ZEALAND

M. P. LEVETT*, J. A. ADAMS, T. W. WALKER

Department of Soil Science, Lincoln College, Canterbury, New Zealand

and E. R. L. WILSON

Department of Horticulture, Lincoln College, Canterbury, New Zealand

(Received for publication 29 February 1984; revision 20 November 1984)

ABSTRACT

The above-ground biomass and litter of an indigenous podocarp-hardwood forest plot in Hochstetter State Forest, Westland, was estimated by sampling thirty 1-m² quadrats after the forest had been felled. Canopy trees were divided into foliage, twigs less than 1 cm diameter, branches and stems 1–5 cm diameter, and branches and stems greater than 5 cm diameter. Understorey vegetation (less than 4 m tall) was divided into foliage and twigs less than 1 cm diameter, and branches and stems greater than 1 cm diameter. Soil litter was divided into leaves and twigs less than 1 cm diameter, and woody detritus greater than 1 cm diameter. Oven-dry weights and weights of sodium, potassium, calcium, magnesium, phosphorus, chlorine, nitrogen, and sulphur were determined for each biomass and soil litter component. For the total above-ground biomass these were 254 t/ha, and 118, 425, 592, 206, 27, 126, 306, and 120 kg/ha respectively. Thirty quadrats were sufficient to reduce the standard error to about 20% of the mean for all components other than woody detritus in the litter. It was estimated that a chipwood logging operation would remove 189 t/ha (dry weight) of the above-ground forest vegetation and 72 kg Na/ha, 282 kg K/ha, 425 kg Ca/ha, 130 kg Mg/ha, 14 kg P/ha, 75 kg Cl/ha, 163 kg N/ha, and 66 kg S/ha. In the absence of fertiliser application this could have a significant effect on long-term productivity in the low-nutrient Westland ecosystem.

Keywords: podocarp-hardwood forest; biomass; nutrients; chipwood logging.

INTRODUCTION

Nutrient immobilisation in forest biomass is an important aspect of ecosystem function and has been given considerable attention in mineral cycling studies (Rodin & Bazilevich 1967). It bears directly on the rate of depletion of soil reserves during forest development and provides a pool of nutrients which are cycled at various rates within the ecosystem. It is an important mechanism for retention of nutrients against leaching (Vitousek & Reiners 1975). Nutrient cycling in throughfall, stemflow, and litterfall is partly dependent on the mineral content of some components of the biomass.

* Present address: Department of Primary Industry, P.O. Box 417, Konedobu, NCD, Papua New Guinea

The size of the nutrient pool in forest biomass depends on site fertility (Duvigneaud & Denaeyer-De Smet 1970), species composition (Rennie 1955), and stage of development of the forest (Wells & Jorgensen 1975; Foster & Morrison 1976). Climatic conditions are probably also important.

Few estimates of mature indigenous forest biomass have been made in New Zealand. The most detailed is that by Beets (1980) for a beech-podocarp forest near Reefton, Westland. Orman & Will (1960), Will (1964), and Madgwick *et al.* (1977) reported on nutrient immobilisation in radiata pine (*Pinus radiata* D. Don) plantations. The only comparable study of nutrients in mature indigenous forest is by Miller (1963), based on a "typical" hard beech (*Nothofagus truncata* (Col.) Kkn.) tree, in the North Island. There are no published data on the bio-element content of South Island forests.

Commercial harvesting of trees for sawlogs and chipwood has stimulated research into the effects of timber removal on nutrient reserves and cycling in forested ecosystems (Rennie 1955; Weetman & Webber 1972). In the early 1970s consideration was given by the New Zealand Forest Service to the utilisation of about 400 000 ha of beech and podocarp-hardwood forest in Westland. This generated considerable interest in the effect of chipwood logging on site quality.

The above-ground biomass and nutrient content of a podocarp-hardwood forest plot in Westland were therefore studied and the quantities of nutrients which might be removed in logs by a chipwood logging operation were estimated.

SITE DESCRIPTION

The study site was located in closed-canopy podocarp-hardwood forest, type PH 17 of the National Forest Survey (Masters *et al.* 1957), in Hochstetter State Forest, Westland, New Zealand (grid reference N.Z. M.S. 1/S45/066949). The soils are well-drained yellow-brown earths (Dystrochrepts) formed from a complex of weathered conglomerate and consolidated muddy sandstone and siltstone (Mew 1980) overlain with 10–70 cm of mor humus. The site was on the upper slope approximately 30 m from the ridge with a predominantly southerly aspect and an average slope of 25°. Mean annual rainfall was approximately 2000 mm and mean daily temperature about 11°C.

The canopy, which had a top height of approximately 15–25 m, was dominated by two hardwood species *Quintinia acutifolia* Kirk (Westland quintinia) and *Weinmannia racemosa* L.f. (kamahi) with emergent *Prumnopitys ferruginea* (D. Don) de Laub. (miro), *Dacrydium cupressinum* Lamb. (rimu), and *Metrosideros umbellata* Cav. (southern rata). A sparse understorey rarely exceeded 4 m in height and consisted mainly of seedlings of Westland quintinia, podocarps (miro and rimu), *Myrsine salicina* Hook.f. (toro), and *Pseudopanax* and *Coprosma* species, and the tree fern *Dicksonia lanata* Col.

The ground vegetation consisted mainly of the creeping ratas *Metrosideros fulgens* Sol. ex Gaertn. and *M. perforata* (J.R. et G. Forst) A. Rich. with a variety of ferns including *Blechnum discolor* (Forst.f.) Keys, *B. minus* (R.Br.) Allan, *Asplenium flaccidum* Forst.f., *A. bulbiferum* Forst.f., *Grammitis billardieri* Willd., *Hymenophyllum* spp., and *Tmesipteris tannensis* Bernh. Other species included *Dendrobium cunninghamii* Lindl., *Archeria traversii* Hook.f., *Libertia* sp., and the blue fungus *Entoloma hochstetteri* (Reichardt) Stevenson. Liverworts and mosses were mainly confined to fallen logs with *Dicranoloma robustum* (H.f. et W.) Par. being the most common.

METHODS

Field Sampling and Sample Preparation

A relatively rapid method using quadrat sampling was employed to estimate the above-ground biomass and the nutrient contents of the forest components. A single plot (625 m²) was established in an unlogged area. Diameter at breast height was recorded on all canopy and understorey species taller than 1.4 m within the plot. In April 1974, the forest on and surrounding the plot was felled and thirty 1-m² quadrats were established randomly within the plot.

The above-ground biomass and nutrient pools in the various forest components were estimated by collecting the felled tree biomass (canopy trees), understorey biomass (including ground vegetation), and soil litter (L horizon) from each quadrat separately. The boundary of each quadrat was defined horizontally from the uphill side using a wooden frame. The biomass was separated by cutting the vegetation vertically through the line of the quadrat boundary using a saw and secateurs. Canopy trees were then separated into foliage, twigs less than 1 cm diameter, branches and stems 1–5 cm diameter, and branches and stems greater than 5 cm diameter. Understorey species were separated into foliage and twigs less than 1 cm diameter, and branches and stems greater than 1 cm diameter. Soil litter was separated into leaves and twigs less than 1 cm diameter, and woody detritus greater than 1 cm diameter. All woody samples included wood plus bark. Individual species were not separated, nor were samples collected for individual trees.

Each component within each quadrat was weighed and subsampled for determination of moisture and nutrient concentrations. Twigs were cut into small lengths (5–10 cm) prior to subsampling. Branches and stems were sampled by cutting discs from the centre of each piece of wood.

Subsamples were dried to constant weight in an air-circulating oven at 70–80°C. All samples were finely ground in a Tema mill. Branch and stem samples were initially coarsely ground in a Wiley mill.

Chemical Analyses

Total sodium, potassium, calcium, magnesium, and phosphorus were determined separately on each biomass fraction from each quadrat. Total nitrogen, sulphur, and chlorine were determined on six composite samples obtained by randomly bulking five quadrat samples proportionately by component weight. For understorey branches and stems greater than 1 cm diameter, the low weight of sampled material necessitated bulking into a single sample for chemical analysis for total nitrogen, sulphur, and chlorine.

Finely ground biomass material was wet-ashed with concentrated nitric and perchloric acids as described by Johnson & Ulrich (1959). Phosphorus in the digest was analysed by the vanadomolybdo-phosphoric acid method (Jackson 1958) and calcium, magnesium, potassium, and sodium were determined by atomic absorption spectrophotometry. Strontium was used as a releasing agent for calcium, and cesium chloride was added to suppress ionisation for sodium and potassium determinations.

Chloride, extracted from ground plant material by shaking overnight with distilled

water (1:250) as described by Johnson & Ulrich (1959), was determined colorimetrically on filtered samples using an autoanalytic procedure based on the ferric-mercuric thiocyanate method (Zall *et al.* 1956). Sulphur was determined by X-ray fluorescence.

Total Kjeldahl nitrogen, including nitrate, was determined on plant material samples by an adaptation of the method given by Goh (1972) for soils. A selenium catalyst was used. Preliminary comparison between mercury and selenium catalysts showed that both methods gave very similar results for finely ground leaves and woody material.

RESULTS AND DISCUSSION

Biomass and Nutrient Contents

The stocking and basal area of the main species in the podocarp-hardwood forest plot are shown in Table 1. A large proportion of the two dominant species (Westland quintinia and kamahi) occurred as saplings with a breast height diameter of less than 10 cm, suggesting a rather young stand with many small stems.

TABLE 1—Stocking and basal area (m²/ha) of the main species in the podocarp-hardwood forest plot

Species	Stocking (stems/ha)	Basal area (m ² /ha)
Quintinia acutifolia	1408	20.16
Weinmannia racemosa	1232	28.29
Metrosideros umbellata	32	1.78
Prumnopitys ferruginea	32	4.16
Dacrydium cupressinum	16	0.69
Myrsine salicina	48	0.02
Coprosma foetidissima	64	0.06
Total	2832	55.16

Mean nutrient concentrations, with 95% confidence intervals, for components of the podocarp-hardwood forest plot are shown in Table 2, with corresponding data for biomass oven-dry weights and nutrient contents in Table 3.

As expected, foliage nutrient concentrations were higher than for any of the woody components in the above-ground biomass (Table 2). In the branches and stems, nutrient concentrations were generally lower in the 1–5 cm diameter component than in the less-than-1-cm-diameter component. The relatively small difference for potassium is similar to that observed by Miller (1963) in hard beech branches. Concentrations in branches and stems greater than 5 cm in diameter were lower for phosphorus, nitrogen, and sulphur but similar for potassium, calcium, and magnesium, compared with those in the 1–5 cm diameter component.

Comparison of foliage nutrient concentrations in New Zealand beech species (Miller 1963; Heine 1973; Adams 1976) and in radiata pine (Madgwick *et al.* 1977; Will

TABLE 2—Mean nutrient concentrations (% by weight), with 95% confidence intervals, in components of podocarp-hardwood forest

Component		Na	K	Ca	Mg	P	Cl	N	S
Canopy trees									
Foliage	Mean	0.11	0.67	0.52	0.34	0.056	0.24	0.79	0.20
	±	0.02	0.06	0.03	0.03	0.003	0.04	0.02	0.05
Twigs < 1 cm diam.	Mean	0.04	0.22	0.34	0.13	0.027	0.11	0.27	0.10
	±	0.01	0.02	0.06	0.02	0.002	0.03	0.04	0.03
Branches and stems 1-5 cm diam.	Mean	0.08	0.16	0.20	0.08	0.014	0.05	0.14	0.066
	±	0.02	0.02	0.02	0.01	0.001	0.01	0.03	0.011
Branches and stems > 5 cm diam.	Mean	0.04	0.15	0.22	0.07	0.008	0.04	0.088	0.039
	±	0.01	0.02	0.02	0.01	0.006	0.02	0.023	0.012
Understorey									
Foliage and twigs	Mean	0.16	0.38	0.33	0.25	0.041	0.24	0.46	0.17
	±	0.02	0.04	0.03	0.02	0.003	0.02	0.18	0.03
Branches and stems > 1 cm diam.	Mean	0.13	0.097	0.089	0.056	0.007	0.12	0.17	0.12
	±	0.23	0.022	0.092	0.002	0.009	N.D.	N.D.	N.D.
Litter									
Leaves and twigs < 1 cm diam.	Mean	0.03	0.11	0.47	0.19	0.031	0.04	0.47	0.11
	±	0.01	0.05	0.01	0.01	0.003	0.01	0.03	0.01
Woody detritus > 1 cm diam.	Mean	0.12	0.34	0.22	0.13	0.006	0.02	0.19	0.039
	±	0.01	0.05	0.01	0.02	0.001	0.01	0.02	0.011

N.D. = not determined

TABLE 3—Dry weight (t/ha) and nutrient content (kg/ha), with 95% confidence intervals, in components of podocarp-hardwood forest

		Dry wt.	Na	K	Ca	Mg	P	Cl	N	S
Canopy trees										
Foliage	Mean	5.8	6.2	38.6	30.2	19.5	3.2	13.6	44.3	11.6
	±	2.1	2.6	13.0	9.6	6.5	1.2	5.3	17.3	5.4
Twigs < 1 cm diam.	Mean	10.7	4.4	23.3	36.3	14.3	2.9	11.2	30.1	11.0
	±	3.8	2.3	8.4	14.9	6.0	1.0	5.5	15.5	6.0
Branches and stems 1-5 cm diam.	Mean	25.5	19.6	41.5	50.5	21.6	3.6	12.9	36.1	16.8
	±	9.0	9.2	16.0	17.8	9.1	1.4	5.8	13.8	5.6
Branches and stems > 5 cm diam.	Mean	209.8	84.3	314.5	469.1	145.9	16.1	83.9	186.6	76.8
	±	75.2	29.4	139.5	192.5	57.4	5.5	66.1	154.6	42.9
Total		251.8	114.5	417.9	586.1	201.3	25.8	121.6	297.1	116.2
Understorey										
Foliage and twigs < 1 cm diam.	Mean	1.8	2.9	6.8	5.6	4.4	0.7	4.4	8.7	3.1
	±	0.5	1.0	1.6	1.4	1.0	0.2	1.5	2.6	0.8
Branches and stems > 1 cm diam.	Mean	0.7	0.9	0.7	0.6	0.4	0.1	0.1	0.2	0.1
	±	1.0	1.6	0.9	0.8	0.6	0.1	0.3	0.6	0.3
Total		2.5	3.8	7.5	6.2	4.8	0.8	4.5	8.9	3.4
Total above-ground biomass		254.3	118.3	425.4	592.3	206.1	26.6	126.1	306.0	119.6
Litter										
Leaves and twigs < 1 cm diam.	Mean	15.2	5.1	17.7	73.0	29.7	4.5	4.7	59.0	14.6
	±	2.9	1.0	4.0	15.2	5.0	0.7	2.2	32.9	6.8
Woody detritus > 1 cm diam.	Mean	66.8	82.9	226.9	146.1	89.5	4.3	13.2	147.4	25.8
	±	91.3	126.1	356.2	218.3	144.3	6.2	19.1	275.6	48.6
Total litter		82.0	88.0	244.6	219.1	119.2	8.8	17.9	206.4	40.4

1978) with those in Table 2 shows some differences. Thus nitrogen and phosphorus concentrations are lower in the podocarp-hardwood forest species while potassium and calcium concentrations are respectively lower and higher than for radiata pine in the central North Island. Of particular interest are the high concentrations of foliage magnesium in the podocarp-hardwood forest species. These are near the upper limit of the usual range reported for forest trees throughout the world. In contrast, nutrient concentrations in the woody components of the above-ground biomass are generally similar in the different forest types except for calcium concentrations which are considerably higher in the podocarp-hardwood forest and in hard beech (Miller 1963) than in radiata pine (Orman & Will 1960; Madgwick *et al.* 1977). These differences may be due partly to the use in this study of bulked samples from several species, the inclusion of bark in branches and stems, and the use of foliage of various ages. However, they do provide a broad indication of differing nutrient immobilisation in the podocarp-hardwood and radiata pine forests.

Sulphur concentrations have been infrequently determined in forest biomass studies in New Zealand. The average sulphur concentration in the podocarp-hardwood foliage was similar to that for foliage of the main tree species at Hubbard Brook, New Hampshire, United States (Likens & Bormann 1970) but higher than that of most Russian forests reported by Rodin & Bazilevich (1967).

Biomass oven-dry weights and nutrient contents are shown in Table 3. The estimate of total above-ground biomass (254 t/ha) for the podocarp-hardwood forest plot is broadly similar to those for other forests in New Zealand: a hard beech forest near Wellington (314 t/ha, Miller 1963); a 26- to 29-year-old radiata pine stand near Rotorua (198 t/ha, Orman & Will 1960); a 22-year-old radiata pine stand in Kaingaroa State Forest (316 t/ha, Madgwick *et al.* 1977); and a beech-podocarp forest near Reefton (306 t/ha, Beets 1980). The understorey comprised less than 1% of the total above-ground biomass which is similar to that reported by Beets (1980). Weights of foliage, branch and stem material, and litter (leaves and twigs) were also similar to Beets' (1980) estimates for comparable components of beech-podocarp biomass. Foliage biomass is lower in these indigenous forests than for radiata pine stands in the North Island (Orman & Will 1960; Will 1964; Madgwick *et al.* 1977).

Although podocarp-hardwood foliage comprised only 2.3% of the total above-ground biomass, its proportion of nutrients was considerably higher – about 5% for sodium and calcium, and 9–15% for the other elements studied (Table 3). In all components of the podocarp-hardwood above-ground biomass, nitrogen, calcium, and potassium were present in greatest amounts by weight. In foliage and in the understorey, the relative abundance was nitrogen > potassium > calcium. In woody samples from canopy trees, nitrogen and calcium decreased and increased respectively with increasing diameter of branches and stems. Hence in branches and stems, the relative abundance of the three elements was calcium > potassium > nitrogen. Nitrogen is usually more abundant than calcium or potassium in foliage (Miller 1963; Ovington & Madgwick 1959; Johnson & Risser 1974) although this is not invariably the case (Ralston & Prince 1965). In the total above-ground components of forest biomass, calcium is more abundant than nitrogen or potassium in many hardwood forests (Miller 1963; Duvigneaud & Denaeyer-De Smet 1968; Ovington & Madgwick 1959; Johnson & Risser 1974) but

in some hardwood and many coniferous forests nitrogen is most abundant (Turner *et al.* 1976; Ralston & Prince 1965; Will 1964; Wright & Will 1958; Switzer & Nelson 1972).

Amounts of nitrogen and phosphorus immobilised in podocarp-hardwood branches and stems (Table 3) were similar to those reported for radiata pine in New Zealand (Orman & Will 1960; Madgwick *et al.* 1977). However, the total phosphorus content of the above-ground biomass in the podocarp-hardwood forest is only about one-third of that in Miller's (1963) hard beech forest although amounts of nitrogen were similar in both. Calcium immobilisation in both foliage and woody components of the podocarp-hardwood forest was considerably higher than for radiata pine stands. The soils within the podocarp-hardwood plot are strongly acid and have very low levels of exchangeable calcium (Mew 1980), reflecting the high immobilisation of calcium in the biomass.

Differences in the relative immobilisation of calcium and magnesium in the podocarp-hardwood plot and in Miller's (1963) hard beech stand are marked. The hard beech stand contained 1120 kg Ca/ha and 123 kg Mg/ha compared with 592 kg Ca/ha and 206 kg Mg/ha in the podocarp-hardwood plot. The reason for or significance of this large difference is not known.

Coefficients of variation (CV) for the most variable concentrations and amounts in the components of the podocarp-hardwood forest plot are presented in Table 4. Individual CV for the 1-m² quadrats for biomass and nutrient contents ranged from 85% to 119% for foliage and woody components in canopy trees for those nutrients (potassium, calcium, magnesium, and phosphorus) determined separately on each component from each quadrat. Bulking samples for nitrogen, sulphur, and chlorine determinations into six composite samples reduced the CV for nutrient weights to 30–75%. Coefficients of variation in the leaf and twig component of the litter were similar for bulked and non-bulked samples and ranged from 42% to 60%. Estimates of biomass and nutrient weights of the woody detritus were particularly variable with CV ranging from 380% to 430% for non-bulked samples and from 140% to 180% for the bulked samples.

Variability in nutrient contents was largely determined by variability in dry weights of the biomass components as CV for nutrient concentrations were considerably less than those for dry weights (Table 4). Thus, in forests of this type, it is important to estimate biomass of the various components as carefully as possible when determining nutrient pools by quadrat sampling. Twenty-five 1-m² quadrats for foliage and 35 for branches and stems would be required to obtain estimates of mean nutrient contents in these biomass components with a standard error within $\pm 20\%$ of the mean (Table 4).

Large woody detritus, such as fallen trees and decaying stumps, was very inadequately sampled by quadrats. Methods such as the line intersect technique (Warren & Olsen 1964; van Wagner 1968) or whole plot sampling would be more appropriate since they involve greater sampling intensity.

The quadrat method used in this study to estimate biomass and nutrient contents of the various forest components is relatively rapid, involving no separation of individual trees or species. This approach was adopted to overcome the constraints of available

TABLE 4—Coefficients of variation for component dry weights, nutrient concentrations, and nutrient contents (of the most variable element), and the number of samples required to reduce the standard error to within 10% and 20% of the mean

Component	C.V.			Number of samples					
	Dry wt.	Nutrient conc.	Nutrient content	± 10% of mean			± 20% of mean		
				Dry wt.	Nutrient conc.	Nutrient content	Dry wt.	Nutrient conc.	Nutrient content
Canopy trees									
Foliage	96	26 (P)	98 (P)	92	7	96	23	2	24
Twigs < 1 cm diam.	95	43 (Ca)	112 (Mg)	91	19	125	23	5	32
Branches and stems 1–5 cm diam.	94	34 (Mg)	112 (Mg)	89	12	125	22	3	32
Branches and stems > 5 cm diam.	96	41 (S)	119 (K)	92	17	142	23	5	35
Understorey									
Foliage and twigs < 1 cm diam. plus branches and stems > 1 cm diam.	74	29 (K)	70 (P)	55	9	49	14	3	13
Litter									
Leaves and twigs < 1 cm diam.	49	38 (K)	60 (K)	24	15	36	6	4	9

resources, the selection of suitable plots being restricted by recent logging activities in the area. The method provides estimates of biomass for several forest components which are similar to those obtained (using whole plot sampling) by Beets (1980) in beech-podocarp forest in Westland. The number of quadrats used (30) was sufficient to provide estimates of most biomass components (except woody detritus on the forest floor) with a reasonable level of precision. The quadrat method used thus appears to have given satisfactory estimates of forest biomass and nutrient contents in this forest type.

Effect of Tree Harvesting

In recent years there has been considerable interest in the possibility of harvesting chipwood as well as sawlogs from Westland forests. A chipwood logging operation would result in removal of all logs with a small-end diameter greater than 10 cm. Nutrient removal under this regime would be greater than at present when only merchantable podocarp sawlogs are harvested.

Over 80% of the biomass of the podocarp-hardwood forest plot was in the large branch and stem component (greater than 5 cm diameter). Of this, about 10% was estimated from the samples collected to be between 5 and 10 cm diameter. This component was not separated for chemical analysis but, if it is assumed that nutrient concentrations in the 5–10 cm diameter wood fraction are approximated by averaging nutrient levels in the 1–5 cm and greater-than-5-cm-diameter branches and stems, then the proportion of nutrients in the biomass which would be removed by a chipwood logging operation can be estimated (Table 5).

Total removal of biomass nitrogen and phosphorus in a chipwood logging operation would be similar to that calculated for radiata pine sawlogs in Kaingaroa Forest (Orman & Will 1960). However, the effect on long-term site productivity is likely to be more significant in the low-nutrient Westland ecosystems (Adams 1978). Losses of calcium and magnesium particularly but also potassium would be considerably greater from the Westland indigenous forest than from Kaingaroa pine forest.

Losses of calcium by chipwood logging may not have a significant effect on tree growth where sites are replanted with pine species which have relatively low calcium requirements. However, where indigenous forest is regenerated and fertiliser applications are not made, the losses of calcium, magnesium, potassium, and phosphorus from the organic nutrient cycle may influence tree growth, since levels of exchangeable cations and available-phosphorus are very low on this site (Levett 1978). It is likely that present forest growth on these soils is closely associated with a very efficient nutrient cycle, largely in the organic horizons.

ACKNOWLEDGMENTS

The authors acknowledge the assistance of the New Zealand Forest Research Institute in providing funds for the study, Mr Neville Clyne and other Forest Service staff who helped with field sampling, Ms Alison Carter who undertook many of the chemical analyses, and Mr A. H. Nordmeyer, Dr G. M. Will, and Dr P. N. Beets for their constructive criticism of the manuscript.

TABLE 5—Dry weight and nutrient content of branches and stems > 10 cm diameter in podocarp-hardwood forest as a percentage of total above-ground biomass and nutrient contents. Estimated nutrient removal by chipwood logging, and nutrients remaining in slash and litter are also shown

		Dry wt.	Na	K	Ca	Mg	P	Cl	N	S
Branches and stems > 10 cm diam.	(%)	74	61	66	72	63	52	59	53	55
Removal by chipwood logging	(kg/ha)	188 800	71.7	282.0	425.0	130.2	13.8	74.5	162.7	65.8
Remaining in slash	(kg/ha)	65 500	46.6	143.4	167.3	75.9	12.8	51.6	143.3	53.8
Remaining in litter	(kg/ha)	82 000	88.0	244.6	219.1	119.2	8.8	17.9	206.4	40.4

REFERENCES

- ADAMS, J. A. 1976: Nutrient requirements of four *Nothofagus* species in north Westland, New Zealand, as shown by foliar analysis. **New Zealand Journal of Botany** **14**: 211-33.
- 1978: Long-term aspects of nutrient loss from forest soils and ecosystems. **New Zealand Journal of Forestry** **23**: 10-20.
- BEETS, P. N. 1980: Amount and distribution of dry matter in a mature beech/podocarp community. **New Zealand Journal of Forestry Science** **10**: 395-418.
- DUVIGNEAUD, P.; DENAEYER-DE SMET, S. 1968: Biomass, productivity and mineral cycling in deciduous mixed forests in Belgium. Pp. 168-86 in Young, H. E. (Ed.) "Symposium on Primary Production and Mineral Cycling in Natural Ecosystems". University of Maine Press.
- 1970: Biological cycling of minerals in temperate deciduous forests. Pp. 199-255 in Reichle, D. E. (Ed.) "Analysis of Temperate Forest Ecosystems". Chapman and Hall Ltd, London.
- FOSTER, N. W.; MORRISON, I. K. 1976: Distribution and cycling of nutrients in a natural *Pinus banksiana* ecosystem. **Ecology** **57**: 110-20.
- GOH, K. M. 1972: Comparison and evaluation of methods for including nitrate in the total nitrogen determination of soil. **Journal of the Science of Food and Agriculture** **23**: 275-84.
- HEINE, M. 1973: A comparison of nutrients in leaves and litter of red, silver and mountain beech. **Mauri Ora** **1973**: 55-60.
- JACKSON, M. L. 1958: "Soil Chemical Analysis". Prentice-Hall Inc., Englewood Cliffs, New Jersey, 498 p.
- JOHNSON, C. M.; ULRICH, A. 1959: Analytical methods for use in plant analysis. **California Agriculture Experiment Station Bulletin 766 (Part II)**: 26-78.
- JOHNSON, F. L.; RISSER, P. G. 1974: Biomass, annual net primary production, and dynamics of six mineral elements in a post oak-blackjack oak forest. **Ecology** **55**: 1246-58.
- LEVETT, M. P. 1978: Aspects of nutrient cycling in some indigenous and exotic forests in Westland, New Zealand. Ph.D. Thesis, Lincoln College, Canterbury University.
- LIKENS, G. E.; BORMANN, F. H. 1970: Chemical analyses of plant tissues from the Hubbard Brook ecosystem in New Hampshire. **Yale University School of Forestry Bulletin** **79**. 25 p.
- MADGWICK, H. A. I.; JACKSON, D. S.; KNIGHT, P. J. 1977: Above-ground dry matter, energy, and nutrient contents of trees in an age series of *Pinus radiata* plantations. **New Zealand Journal of Forestry Science** **7**: 445-68.
- MASTERS, S. E.; HOLLOWAY, J. T.; McKELVEY, P. J. 1957: "The National Forest Survey of New Zealand, 1955." Government Printer, Wellington.
- MEW, G. 1980: Soils, forestry and agriculture of the Grey Valley, South Island, New Zealand. **New Zealand Soil Survey Report** **46**.
- MILLER, R. B. 1963: Plant nutrients in hard beech. I. The immobilisation of nutrients. **New Zealand Journal of Science** **6**: 365-77.
- ORMAN, H. R.; WILL, G. M. 1960: The nutrient content of *Pinus radiata* trees. **New Zealand Journal of Science** **3**: 510-22.
- OVINGTON, J. D.; MADGWICK, H. A. I. 1959: The growth and composition of natural stands of birch. II. The uptake of mineral nutrients. **Plant and Soil** **10**: 389-400.
- RALSTON, C. W.; PRINCE, A. B. 1965: Accumulation of dry matter and nutrients by pine and hardwood forests in the Lower Piedmont of North Carolina. Pp. 77-94 in

Youngberg, C. T. (Ed.) "Forest-soil relationships in North America". Oregon State University Press.

- RENNIE, P. J. 1955: The uptake of nutrients by mature forest growth. **Plant and Soil 7**: 49-95.
- RODIN, L. E.; BAZILEVICH, N. I. 1967: "Production and Mineral Cycling in Terrestrial Vegetation". Oliver and Boyd, Edinburgh.
- SWITZER, G. I.; NELSON, L. E. 1972: Nutrient accumulation and cycling in loblolly pine (*Pinus taeda* L.) plantation ecosystems: the first twenty years. **Soil Science Society of America Proceedings 36**: 143-7.
- TURNER, J.; COLE, D. W.; GESSEL, S. P. 1976: Mineral nutrient accumulation and cycling in a stand of red alder (*Alnus rubra*). **Journal of Ecology 64**: 956-74.
- van WAGNER, C. E. 1968: The line intersect method in forest fuel sampling. **Forest Science 14**: 20-6.
- VITOUSEK, P. M.; REINERS, W. A. 1975: Ecosystem succession and nutrient retention: a hypothesis. **BioScience 25**: 376-81.
- WARREN, W. G.; OLSEN, P. F. 1964: A line intersect method for assessing logging waste. **Forest Science 10**: 267-76.
- WEETMAN, G. F.; WEBBER, B. 1972: The influence of wood harvesting on the nutrient status of two spruce stands. **Canadian Journal of Forestry Research 2**: 351-69.
- WELLS, C. G.; JORGENSEN, J. R. 1975: Nutrient cycling in loblolly pine plantations. Pp. 137-58 in Bernier, B.; Winget, C. H. (Ed.) "Forest Soils and Forest Land Management". Proceedings of the 4th North American Forest Soils Conference, Quebec, 1973. Laval University Press, Quebec.
- WILL, G. M. 1964: Dry matter production and nutrient uptake by *Pinus radiata* in New Zealand. **Commonwealth Forestry Review 43**: 57-70.
- 1978: Nutrient deficiencies in *Pinus radiata* in New Zealand. **New Zealand Journal of Forestry Science 8**: 4-14.
- WRIGHT, T. W.; WILL, G. M. 1958: The nutrient content of Scots and Corsican pines growing on sand dunes. **Forestry 31**: 13-25.
- ZALL, D. M.; FISHER, D.; GARNER, M. O. 1956: Photometric determination of chlorides in water. **Analytical Chemistry 28**: 1665-8.