RESEARCH NOTE

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ORGANIC CONSTITUENTS OF FOREST HUMUS LAYERS IN THE COASTAL WESTERN HEMLOCK BIOGEOCLIMATIC ZONE OF BRITISH COLUMBIA IN RELATION TO FOREST ECOSYSTEMS

1. PROXIMATE ANALYSIS

by

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ORGANIC CONSTITUENTS OF FOREST HUMUS LAYERS IN THE COASTAL WESTERN HEMLOCK BIOGEOCLIMATIC ZONE OF BRITISH COLUMBIA IN RELATION TO FOREST ECOSYSTEMS. 1. PROXIMATE ANALYSIS

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ABSTRACT

A proximate analysis procedure, involving the estimation of lipid, soluble polysaccharide, hemicellulose, cellulose, 'protein', and 'lignin-humus' fractions, was applied to replicated samples of humus layers derived from soils of xeric, mesic and hygric hygrotopes in the dry subzone of the Coastal western hemlock biogeoclimatic zone, as well as to tissue samples and samples of decayed wood. Additional chemical characteristics of humus layer samples were also determined.

Differences between ecosystems were noted with respect to proximate analysis, pH, % base saturation and ratios of exchangeable Ca to exchangeable K and Mg. These differences were apparently related to moisture regime.

Proximate analysis reflects the degree of decomposition of humus layer or litter samples, and the rates of cellulose to lignin-humus fractions is suggested as a relatively sensitive index of this property. Use of a hierarchical grouping analysis technique indicated that proximate analysis can discriminate between materials of diverse origin. In general, however, it was concluded that proximate analysis, while a useful supplement to other chemical data, is not in itself sufficient to distinguish between humus layers of most forest ecosystems, or to reveal differences in the nature of humification products.

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INTRODUCTION

Forest humus layers constitute an important component of forest ecosystems (biogeocoenoses), but one which as yet is not fully understood, either with respect to its significance in soil genesis, or its importance in determining forest management decisions.

Organic soil horizons are undoubtedly of importance in relation to biological activity, nutrient release, cation retention and humus formation and translocation. Physical properties of forest soils, including thermal properties, infiltration and water retention are also profoundly influenced by forest humus layers. While considerable information is available on the distribution of nutrient elements in forest humus layers in a variety of ecosystems, very little is known of the nature and distribution of organic components. Furthermore, much of the available information cannot be related to carefully defined ecosystem units.

The present study was part of a programme carried out at the University of British Columbia Research Forest, at Haney, B.C., designed to evaluate relationships between forest ecosystems (defined by synecological methods) and the properties and genesis of forest humus layers. The objectives of the study reported here, were 1. to find out whether significant differences could be detected between selected forest ecosystems on the basis of proximate analysis of forest humus layers; and 2. to investigate the possible influence of understory vegetation and decayed wood on the distribution of organic fractions, as indicated by proximate analysis. A subsequent paper will report on a study of humus fractions on the same sites.

MATERIALS AND METHODS

Sampling Sites

Samples of organic horizons were collected from forest ecosystems in the U.B.C. Research Forest, which lies in the Coastal western hemlock (CWH) biogeoclimatic zone (Krajina 1959, 1965 and 1969). Plots were classified into ecosystem units at several levels of generalization, following the analysis of vegetation by the phytosociological techniques of the Zürich-Montpellier School (Braun-Blanquet 1928, 1951, Krajina 1933, Becking 1957) and of corresponding habitats as adopted by Krajina and his students. Classification of both vegetation and soils was applied to form any ecologically significant unit. Classification, characterization and mapping of the ecosystem units are described elsewhere (e.g. Brooke *et al.* 1970, Orloci 1964 and 1965).

The three ecosystem units used for proximate analysis in the present study were selected on soils with xeric, mesic and hygric hygrotopes in the Drier Douglas-fir - western hemlock subzone of the Coastal western hemlock zone (CWHa). Xeric habitats were well drained, whereas the hygric habitats were characterized by permanent subsurface flow of seepage water. Some chemical data is also presented for three units of the same hygrotopes in the Wetter Pacific silver fir - western hemlock subzone (CWHb). Although some species of tree layers and soil subgroups varied between individual plots of the same hygrotope; shrub, herb and moss layers were very similar. This similarity formed the basis on which these plots were grouped into units at several levels of generalizations, out of which a plant alliance was used in the study.

Detailed descriptions of the units, with respect to vegetation and soil, were given by Orloci (1964). Brief descriptions are presented below:

I. CWHa 1. GAULTHERIA - DOUGLAS-FIR plant alliance [*Gaultherio (shallonis) - Pseudotsugion menziesii*]

Forest ecosystems (plot numbers: 021, 030, 057 and 083), classified into this ecosystem unit at the abstration level of plant alliance are characteristic of xeric habitats, i.e. shallow, very rapidly drained, coarse textured soils, located on upper slopes and ridges. Associated soils were loamy sand, Lithic Mini Humo-Ferric Podzol, Lithic Podzol and Lithic Folisol with mor humus developed from moraine veneer over quartzdiorite bedrock. Present forest cover was 90-year old secondary Douglas-fir stands.

2. MOSS - WESTERN HEMLOCK plant alliance [*Plagiothecio (undulati) - Rhytidiadelpho (lorei) - Pseudotsugo (menziesii) - Tsugion heterophyllae*]

Forest ecosystems (plot numbers 007, 024, 032, 124) classified in this alliance are characteristic of mesic habitats, i.e. moderately deep and moderately well drained soils located on middle slopes or flat divides. Associated soils were loamy sand to sandy loam, Mini and Orthic Humo-Ferric Podzols with mor humus developed from moraine blanket over quartzdiorite bedrock. Present forest cover was Douglas-fir (plot no. 007 and 032) and western hemlock (plot no. 024 and 124) 90-year old secondary stands.

3. TIARELLA - POLYSTICHUM - WESTERN REDCEDAR plant alliance [*Plagiomnio (insignis) - Tiarello (trifoliatae) - Polysticho (muniti) - Thujion plicatae*]

Forest ecosystems (plot no. 015, 098, 135 and 148) classified in this alliance are characteristic of hygric habitats affected by lateral flow of seepage water, i.e. moderately deep to deep, imperfectly drained soils located on lower concave slopes.

Associated soil were sandy loam and clay loam (Gleyed) Sombric Humo-Ferric and Ferro-Humic Podzols with mull humus developed from glacio-fluvial and glaciomarine deposits (plot no. 098 and 148) respectively; and loamy, skeletal Orthic Regosol and Orthic Dystric Brunisol with mull humus developed from colluvial deposits (plot no. 015 and 135). Forest cover was variable; however, a constant component of 90-year old secondary stands was western redcedar.

II. CWHb 1. Vaccinium - Gaultheria - Douglas-fir - western hemlock plant association [*Pleurozio (schreberi) - Rhytidiopsido (robustae) - Gaultherio (shallonis) - Vaccinio (alaskaensis) - Pseudotsugo (menziesii) - Tsugetum heterophyllae*]

Forest ecosystems (plot no. 053, 055, 056 and 063), classified into this association, are characteristic of xeric habitats, i.e. very shallow, rapidly drained soils, located at upper slopes and narrow ridges. Associated soils were coarse textured Lithic Podzol, Lithic Orthic Humo-Ferric Podzol and Lithic Folisol with mor humus developed from moraine veneer over quartzdiorite bedrock. Present forest cover was formed either by old growth stands of Douglas-fir and western hemlock (plot no. 060 and 063) or by secondary, 90-year old stands of western hemlock and Douglas-fir.

2. Vaccinium - moss - western hemlock plant association [*Rhytidiopsido (robustae) - Vaccinio (alaskaensis) - Menziesio (ferrugineae) - Tsugetum heterophyllae*]

Forest ecosystems (plot no. 044, 087, 089 and 125), classified into this association, are characteristic of mesic habitats, i.e. rather shallow, moderately well drained soils, located on middle slopes or flat divides. Associated soils were sandy loam and loamy sand Lithic Podzol and Lithic and Orthic Humo-Ferric Podzol with mor humus developed from moraine deposits over quartzdiorite bedrock. Present forest cover was 90-year old secondary stands of western hemlock with amabilis fir.

These two plant associations belong to the alliance VACCINIUM - MOSS - WESTERN HEMLOCK [*Rhytidiopsido (rubustae) - Vaccinio (alaskaensis) - Menziesio (ferrugineae) - Tsugion heterophyllae*]

3. BLECHNUM - AMABILIS FIR - WESTERN HEMLOCK plant alliance [*Rhytidiadelpho (lorei) - Plagiothecio (undulati) - Blechno (spicantis) - Vaccinio (alaskaensis) - Menziesio (ferrugineae) - Abieto (amabilis) - Tsugion heterophyllae*]

Forest ecosystems (plot no. 062, 095, 114 and 149), classified into this alliance, are characteristic of hygric habitats affected by lateral subsurface flow of seepage water, i.e. moderately deep to deep, imperfectly drained soils, located on lower concave slopes.

Associated soils were sandy loam Gleyed Mini and Orthic Ferro-Humic Podzols with mor and moder (under secondary stands) humus, frequently with ortstein, developed from moraine and colluvial deposits. Present forest cover was formed either by old growth stands of western hemlock, western redcedar and Douglas-fir (plot no. 062 and 095) or by secondary, 90-year old stands of western hemlock, amabilis fir and western redcedar.

Samples

For each plot, a composite sample of ectorganic or endorganic layers (*sensu* Wilde 1971) was collected in the summer of 1973 or 1974. The samples were air-dried and ground in a Wiley mill. Following descriptions and chemical analysis, soils were classified according to the System of Soil Classification for Canada (1974), and the humus forms classified as mull, moder or mor according to Bernier (1968). Out of the total of 158 established plots, only four samples from four plots were selected for each unit in this study.

Samples of decayed wood and of foliage were also collected for evaluating the contribution of these materials to the humus layers. Five foliage samples of salal (*Gaultheria shallon* Pursh.) and of western sword-fern [(*Polystichum munitum* (Kaulf.) Presl] were taken. Salal is a major component of the ground cover on xeric habitats in association with Douglas-fir, whereas western sword-fern is a major component on hygric habitats in association with western red cedar. The triplicate samples of decayed wood were from Douglas-fir and western red cedar, in an advanced stage of decomposition, and were collected from debris left after logging of old growth in the 1930's. In the mesic MOSS - WESTERN HEMLOCK alliance, in particular, decayed wood represented a significant contribution to the surface organic accumulation.

Analytical Methods

Standard soil analyses followed procedures described by Black *et al.* (1965). Total carbon was measured with a Leco Induction Furnace and carbon analyser, total nitrogen by semimicrokjeldahl, and pH electrometrically in water and in 0.01 M $CaCl_2$. Cation exchange capacity and exchangeable cation measurement were based on saturation with 1 N ammonium acetate at pH 7. Extractable Fe and Al were determined by atomic absorption spectroscopy on extracts obtained with 0.1 M sodium pyrophosphate (Bascomb 1968).

Proximate analysis procedures were a modification of those described by Stevenson (1965). Details are given below, indicating the modifications.

Fraction 1. Lipids (fats, waxes, oils and resins):

10 g samples were extracted with 100 ml ethanol-benzene (1:1) for 3 hours, with shaking. After filtering (Whatman No. 42), the residue was washed with a further 100 ml ethanol-benzene and 50-75 ml ethanol. After removal of solvent, and drying at $100^{\circ}C$, the yield

of fraction 1 was determined gravimetrically, and corrected for ash content.

Fraction 2. Water soluble polysaccharides:

After removal of solvent, 100 ml distilled water were added to residue from first extraction and boiled under reflux for two hours. Extract was filtered hot through same filter paper used for fraction 1. Residue was washed thoroughly with hot water. After making filtrate plus washings to 1 litre, an aliquot was evaporated and the yield of fraction 2 obtained by weighing the oven dried residue, and correcting for ash content (ignition at 550°C).

Fraction 3. Hemicellulose:

The residue from the hot water extraction was dried at 100°C, weighed and one half of the residue transferred to a 500 ml flask. 300 ml 0.65 N HCl were added, and the sample hydrolysed in an autoclave for one hour at 15 P.S.I. After cooling and filtering, the residue was washed thoroughly with 0.65 N HCl, and the filtrate plus washings adjusted to 500 ml. Aliquots (20 ml) of these hydrolysates were then analysed for reducing sugars by addition of Fehlings solution and backtitrating excess Fehlings solution with standard glucose solution, as described by Stevenson (1965).

Fraction 4. Cellulose:

The residue from the HCl hydrolysis was oven dried at 100°C and weighed. Portions of the residue (2-3 g) were treated with 25 ml of 80% H_2SO_4 and allowed to stand for 2.5 hr at room temperature. The sample was then diluted by addition of 875 ml distilled water, and hydrolysed in the autoclave for one hour. After cooling, filtering, and washing, reducing sugars in the hydrolysate were determined by the same procedure as used for the hemicellulose fraction.

Fractions 5 and 6. Protein and 'lignin-humus':

Residue from the H_2SO_4 hydrolysis was oven dried and weighed and total C and total N content determined. Protein content was estimated as N% x 6.25. The lignin-humus fraction was calculated as:- organic matter in residue (C% x 1.724) minus protein. Results of the proximate analysis are expressed on a moisture-free, ash-free basis. Recovery of organic plus mineral constituents varied from 83% to 93% of original sample weight.

Proximate analysis has a number of well recognized limitations, especially when applied to soil materials. These will be discussed later. Even for plant tissue, the procedure can only be assumed to give an approximate picture of the distribution of major classes of organic materials. However, more sophisticated procedures are extremely time consuming.

RESULTS AND DISCUSSION

Chemical characteristics and humus forms for the samples representing each ecosystem are presented in Table 1. Considerable variation in form and thickness of humus layers is apparent for any given unit. Variations in total carbon content result from variations in mineral content, reflecting the humus form present. Low pH values were observed for all samples. pH values measured in $CaCl_2$ solution were always lower (on average by 0.46 pH units) than the values measured in water. Values for C/N ratio also reflected humus forms, being generally highest when mor types were present, and lowest for mull types.

Comparison of ecosystem units with respect to mean values for a number of chemical characteristics (Table 2), indicated some trends apparently related to moisture regime. For each subzone, pH and percent base saturation were highest for the hygric habitats. (This may be due to an influx of bases through seepage, or to a more effective cycling of subsoil nutrients by the vegetation characteristic of the hygric habitats.)

In the CWHa subzone, highest N levels were found for the mesic and lowest levels for the hygric habitats. N levels in the CWHb subzone increased from xeric to mesic to hygric habitats. In contrast, the C/N ratio, which tends to reflect both degree of litter decomposition and N mineralization rates, was lowest at the hygric habitats in both subzones. In particular, the low C/N (17.0) and high pH of the TIARELLA - POLYSTICHUM - WRC alliance indicate a greater biolgical activity than at the other units.

The distribution of exchangeable bases showed an interesting relationship to moisture regime. For both CWHa and CWHb subzones, an increase in moisture (xeric to mesic to hygric) was associated with increasing levels of exchangeable Ca but decreasing levels of exchangeable K and Mg. The magnitude of the effect is most clearly shown by changes in the Exch. Ca:Exch. K and Exch. Ca:Exch. Mg ratios (Table 2). Such differences in Ca:K ratios are likely to be of considerable nutritional significance, although it is not clear whether they have influenced the establishment of present vegetation, or are the result of vegetational differences. The depletion of K and Mg relative to Ca, with increasing moisture, may result from increased leaching of those cations less strongly held on the cation exchange sites. It was noted that exchangeable K levels represented, on average, over 90% of the total soil K values, whereas exchangeable Ca, although variable, represented on average only about 53% of the total Ca present in the humus layer samples. Thus, continuing decomposition would tend to increase the levels of Ca available for dominating the cation exchange sites.

Table 1. Some chemical characteristics and humus forms of the samples

Ecosystem unit*	Plot No.	Humus form	Thickness cm	pH (water)	Total C %	Total N %	C/N
CWHa, GAULTHERIA - DOUGLAS-FIR (xeric)							
	021	F-mor	7	4.18	37.39	1.22	30.6
	030	H-mor	11	3.64	43.71	1.17	37.4
	057	Moder	4	4.06	29.04	1.09	26.6
	083	F-mor	12	3.69	51.48	1.78	29.2
CWHa, MOSS - WESTERN HEMLOCK (mesic)							
	007	F-mor	4	4.23	50.23	1.54	32.6
	024	H-mor	35	3.85	54.14	1.60	33.8
	032	H-mor	12	3.98	47.65	1.28	37.2
	124	F-mor	7	3.56	52.58	1.33	39.5
CWHa, TIARELLA - POLYSTICHUM - WESTERN REDCEDAR (hygric)**							
	015	Mull (Ah)	30	5.33	15.07	1.16	13.0
	098	Moder (Ah)	15	4.56	15.07	0.74	20.4
	135	Mull (H)	10	5.60	41.91	1.81	23.2
	148	Mull (Ah)	10	5.20	8.39	0.73	11.5
CWHb, Vaccinium - Gaultheria - Douglas fir - western hemlock (xeric)							
	053	F-mor	10	3.55	53.33	1.31	40.7
	055	F-mor	12	3.56	52.93	1.17	45.2
	056	F-mor	11	3.80	49.39	1.25	39.5
	063	F-mor	9	3.70	53.80	1.34	40.1
CWHb, Vaccinium - moss - western hemlock (mesic)							
	044	H-mor	15	3.53	49.33	1.58	31.2
	087	H-mor	18	3.56	53.97	1.02	52.9
	089	F-mor	10	3.60	53.22	1.77	30.1
	125	H-mor	14	3.90	49.74	1.50	33.2
CWHb, BLECHNUM - AMABILIS FIR - WESTERN HEMLOCK (hygric)							
	062	F-mor	12	3.84	53.10	1.47	36.1
	095	H-mor	15	3.87	53.04	1.31	40.5
	114	Moder	12	4.37	44.58	1.57	28.4
	149	Moder	5	3.94	46.72	2.20	21.2

*Categorical rank of plant alliance and plant association was designated by capital and small letters respectively.

**The samples in this alliance originated from Ah or low organic matter H horizons. Soil organic layers here were very thin and consisted entirely of litter.

Table 2. Mean values of chemical characteristics for ecosystem units.

Ecosystem unit	pH	Total C %	Total N %	C/N	Exchangeable Cations (me/100 g) Ca	Mg	Na	K	CEC me/100 g	% Base Saturation	Pyrophosphate extractable Fe %	Al %	Exch Ca / Exch K	Exch Ca / Exch Mg
CWHa														
GAULTHERIA - DF	3.89	40.4	1.31	30.9	10.3	3.17	0.88	2.44	100.7	17.4	0.11	0.21	4.25	3.40
MOSS - WH	3.90	51.2	1.44	35.8	14.5	2.44	0.68	1.88	170.2	12.1	0.04	0.15	8.33	6.06
TIARELLA - *POLYSTICHUM* - WRC	5.15	20.1	1.11	17.0	18.3	1.88	0.12	0.36	74.6	23.2	0.45	1.10	47.40	8.49
CWHb														
Vaccinium - *Gaultheria* - DF - WH	3.65	52.4	1.37	41.4	8.9	3.21	1.26	2.53	132.0	12.1	0.06	0.15	3.68	2.83
Vaccinium - moss - WH	3.66	51.6	1.47	36.8	11.1	2.86	0.50	2.38	108.1	16.0	0.05	0.12	5.39	3.94
BLECHNUM - AF - WH	3.94	49.4	1.63	31.5	17.6	2.63	0.64	1.28	122.7	18.4	0.10	0.29	19.08	6.67

Tree species were abbreviated as follows: AF - amabilis fir [*Abies amabilis* (Dougl.) Forbes], DF - Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco], WH - western hemlock [*Tsuga heterophylla* (Raf.) Sarg], and WRC - western redcedar (*Thuja plicata* Donn ex D. Don in Lamb.)

It is interesting to note in this respect that ferns, being dominant herbs in the understory on hygric habitats, were found to have a high concentration of potassium in leaf tissues out of 54 common species of shrubs, herbs and mosses in the Research Forest. Concentrations (in % of oven-dried weight) were: 3.7 for *Athyrium filix-femina* (L.) Roth; 3.0 for *Gymnocarpium dryopteris* (L.) Newn.; 2.6 for *Dryopteris austriaca* (Jacq.) Woynar *ex* Schinz & Thell: and 1.8 for *Polystichum munitum* (Kaulf.) Presl. However, some other species, limited to these habitats in a smaller number, were found to have yet higher potassium concentrations e.g. 4.1 for *Trillium ovatum* Pursh.; 3.8 for *Oplopanax horridus* (J.E. Smith) Miq.; and 3.4 for *Sambucus pubens* Michx.

It is suggested that these species play an important role in preventing outflow of potassium out of the hygric ecosystems.

Pyrophosphate extractable Al and Fe, were markedly higher in the samples from the hygric habitats, especially in the CWHa subzone. Concentrations of Al and Fe in humus layers were found to be correlated with those in B horizon. Thus B horizons in soils on hygric habitats exhibited the highest concentrations of translocated Al and Fe.

Proximate analyses were carried out on samples for three alliances from the CWHa subzone, together with samples of two major ground cover species and of decayed wood (Table 3).

As indicated by the standard deviations (Table 3), variation in levels of each organic fraction was at times considerable, especially in the case of humus layers of the TIARELLA - POLYSTICHUM alliance. Nevertheless, significant differences in fraction distribution between sources were observed.

Proximate analysis gives a rough picture of the distribution of major chemical constituents. Since some constituents are degraded much more rapidly than others, fraction distribution gives an indication of the extent to which decomposition, and associated humus synthesis, has proceeded. A comparison of fraction distribution for fresh tissue with that of humus layers indicates the nature of the changes occurring during litter decomposition, namely decrease in lipid, soluble polysaccharide and cellulose fractions, and an increase in the so-called 'protein' and 'lignin-humus' fractions. However, the conventional designations for the latter two fractions are not entirely appropriate. While the 'protein' fraction probably consists largely of protein in undecomposed material, a large fraction of the N of humified materials is probably present in other forms, as yet not satisfactorily characterized. The 'lignin-humus' fraction contains both intact and slightly modified lignin, which will predominate in plant materials and relatively unhumified soil horizons; and humus fractions, which will predominate in well humified materials. The increase in lignin-humus fraction with decomposition is a function both of humus formation, and of relative enrichment in lignin through degradation of other less resistant plant constituents. Changes in the hemicellulose fraction with decomposition are less marked, since degradation of plant polysaccharides can be accompanied by synthesis of microbial heteropolysaccharides, which are recovered in the same fraction.

Table 3. Organic fraction distribution and effects of material on organic fractions

(fractions expressed as % of original organic matter)

Material	# samples	OM% O.D. basis	Lipid 1	Sol. PSS 2	Hemicell. 3	Cellulose 4	'Protein' 5	'Lignin-Humus' 6
HUMUS LAYERS								
GAULTHERIA - DF	4	69.7±	5.70±0.98bc	5.65±2.20a	16.43±4.16b	7.77±1.05a	6.00±2.03ab	56.70±5.66b
MOSS - WH	4	88.2±	6.27±1.03c	5.09±0.45a	16.61±2.03b	9.97±1.16ab	5.23±1.64ab	56.80±2.17b
TIARELLA - POLYSTICHUM - WRC	4	34.7±	1.88±0.82a	3.78±1.97a	8.82±3.29a	3.21±2.09a	12.67±9.45b	69.72±13.24b
TISSUE								
Gaultheria shallon	5	93.4±	14.48±1.58e	13.52±2.01b	17.24±3.27b	26.55±3.82c	4.37±1.22a	23.88±3.80a
Polystichum munitum	5	95.2±	11.00±1.44d	12.02±3.08b	18.62±2.44b	28.49±4.80cd	4.65±0.48a	25.03±7.50a
DECAYED WOOD								
Douglas-fir	3	99.0±	3.01±1.79ab	3.63±1.80a	17.06±0.90b	34.21±6.35d	1.23±0.05a	38.25±7.16a
Western redcedar	3	99.5±	2.59±1.14a	2.74±0.30a	12.21±6.00ab	17.44±1.29b	1.89±0.12a	63.13±7.98b
		P =	.0000	.0000	.0056	.0000	.0118	.0000

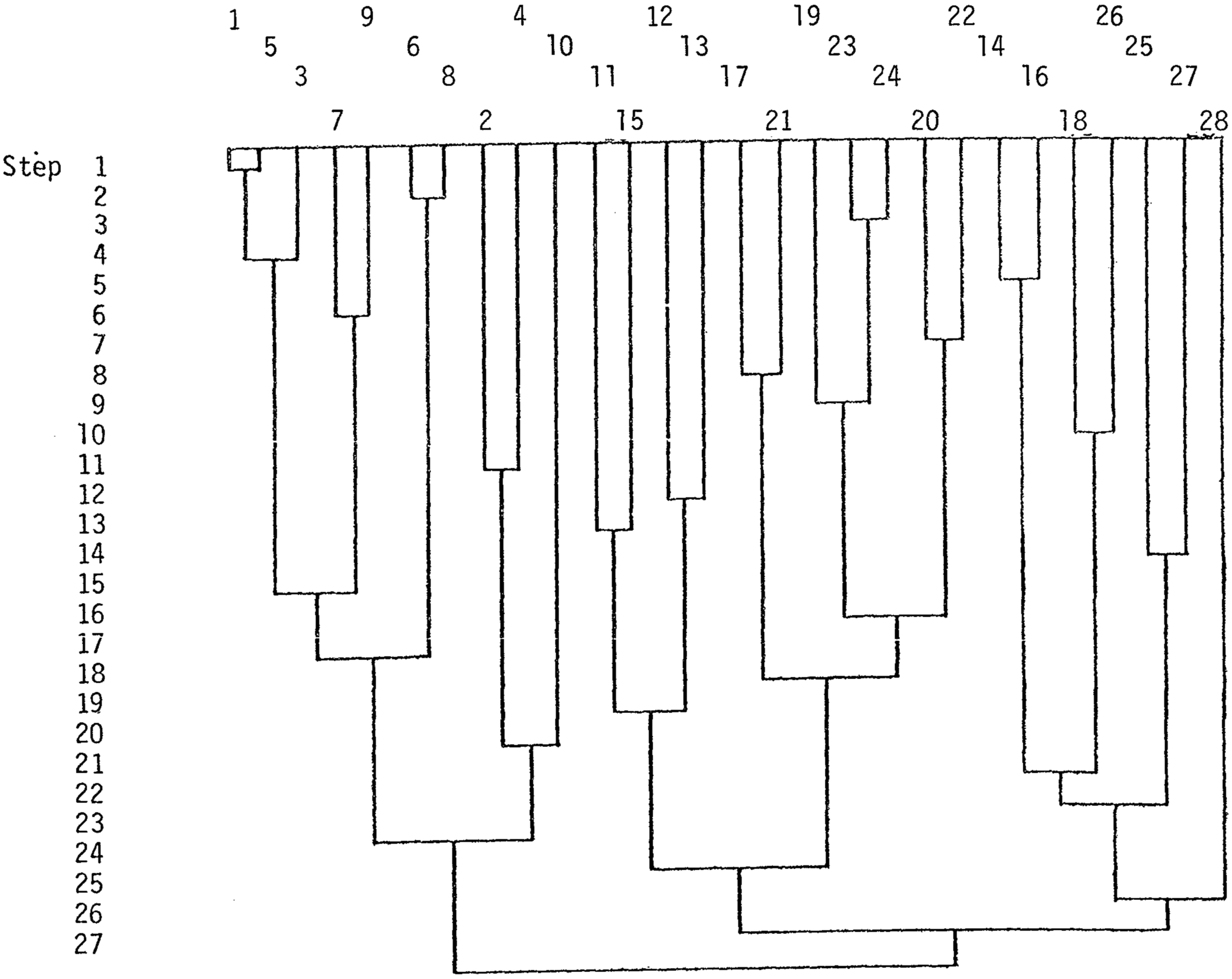
Values within column carrying the same letter superscript were not significantly different at the P = 0.05 level, using Duncan's Multiple Range Test.

The results of the proximate analysis for the humus layers of the three alliances indicated that the hygric habitats had significantly lower levels of lipid and hemicellulose fractions than the other habitats. Furthermore, average cellulose values were lower, and 'protein' and 'lignin-humus' values were higher. On the other hand, only minor differences were found between the xeric and mesic habitats. These results indicate that the TIARELLA - POLYSTICHUM - WRC alliance was characterized by a much higher degree of decomposition, and hence of biological activity, in terms of decomposition rates. It is suggested that the ratio of cellulose to lignin-humus level is a relatively sensitive index of intensity of decomposition. The values of this ratio were 0.05, 0.14 and 0.18 for the hygric, xeric and mesic sites respectively. Corresponding ratios for foliage of *Gaultheria shallon* and *Polystichum munitum* were greater than 1.0, and for decayed wood, between 0.2 and 0.9. In general, the proximate analyses for humus layers of the CWHa ecosystems confirmed the indications of C/N ratio, pH and predominant humus forms, that the hygric habitats were characterized by substantially the highest decomposition rates, and mesic habitats had slightly lower rates than xeric habitats. While low pH would be expected to contribute to lower biological activity at both the exeric and mesic habitats, slower decomposition at the mesic habitats (relative to xeric) is less easily accounted for. The greater observed abundance of decayed wood affecting temperature and moisture status of humus layers at these mesic habitats may be partly responsible.

The results for the decayed wood of Douglas-fir and western redcedar indicated not only marked differences between species, but also between decayed wood and both leaf tissue and humus layers. Clearly, major differences in amounts of woody materials present, will influence the fraction distribution of humus layers. Relative to leaf or coniferous needles, wood is relatively low in lipid, soluble polysaccharide and protein, but high in lignin. (Wood is also more slowly decomposed, and thus tends to make up a proportion of the humus layer that increases with age of the stand.) In particular, the high lignin and relatively low hemicellulose and cellulose in the very slowly decomposing wood of western redcedar, may well be partly responsible for the similar trends in humus layers of the TIARELLA - POLYSTICHUM - WRC, as compared to the other units. Little evidence was found indicating that foliage of *Gaultheria shallon* or *Polystichum munitum* produced recognizable effects on the proximate analysis of humus layers in ecosystems in which these species were major components.

To further test the ability of proximate analysis to discriminate between organic samples of diverse origin, a hierarchical grouping analysis (as applied by Kloosterman and Lavkulich 1973) was carried out on the data from the samples of humus layers, plant tissue and decayed wood. Such a technique assesses the extent to which natural groupings exist among a set of samples. In the present study the objective was to ascertain to what extent proximate analyses could be used to reproduce the original groupings on which sampling was based (Table 3). The results are presented in a dendrogram (Table 4) in which successive groupings represent decreasing degrees of similarity, with an associated error term. It was noted that in the successive grouping process, a substantial error increase occurred at step 23 on decreasing from five groups to four. This represented a

TABLE 4. Dendrogram of proximate analysis by hierarchical grouping analysis for 28 samples of humus layers



level of grouping that minimized the number of groups without introducing excessive error, suggesting that five 'natural' groups were present in the set of samples. The composition of these groups is given in Table 5. The first group contained all the samples of salal and western sword-fern tissues and excluded all other materials. The second group contained only decayed wood samples, including all those of Douglas-fir and one of the western redcedar samples. The third group contained seven out of eight samples of humus layers from the xeric and mesic habitats, indicating little differences between these materials. The fourth group was more mixed, containing three out of four humus layers of the TIARELLA - POLYSTICHUM - WRC alliance, two samples of decayed wood of western redcedar and one sample from the GAULTHERIA - DOUGLAS-FIR alliance. The latter sample was from a plot in which a signficant understory of western redcedar had developed. The final group contained only one sample of humus layers from a hygric habitat, characterized by a mull humus form exhibiting substantially lower organic matter content than any of the other samples examined.

It was concluded that proximate analysis was relatively efficient in discriminating between foliage, decayed wood and humus layers, it was only partially successful in distinguishing humus layers derived from different forest ecosystems. In view of the recognized limitations of this analytical approach, and in particular the inability to distinguish between lignin and the more resistant humus fractions, this is not entirely surprising.

SUMMARY AND CONCLUSIONS

The results presented indicate that forest ecosystems, defined by synecological methods, possess soil organic layers distinguishable on the basis of chemical properties. On the basis of proximate analysis alone, the TIARELLA - POLYSTICHUM - WESTERN REDCEDAR alliance could be distinguished from those of the GAULTHERIA - DOUGLAS-FIR and the MOSS - WESTERN HEMLOCK alliances, but the latter two could not be separated. The ratio of cellulose content to content of the 'lignin-humus' fraction appeared to be a relatively sensitive index of the intensity of organic matter decomposition in forest humus layers.

Differences in composition of organic soil horizons are highly dependent on litter decomposition processes, which in turn are dependent on the nature and activity of the microbiological population, and on the composition of the litter. Thus, differences in the organic constituents of humus layers can be related both to the species composition, especially dominant tree species, and to the microenvironment within the humus layers. In the latter context, pH, temperature and moisture regime are of particular importance.

Table 5. Sample identification and classification obtained by hierarchical grouping analysis.

Samples Grouped	Sample Origin and Number		
1	G.S.	002	GROUP 1
5	G.S.	028	
3	G.S.	005	
7	P.M.	002	
9	P.M.	006	
6	P.M.	001	
8	P.M.	005	
2	G.S.	003	
4	G.S.	023	
10	P.M.	029	
11	DWDF	025	GROUP 2
15	DWWRC	023	
12	DWDF	030	
13	DWDF	032	
17	GA-DF	021	GROUP 3
21	MO-WH	007	
19	GA-DF	057	
23	MO-WH	032	
24	MO-WH	124	
20	GA-DF	083	
22	MO-WH	024	
14	DWWRC	001	GROUP 4
16	DWWRC	026	
18	GA-DF	030	
26	T-P-WRC	098	
25	T-P-WRC	015	
27	T-P-WRC	135	
28	T-P-WRC	148	GROUP 5

Abbreviations used: G.S. - *Gaultheria shallon*, P.M. - *Polystichum munitum*, DWDF - Decayed wood of Douglas-fir, DWWRC - Decayed wood of western redcedar, GA-DF - *GAULTHERIA* - DF, MO-WH - MOSS - WH, T-P-WRC - *TIARELLA* - *POLYSTICHUM* - WRC.

Ecosystem classification of forests, integrating all ecosystem components, appears to be a useful approach to the study of humus formation, and the relationships of humus layers to other ecosystem components. The use of proximate analysis for organic layers provides a useful supplement to other chemical data, but is not in itself sufficient to distinguish forest ecosystems in the Coastal western hemlock zone or to reveal differences in the nature of humification products.

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