

Chapter (non-refereed)

Heal, O. W.. 1979 Decomposition and nutrient release in even-aged plantations. In: Ford, E. D.; Malcolm, D. C.; Atterson, J., (eds.) *The ecology of even-aged forest plantations*. Cambridge, Institute of Terrestrial Ecology, 257-291.

Copyright © 1979 NERC

This version available at <http://nora.nerc.ac.uk/7076/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the authors and/or other rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

This document is extracted from the publisher's version of the volume. If you wish to cite this item please use the reference above or cite the NORA entry

Contact CEH NORA team at
nora@ceh.ac.uk

DECOMPOSITION AND NUTRIENT RELEASE IN EVEN-AGED PLANTATIONS

By O.W. HEAL

Institute of Terrestrial Ecology, Merlewood Research Station,
Grange-over-Sands, Cumbria, U.K.

SUMMARY

The decomposition sub-system is a complex interacting set of organisms and processes whose activities are central to the availability of nutrients to plants and to the maintenance of the nutrient capital of the ecosystem. Information on decomposition and nutrient release in plantations is sparse and much is inferred from accumulation patterns on the forest floor. This paper describes the general principles of the control of decomposition and nutrient release, and examines their application and implications to even-aged plantations.

Decomposition comprises katabolism, comminution and leaching, commonly measured by weight loss and respiration which are correlated with rates of nutrient release with an approximate release sequence $K > Mg > Ca > Mn > C > P > N > S$.

Decomposition is a function of three factors: climate, soil and resource quality, acting through the heterotrophic organisms. The broad limits to decomposition, set by site conditions, are modified by management and forest development.

Decomposition of different litters is related to the proportions of ethanol soluble and ethanol insoluble fractions and in some cases to initial nitrogen concentration. Two exponential curves provide a reasonable representation of the main phase of decomposition, followed by long-term decomposition of resistant humus fractions.

During decomposition nutrients are 'immobilized' in micro-organisms and faunal tissues, but the concept of immobilization, with mineralization at critical C:nutrient

ratios, masks the short-term recycling of nutrients through microbial turnover.

The temporal pattern of decomposition and nutrient release includes pedogenetic trends over millenia, successional changes over decades or centuries, and seasonal and diurnal rhythms. In plantations the successional sequence is very distinct with additional pulses introduced by management.

There is little evidence of the variation in nutrient release during a crop rotation but phases of nutrient supply and demand are apparently not synchronized as closely as in mixed-aged stands. The proportion of the ecosystem nutrients retained in the forest floor and the turnover time increases with latitude. The organic accumulation, while acting as a stabilizing influence in high latitudes, reduces nutrient flow to the trees. A manipulated increase in rate of turnover is expected to increase primary production.

RÉSUMÉ

Le sous-système de la décomposition est un système interactif d'organismes et de processus dont l'activité est indispensable à la disponibilité et au capital d'éléments nutritifs de l'écosystème. Les renseignements que l'on possède à présent sur la décomposition et la libération d'éléments nutritifs dans les plantations sont minces et nous basons nos connaissances sur les types d'accumulation trouvés dans les sols des forêts. Notre exposé décrit les principes généraux du contrôle de la décomposition et de la libération d'éléments nutritifs et nous examinons leur application et les conclusions que l'on peut en tirer dans le cas de forêts équiennes.

La décomposition comprend le katabolisme, le broyage et le lessivage qui se mesurent habituellement par la perte de poids et la respiration, qui sont corrélées avec le taux d'éléments nutritifs libérés, selon l'ordre-type suivant: $K > Mg > Ca > Mn > C > P > N > S$.

La décomposition dépend de trois facteurs, climat, sol et qualité en ressources, qui agissent par l'intermédiaire d'organismes hétérotrophiques. Les limites générales de la décomposition, dictées par les conditions de la station, sont modifiées par la gestion et le

développement des forêts.

La décomposition de litières différentes est proportionnelle à des fractions solubles et insolubles dans l'éthanol et dans certains cas à la concentration initiale d'azote. La phase principale de décomposition, suivie de la longue décomposition de fractions d'humus plus résistant, peut être représentées par deux courbes exponentielles.

Pendant la décomposition, les éléments nutritifs sont 'immobilisés' dans des micro-organismes et des tissus de la microfaune mais le concept même d'immobilisation, avec une minéralisation à des rapports critiques de C:éléments nutritifs, masque le recyclage à court terme des éléments nutritifs par l'intermédiaire du cycle microbien.

Du point de vue temporel, la décomposition et la libération des éléments nutritifs présentent des tendances pédogénétiques sur une période de mille ans, des changements de succession sur des décennies ou des siècles et des rythmes saisonniers et diurnes. Dans les plantations, l'ordre des successions est très distinct, montrant des pulsations supplémentaires dûe à la gestion.

Il n'est pas évident que la libération d'éléments nutritifs varie pendant une révolution mais on peut dire que les phases d'offre et de demande d'éléments nutritifs ne sont pas aussi étroitement synchronisées que dans les peuplements d'âge mixte. La proportion d'éléments nutritifs de l'écosystème retenus au sol de la forêt et la durée du recyclage augmentent avec la latitude. L'accumulation organique qui a un effet stabilisateur à des latitudes élevées réduit le flux d'éléments nutritifs vers l'arbre. Une augmentation de la rapidité du cycle - amenée artificiellement pourrait augmenter la production primaire.

ZUSAMMENFASSUNG

Das Subsystem der Verwesung besteht aus einem komplexen Zusammenwirken von Organismen und Prozessen, deren Wirken von zentraler Bedeutung für die Pflanzenverfügbarkeit von Nährstoffen und für die Aufrechterhaltung des Nährstoffvorrats im Ökosystem ist. Kenntnisse über Verwesung und Freisetzung von Nährstoffen in Forstpflanzungen sind spärlich und vieles

muss man aus Anhäufungsmustern auf dem Waldboden ableiten. Dieser Beitrag beschreibt die Gesetzmässigkeiten, denen Verwesung und Freisetzung von Nährstoffen unterliegen und untersucht ihre Übertragbarkeit auf gleichaltrige Pflanzungen.

Verwesung umfasst Katabolismus, Zerkleinerung und Auswaschung. Man misst sie üblicherweise am Gewichtsverlust und der Atmung. Diese Grössen sind korreliert mit den Nährstoff-Freisetzungsraten (ungefähre Reihenfolge $K > Mg > Ca > Mn > C > P > N > S$).

Verwesung ist eine Funktion der drei Faktoren Klima, Boden und Angreifbarkeit für heterotrophe Organismen. Die durch Standortbedingungen gesetzten Grenzen der Verwesung werden durch Bewirtschaftung und Waldentwicklung modifiziert.

Die Verwesung verschiedener Streuarten ist abhängig vom Anteil der Äthanol-löslichen und Äthanol-unlöslichen Fraktionen; in einigen Fällen auch vom ursprünglichen Stickstoffgehalt. Zwei Exponentialkurven geben eine zutreffende Darstellung der Hauptphase der Zersetzung, auf die dann der langfristige Abbau resistenter Humusfraktionen folgt.

Während der Verwesung werden Nährstoffe in Mikroorganismen und tierischen Geweben 'immobilisiert'. Das Konzept der Immobilisierung, mit einer Mineralisierung bei kritischen Kohlenstoff : Nährstoff Verhältnissen, verdeckt jedoch das kurzfristige Recycling von Nährstoffen durch mikrobiellen Umsatz.

Das Zeitschema der Verwesung und der Freisetzung von Nährstoffen schliesst ein die pedogenetischen Tendenzen über Jahrtausende, Sukzessionswechsel über Jahrzehnte oder Jahrhunderte sowie jahreszeitliche und tägliche Rhythmen. In Pflanzungen sind Sukzessionsfolgen sehr ausgeprägt; sie sind zusätzlich beeinflusst durch Bewirtschaftungsmassnahmen.

Es gibt wenig Anhaltspunkte für die Schwankungen in der Freisetzung von Nährstoffen während der Umtriebszeit. Phasen der Nährstoffanlieferung und des Nährstoffbedarfs sind jedoch offensichtlich nicht so gut aufeinander abgestimmt wie in verschiedenaltigen Beständen. Der Anteil der Nährstoffe des Ökosystems, die im Auflagehumus

enthalten sind, und die Umsatzzeit nehmen mit dem Breitengrad zu. Die Anhäufung in organischer Form, die in hohen Breitengraden einen stabilisierenden Einfluss ausübt, reduziert gleichzeitig die Nährstoffzufuhr zu den Bäumen. Es ist zu erwarten, dass eine gesteuerte Zunahme der Umsatzrate die Primärproduktion steigert.

INTRODUCTION

The decomposition sub-system in forests, as in other ecosystems, is not just a 'black-box', best left unopened and considered as a component which accepts and releases elements. It is Pandora's box containing a complex interacting set of organisms and processes whose activities are central to the availability of nutrients to plants and to the maintenance of the nutrient capital of the ecosystem. The sub-system, therefore, demands our understanding, on the assumption that better understanding will lead to better management, although much of the experience in agriculture suggests that a pragmatic approach to management can be very successful. Forestry, however, has not had the benefit of centuries of experience from trial and error and of a century of intensive soil research. Thus management of nutrient processes in forests has the opportunity, and the need, to use the research tool more directly than has agriculture and also to make use of the understanding from research in agriculture and from basic science.

The information on decomposition and nutrient release in forest plantations is sparse and scattered. Therefore, I have adopted the approach of describing first the general principles of decomposition, then of examining their application to even-aged forests in order to describe the pattern of processes during a rotation, and finally of discussing some implications, including comparisons with other systems. The emphasis throughout is on the organic horizons of the forest floor and on coniferous plantations.

DECOMPOSITION

The term decomposition has been used in a wide variety of senses, but here it is used to include three main processes: katabolism, comminution and leaching. Katabolism, the disruptive processes of chemical change by organisms, involving the breakdown of carbohydrates, proteins and other organic compounds for heterotrophic anabolism with the associated release of simpler, insoluble, soluble or gaseous compounds or elements. Thus the katabolism of organic compounds by heterotrophic organisms results in the incorporation of elements into their tissues, i.e. immobilization, and release of elements into the soil and

aerial environment, i.e. mineralization. However, it must be emphasized that the tissues of the heterotrophs are themselves subject to decomposition with subsequent mineralization of elements. Comminution is the reduction in particle size by a combination of biological and physical mechanisms and results in redistribution of organic matter in the soil. Leaching is the physical process of transport of water-soluble or fine particulate material from organic matter. The combination of the processes of katabolism, comminution and leaching results in measurable parameters of weight loss, change in chemical composition and release of gaseous and water-soluble material from the organic matter but the component processes are often indistinguishable.

Weight loss is a common measure of decomposition which combines all losses and is biased towards the major organic substrates which constitute most of the organic matter. Respiration provides a direct measure of carbon katabolism which usually correlates well with weight loss and with the rate of release of nutrient elements, although each element has a different pattern and rate of release. Potassium is not organically bound and is released rapidly through leaching. Calcium and magnesium are mainly contained in plant structural components, are released more slowly and accumulate in fungi and fauna (Cromack et al. 1977). Phosphorus, nitrogen and sulphur are mobilized during katabolism, but, because their concentration in microbial tissue is higher than that in plant tissues, they tend to be retained within the microbial population and released slowly. Thus the release sequence tends to be $K > Mg > Ca > Mn > C > P > N > S$, largely reflecting the demand by decomposers but with some variation in different litters, depending on the relative concentration of the elements (Will 1967; Attiwell 1968; Wood 1974; Toth, Papp & Lenkey 1975; Gosz, Likens & Bormann 1973).

FACTORS CONTROLLING DECOMPOSITION

Although there is a wide variety of types of organic matter decomposing in various environments, within any ecosystem, the rate of decomposition is basically a function of three groups of factors: climate, soil and resource quality, the term 'resource' being used for organic matter composed of a number of chemical compounds, while the term 'substrate' is used in the biochemical sense of a chemical entity that reacts in a specific manner with an enzyme. These factors control the activities of the heterotrophic microflora and fauna and can be represented as a module (Fig. 1) which is repeated for different types of resource, e.g. needle, leaf, stem or root within an ecosystem and in different ecosystems (Bunnell & Tait 1975; Swift, Heal & Anderson, in press). The rate of decomposition in planted forests is determined by:

- (1) The microclimate of the forest floor, which is basically

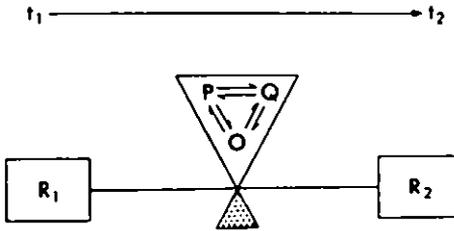


Fig. 1. Module of decomposition of organic matter. The decomposition of a resource from state R_1 to R_2 over time t_1 to t_2 is controlled by physico-chemical (P) factors of the environment and resource quality (Q) acting through heterotrophic organisms (O). (From Swift, Heal & Anderson in press).

that of the local climate modified by the vegetation canopy, which varies with tree species, planting density, growth rate and management.

- (2) The soil on which the forest floor develops, the degree of soil influence itself depends on the extent of site preparation and exposure of the mineral soil.
- (3) The chemical and physical composition i.e. resource quality of the organic matter input to the forest floor which is dependent on the initial vegetation, the type of tree and the associated management.

The rate of decomposition will vary, therefore, during a forest rotation because the forest and its management modify the controlling factors and the amount of organic matter available for decomposition.

Climate

Although there are no detailed studies of the influence of climate on decomposition through the cycle of an even-aged forest, a general picture can be drawn from the scattered data and from results in other systems. The model of the influence of temperature and moisture on microbial respiration by Bunnell et al. (1977) has proved reasonably applicable to a range of litters, including aspen and dwarf shrub, in tundra, boreal forests and temperate bogs. It provides a succinct statement of the effect of the major climatic variables, with respiration rate of the litter ($R(T,M)$) in $\mu\text{l O}_2/\text{g}$ expressed as:

$$R(T, M) = \frac{M}{a_1 + M} \times \frac{a_2}{a_2 + M} \times a_3 \times a_4^{((T-10)/10)}$$

where T is temperature in °C; M is moisture in per cent dry weight; a_1 is the percentage moisture at which activity is at half its optimal value, thus representing availability of water for metabolism by decomposer organisms; a_2 is the percentage moisture at which gas exchange is limited to half its optimal value, thus representing the decreasing oxygen supply to organisms with increasing water content; a_3 represents the effect of substrate composition as the respiration rate in $\mu\text{l O}_2/\text{g/hr}$ at 10 C, when neither moisture nor oxygen are limiting; a_4 is the Q10 coefficient determining the respiration response to temperature.

The model has been fitted to data from the litter, fermentation and humus layers of an aspen (*Populus tremuloides*) forest (Fig. 2). The calculated response surfaces show the retarding effect of both low and high moisture levels and also the decrease in respiration rate which occurs as the organic matter ages. Respiration rate of the three organic layers, measured seasonally, was influenced more strongly by temperature than by moisture, with the importance of temperature increasing with depth as the variability in moisture decreased (Van Cleve & Sprague 1971). The site studied, a fifty year-old stand in central Alaska, is a silt loam in a cold, dry climate in which moisture levels are moderate to low, but in forests on poorly drained soils and wet climates, the respiration rates will be inhibited by high moisture levels which retard oxygen diffusion. The principles of oxygen depletion in mineral soils (Greenwood 1968) probably apply to organic matter with the additional emphasis that the development of anaerobic microsites is related to the respiration rate and is, therefore, likely to be greatest in fresh and rapidly decomposing organic matter and to be temperature dependent. Thus respiration rates, commonly measured as oxygen uptake or carbon dioxide output, may omit a significant katabolic component of anaerobic respiration.

The rate of respiration by the microflora, although usually taken as a measure of carbon release, is also directly related to mineralization of the physiologically active plant nutrients (Witkamp 1966; Attiwell 1968; Wollum & Davey 1975). The reduction - oxidation state of the elements, however, depends on the degree of oxygen depletion which is dependent not only on moisture content but also on microbial activity (Fig. 3).

The rate of decomposition of organic matter in the cycle of an even-aged plantation will, therefore, vary with the changing temperature and moisture regimes. The forest floor temperature will follow air temperature but show reduced

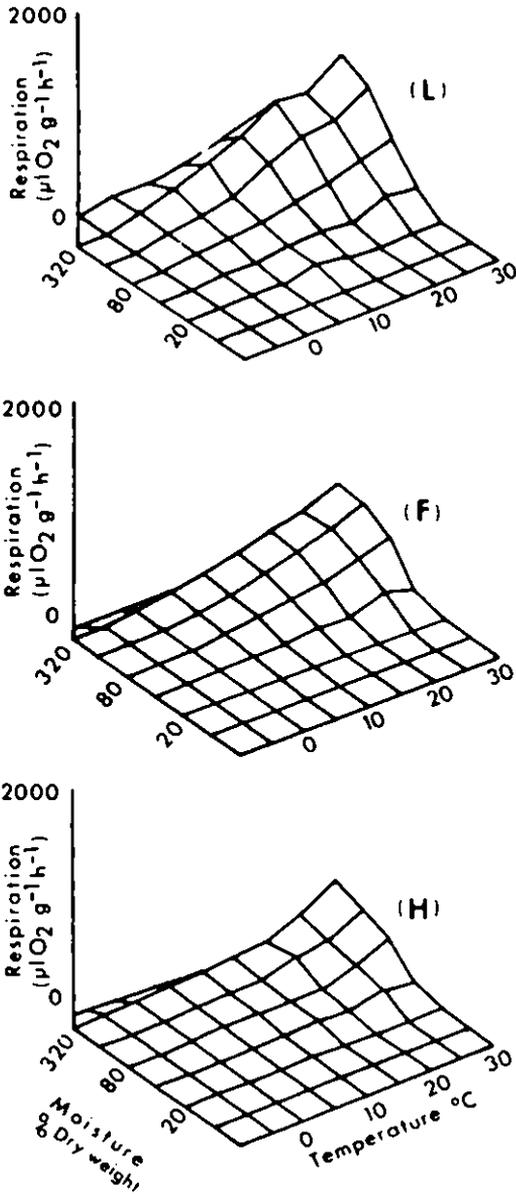


Fig. 2. Respiration rates of litter (L), fermentation (F) and humus (H) layers of aspen (*Populus tremuloides*) forest floor in Alaska, in relation to temperature and moisture. (From Bunnell et al. 1977).

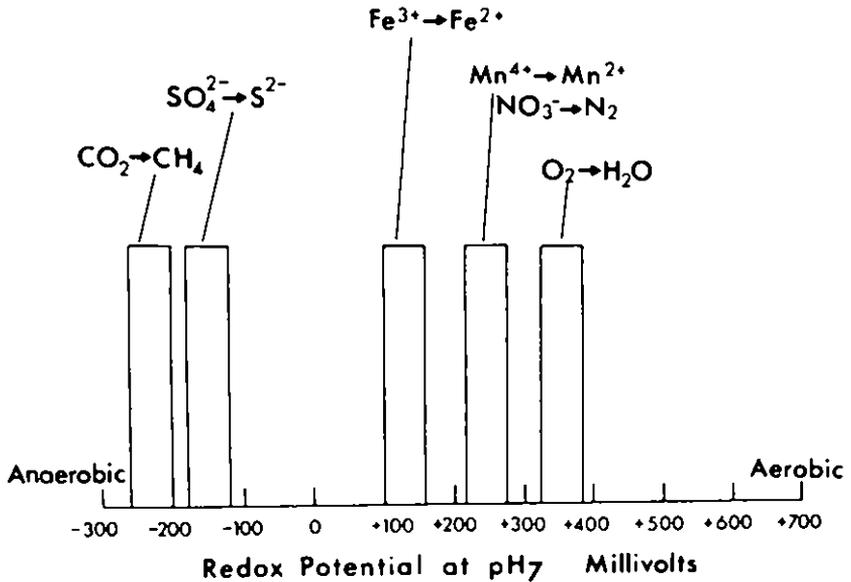


Fig. 3. Approximate critical redox potentials at which various redox systems are reduced. (From Patric 1978).

diurnal and seasonal maxima and minima as the stand ages and canopy closes, although fluctuation will be increased at thinning (Hansen 1937; Odin 1974; Edgerton & McConnell 1976; Piene & Van Cleve 1978). On mineral soils development of the organic layers will also reduce fluctuation because of their low thermal and water conductivity resulting from their low bulk density. The higher temperature minima and resulting longer decomposer season which occur as the forest develops will not compensate fully for the higher temperature maxima in unforested areas because the relationship of microbial respiration to temperature is basically exponential. In addition, freeze-thaw cycles which include nutrient release will also be depressed in the forest (Birch 1964; Witkamp 1969). The principle of reduced temperature fluctuations is reasonable but direct evidence is very limited. Piene & Van Cleve (1978) found that thinning in a *Picea glauca* forest in Alaska increased the rate of litter decomposition as a result of higher temperatures and more favourable moisture conditions. However, Brown (1976) found no detectable difference in surface temperatures in cut and uncut strips of black spruce (*Picea mariana*) on a peat bog in Minnesota. He concluded that temperature related microbial activity was not

expected to vary as a result of felling.

The varying effect of moisture during a forest cycle is more complex than that of temperature, as well as interacting with it, because of the balance between aerobiosis and anaerobiosis. The increase in evapotranspiration and canopy interception as the forest develops will reduce water input to the litter surface and moisture levels in the soil. The degree of soil drying will vary with tree species, soil type, cultural technique and thinning (Hansen 1937; Lull & Axley 1958; Haberland & Wilde 1961; Binns 1968; Read, Armstrong & Weatherall 1973; Pyatt 1973; Helvey 1975; Williams, Cooper & Pyatt 1978). Moisture content and temperature will also vary spatially within a plantation, especially in the pre-thicket stage, where ploughing has occurred, with greater temperature variation and lower moisture levels on ridges than in furrows. The changes in moisture content in organic horizons are reasonably predictable, but they are associated with more complex changes in other factors both in the organic and mineral horizons. Over the longer term, bulk density tends to increase as a result of decreasing moisture which causes a partially reversible compaction, especially in soils with a high organic content, while pH tends to fall and is related to alteration in the exchange capacity (e.g. Wilde 1964; Hamilton 1965; Pyatt 1973; Grieve 1978; Williams, Cooper & Pyatt 1978).

Thus during the development of a forest the change in physical and chemical factors outlined above is expected to cause the following changes in the rates of decomposition and release of minerals:

- (1) a gradual decrease at moist and dry sites because of decreasing fluctuation in temperature and decreasing moisture content as the canopy develops, reaching a constant level after canopy closure. At thinning, decomposition and release will increase for a few years with increased temperature and moisture and at felling the rate will rise considerably through the canopy removal.
- (2) In wet sites either an increase or a decrease with tree growth, depending on the balance between the retarding effect of reduced amplitude of temperature variation and the stimulating effect of increased aeration through lower moisture levels.

Soil factors

The initial soil conditions, like climate, set broad limits to the rate of decomposition with a direct relationship to soil pH and concentration of minerals. Such a simplistic statement is inadequate, but there are surprisingly few studies which have examined decomposition in a wide range of soils and determined the influence of specific edaphic factors (Williams & Gray 1974; Dickinson 1974). One reason for the lack of information is that many factors are correlated and it

is virtually impossible to modify individual variables. In addition there is a strong interaction between climatic and soil factors which confounds analysis of decomposition in field conditions (Heal & French 1974).

Comparative studies have shown that decomposition of litter on the surface is correlated with pH, phosphorus and calcium concentrations and is higher in soils with mull humus than in those with moder, mor or peat (Bocock & Gilbert 1957; Witkamp & Van der Drift 1961; Frankland 1966; Heal & French 1974). Such studies correspond with results from research on particular processes such as cellulose decomposition, organic phosphate mineralization and nitrification (Alexander 1977). The chemical characteristics of the soil are intimately linked with physical characteristics, particularly texture and particle size, which have a great influence on adsorption characteristics, exchange capacity and pH. The chemical and physical characteristics influence decomposition by their effects on the organisms and on the rate of enzyme activity, but they also affect retention of nutrients in the soil and their availability to decomposers. Because clay particles have a high ion exchange capacity, retention of nutrients is particularly related to the amount and composition of the clay fraction (e.g. Kolenbrander 1971). The soil moisture regime is closely related to soil structure (Salter, Berry & Williams 1966) through its associated aeration characteristics, the microsite phenomenon being applicable to pH and other physical factors as well as oxygen. The complex combination of soil factors which influence nutrient movements under varying soil conditions are well described by Nye & Tinker (1977) and the dynamics of nutrients within ecosystems are defined in various computer simulations (Beek & Frissel 1973; Innis 1978; Tanji & Gupta 1978).

There is a vast literature on nutrient transformations in soils, especially nitrogen and phosphorus in agricultural soils (Frissel & Damen 1977), but the pattern of variation in decomposition and mineral release as related to different soils in forests is poorly documented. During the cycle of a conifer stand there is an accumulation of organic matter on the forest floor which reaches a maximum and may then decline in older stands (Ovington 1959; Page 1968, 1974; Kholopova 1972; Jorgensen, Wells & Metz 1975). This accumulation, representing the balance between input and loss, is greater than under comparable deciduous stands and tends to have lower pH, lower nitrogen content and a different balance of exchangeable nutrients (Ovington 1953, 1954; Nihlgard 1971; Tappeiner & Alm 1975). The changes in composition of the forest floor result in alterations to the lower horizons but the direction, degree, time-scale and consequences of such alterations are the subject of considerable debate (Stone 1975). The arguments will not be repeated here except to say

that soil properties are affected by the chemical and physical composition of the incoming organic matter and its decomposition characteristics. Although not proven because of technical difficulties, such as accumulated sampling errors, comparability of sites and the range of variables to be measured, the theoretical and practical evidence indicates that conifers will cause soil changes which tend to reduce the rate of decomposition and nutrient release as compared with deciduous species.

Resource quality

It is obvious that different resources, e.g. deciduous or coniferous leaf litter or wood, have different rates of decomposition. Such variations occur between species, between different parts of the same plant, within the same species grown under differing soil conditions, and within the same plant as it matures and senesces. Thus, while it is convenient to define the resource as Pinus contorta needles or Pseudotsuga menziesii branches, such names are insufficient to describe the important physico-chemical characteristics which determine the rate of decomposition of that resource. Although our current understanding of the control of decomposition by resource factors is poor, four factors, which are often inter-correlated, are recognized:

- (1) Carbon sources - a range of organic substrates act as carbon and energy sources for micro-organisms and their chemical composition controls their susceptibility to katabolism, e.g. Minderman (1968). The combination of carbon substrates within a resource modifies its rate of decomposition (Fig. 4). Although many substrates are involved, the decomposition rate is largely determined by, or at least correlated with, the percentage of lignin (Van Cleve 1974). Bunnell, Tait & Flanagan (1977) developed these principles and found that ethanol soluble components were katabolized at 5-10 times the rate of ethanol insoluble components. From this they showed that a double exponential model, expressing both rapid and slow decomposing constituents, defined by the proportion of ethanol soluble and non-soluble fractions, provided a good fit between observed and predicted loss rates for a number of different litter types.
- (2) Nutrient sources - the chemical elements of importance in plant growth are also important in microbial and faunal growth, and are provided by katabolism of organic matter. The concentration of nutrient elements in fresh organic matter is generally related directly to the rate of decomposition and mineral release as shown by the strong positive correlation between weight loss and initial nitrogen concentration (e.g. Witkamp 1966; Jensen 1974; Van Cleve 1974). There is, however, an opposing trend, that during decomposition, the rate of decomposition

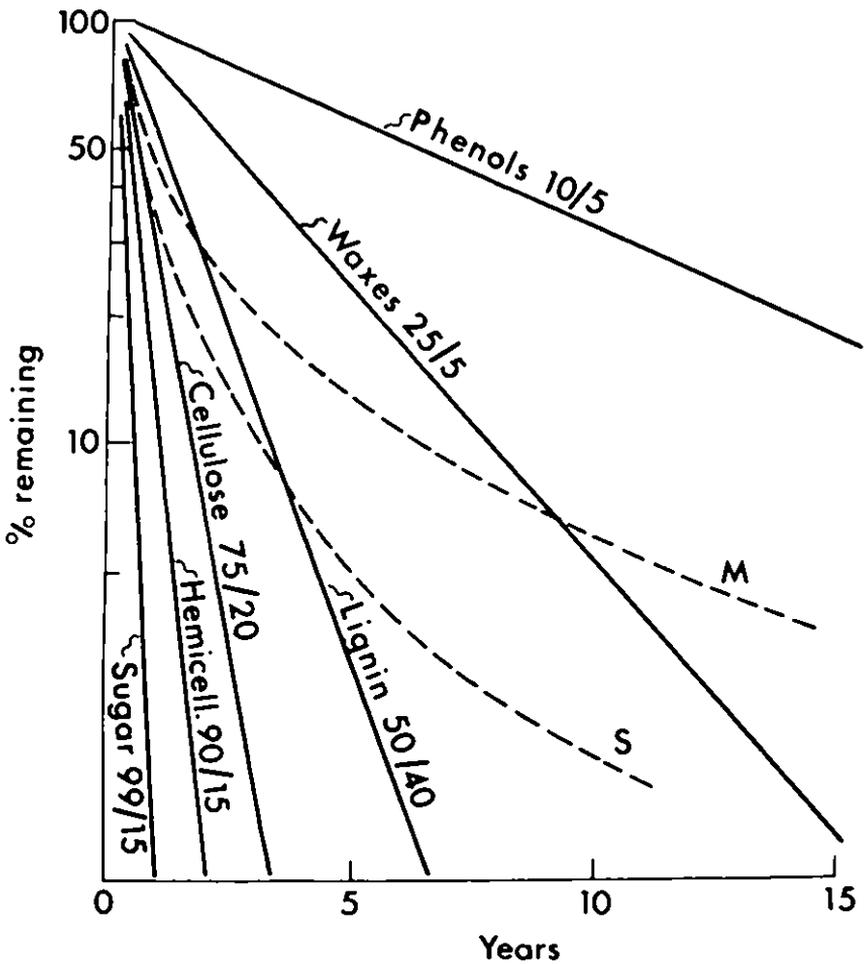


Fig. 4. Decomposition curves of substrates which constitute woodland litter. For each substrate the first number indicates the percentage of the substrate lost in one year, the second number is the approximate percentage in weight of the original litter. The curve S is the annual summation of the residual amounts of substrates remaining. The curve M is the approximate course of decomposition based on observed values. (From Minderman 1968).

declines while the nutrient concentration often increases as a result of loss of gaseous carbon and immobilization of nutrients by the microbial population. The lowest rates of decomposition are found in 'humus' which has a high nutrient concentration, but the nutrients are combined in complex organic molecules which are the result of decomposition.

- (3) Modifiers - chemical compounds, either present in the initial litter or produced by micro-organisms, whose presence in organic matter retards or stimulates microbial and faunal activity. A wide variety of compounds are involved but for technical reasons they have not been measured in comprehensive studies of decomposition. Their presence probably accounts for much of the variation in decomposition which is not explained by the composition of carbon and nutrient sources. Phenolic and quinonic compounds and tropolones extracted from conifer wood have been shown to be toxic to fungi (Scheffer & Cowling 1966); polyphenols retard leaf litter decomposition and inhibit earthworm feeding (King & Heath 1967; Satchell & Lowe 1967) and may cause low rates of decomposition of roots (Sinha 1972); and of course Handley (1954) developed the hypothesis of the role of phenol tanned proteins in mull and mor formation. No general relationship between decomposition rate and concentration of modifier compounds has been described, but evidence suggests that conifers tend to have evolved these inhibiting compounds to a greater extent than many other plants (e.g. Bauzon, van den Driessche & Dommergues 1969). Variation in decomposition of the same litter from different sites and ages may be attributed to nutritionally induced differences in polyphenol complexing of litter materials, as in Pinus radiata needles (Lamb 1976).
- (4) Physical factors - the surface properties, toughness, particle size and other physical properties of the organic matter influence their rate of decomposition, particularly through their influence on moisture uptake and retention and on the resistance to attack by micro-organisms and fauna. The main feature is the physical character of coniferous forest litter with its hydrophobic surface and small surface area to volume. Thus, in comparison with most deciduous leaf litter, they tend to have a low uptake but high retention of moisture, and retain their physical shape until late in the process of decomposition. These needle characteristics result in a lower leaching loss of soluble organic compounds and nutrients than in deciduous litters. Water soluble organic compounds thus decompose to a greater extent inside needles than inside leaf litter (Nykvist 1963).

The four groups of factors which constitute resource quality combine to determine the relative rate of decomposition and nutrient release from different litters at a given site, with the environmental factors determining the absolute rate at different microsites. Although examples are cited in which a correlation exists between decomposition rate and concentrations of organic fractions or nutrients, there are many examples in which correlations were not detected (e.g. Melin 1930; Mikola 1955; Daubenmire & Prusso 1963). Much depends on the range of resource quality which is examined, the range of chemical components determined and the extent to which interactions between factors are expressed.

The variation in rate of decomposition of different litters, as expressed by weight loss, has been determined in many comparative studies. These show a general pattern of decreasing rate over the series:

herb leaves > grass leaves > deciduous tree leaves >
 conifer needles > moss > deciduous wood > conifer wood,
 (Mikola 1955; Daubenmire & Prusso 1963; Bocock 1964; Voigt 1965; Mangelot 1966; Witkamp 1966; Satchell & Lowe 1967; Kira & Shidei 1967; Attiwell 1968; Mommaerts-Billiet 1971; Gosz, Likens & Bormann 1973; Dickinson & Pugh 1974; Heal & French 1974; Swift et al. 1976; Heal, Latter & Howson 1978). Rates of loss have usually been measured for only the first year or two of decomposition but within this period the fastest rates are about ten times those of the slowest. There is considerable overlap between loss rates of the groups identified and it is particularly difficult to isolate the relative importance of different chemical and physical characteristics within groups. The initial state of the litter influences its subsequent decay rate, with faster rates recorded for green litter from which soluble fractions have not been resorbed before death - a factor relevant to the decomposition of brush. The decomposition of wood is also dependent on the proportions of bark, sapwood and heartwood, which vary considerably in chemical and physical composition and in decomposition rate (Gosz, Likens & Bormann 1973; Kaarik 1974).

The data on rate of decomposition of roots are very few but indicate slower rates than for leaf material of the same species (Jenkinson 1965; Smith 1966; Malone & Reichle 1973; Sinha 1972). The results are mainly for agricultural crops but are probably similar in non-cultivated species, with tree and shrub roots having rates comparable with those of above-ground wood (Kaarik 1974; Waid 1974; Heal & French 1974). Root exudates constitute a very variable fraction of the total plant production, mainly as organic acids, sugars and amino acids whose rate of decomposition is probably high compared with other inputs (Smith 1969, 1970; Nye & Tinker 1977).

Thus, during the life of an even-aged plantation there is a changing pattern of quality of organic matter input, and

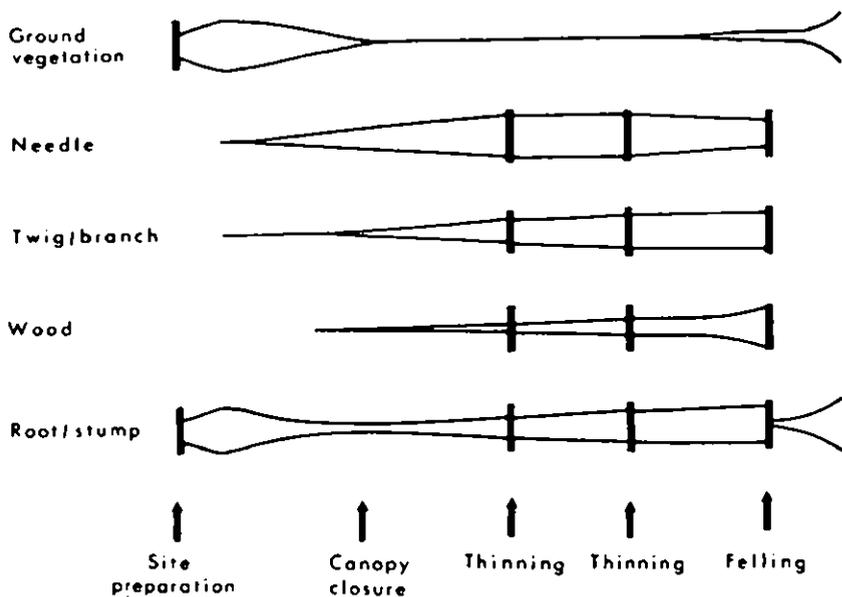


Fig. 5. Schematic input of various resources to the forest floor during a rotation. Bars represent major inputs of fresh material with relatively high soluble organic and nutrient content.

therefore, a changing rate of decomposition. The general phases of input are a gradual reduction in ground flora components compensated by needles and by twigs and branches as the forest matures. The production of dead roots probably increases with time but data are very sparse. A series of inputs result from management practices with the particular characteristic that they usually comprise fresh plant material, needles, wood and roots, from which soluble organic material and nutrients have not been resorbed by the plant. At planting, fresh ground vegetation may be killed as a result of sward inversion; brushing adds dead twigs and branches; thinning contributes green needles, fresh twigs, branches, stumps and roots, with a similar major input at final felling. Felling is followed by a period of negligible input until the ground flora redevelops, this being characterized by fast growing species whose litter probably has a high decay rate. The general sequence of events, represented in Fig. 5, is recognized from well-documented, quantitative measurements of

above-ground input in plantations at varying stages of development (Bray & Gorham 1964; Turner 1975; Miller, Cooper & Miller 1976; Carey & Farrell 1978), and occasionally for a complete age sequence for a species, e.g. Pinus sylvestris (Ovington 1959), P. radiata (Will 1964; Florence & Lamb 1974).

The varying types of organic matter decompose at differing initial rates, but the composition changes with time as material is concentrated in microflora or converted to humus. The rate of decomposition of some of these residual fractions is very slow and as a result there are pools of organic matter and nutrients with different turnover rates. This is clearly expressed in the model developed by Jenkinson & Rayner (1977) based on data from the Rothamsted field experiments and on measured organic matter fractions and rates of decomposition. The input (1 tC/ha/yr) is separated into two fractions: 'decomposable plant material' and 'resistant plant material' in proportions 0.837 and 0.163, respectively. Each of these fractions decomposes to produce 'soil biomass', 'physically stabilized organic matter' and 'chemically stabilized organic matter' in proportions of 0.076, 0.125 and 0.0035, respectively, with the release of carbon dioxide. These three fractions are repeatedly decomposed, yielding the same fractions at each step. The estimated half life of the fractions varied considerably and the predicted accumulation of the fraction when the model was run to 10,000 years assuming steady state (Table 1) was acceptably close to measured accumulations. The model indicates that small changes in input to the residual fractions, or changes in their turnover time, can cause large changes in the amounts of accumulated organic matter, and nutrients.

A change in rate of decomposition and accumulation can result from input of residues which tend to produce more or less of specific humus fractions. Alternatively, a change in the aerobic / anaerobic balance during the forest development can modify the production of such compounds. For example, Sinha (1972) showed that anaerobic decomposition of oat roots produced more fulvic acid and less humic acid and humins than did aerobic decomposition, the rate of decomposition of these fractions being in the sequence: fulvic acid > humic acid > humins (Campbell et al 1967).

IMMOBILIZATION AND RELEASE

The pool of organic matter with high rate of turnover may be small but provides a rapid supply of recycled nutrients, while the larger pools of resistant organic matter with slow turnover provide a continuous supply of nutrients. The supply from the resistant organic matter, although representing a very small contribution from each year's input, represents a considerable accumulated release in any one year. The turnover of the microbial and faunal biomass are key factors in the

Table 1. Turnover (half-life) and accumulation of fine fractions of organic matter in a cropped agricultural system at steady state (from Jenkinson & Rayner 1977).

Fraction	Half-life (years)	Accumulation (tC/ha)
Decomposable plant material	0.165	0.01
Resistant plant material	2.31	0.47
Soil biomass	1.69	0.28
Physically stabilized o.m.	49.5	11.3
Chemically stabilized o.m.	1980	12.2

mobilization of nutrients in the pools. The concentration of many elements in the decomposer organisms (Table 2) is much higher than in plant residues. As the carbon compounds are used as energy sources by the microflora, carbon is released as carbon dioxide or as anaerobic respiratory products, and only a small fraction is converted into microbial tissue. In contrast nutrients are first mineralized from the plant residue, absorbed and converted into microbial tissue. The transfer of nutrients from plant to microbial compounds, commonly referred to as immobilization, results in the well-known fall in the C:N or C:element ratio. The decline in the ratio is considered to continue until it approximates to that of microbial tissue, at which stage the nutrient concentration is in excess of that required by the microflora and therefore the excess becomes available for plant uptake.

The changing concentration or ratios of elements indicate the stage at which there is net release of the element from the intimate mixture of plant residue and microbial population. Critical levels approximate to 2 per cent for nitrogen (C:N c.25:1), 0.1 per cent for phosphorus (C:P c.500:1), 0.20 per cent for sulphur (C:S c.250:1) and 0.10 per cent for potassium (C:K c.500:1) (Gosz, Likens & Bormann 1973; Dowding 1974; Toth, Papp & Lenkey 1975). Such generalizations are dangerous, however, because there is considerable variation between types of resource and in methods of analysis and release is inferred, not measured. The expression of concentration or ratio also ignores the state of the element, thus release will depend on the availability of the element, including carbon, to micro-organisms, and also on the availability of other elements.

The concepts of immobilization and critical concentrations or ratios provide a convenient outline of the main sequence of events during decomposition and of differences between resources, but they mask the dynamic nature of the processes, particularly those involving the

Microflora	Mg				Source
Fungal mycelium	1.74	0.48	0.33	4.28	
mean					
range	0.23-4.31	0.02-1.31	0.16-0.61	0.68-9.50	Swift (1977)
(n)	(30)	(19)	(19)	(18)	
Fungal mycelium	2.80	0.24	0.12	-	
Fungal fruit bodies	4.40	1.00	4.90	-	Ausmus, Edwards & Witkamp (1976)
Fungal rhizomorphs	4.13	0.93	3.16		
Bacteria	4.00	0.91	1.50		
Actinomycetes	4.20	1.00	4.00		
Fauna					
Oligochaeta	10.5	1.1	0.5	0.3	Allen et al. (1974).
Diplopoda	5.8	1.9	0.5	14.0	McBrayer et al. (1974).
Insecta	8.5	6.9	0.7	0.3	
Detritivores	7.74	0.80	0.13	10.30	
Fungivores	7.74	1.39	0.40	3.95	Allen et al. (1974)

Table 2. Nutrient concentration (% dry weight) of microflora and soil fauna.

microflora. Measurements of the standing crop of microflora in various resources have been used, in conjunction with nutrient concentrations of the microflora, to calculate the quantities of nutrients immobilized. The calculated percentage of the total nutrient which is immobilized varies greatly, e.g. 2-3 per cent for nitrogen and phosphorus in the forest floor of black spruce (*Picea mariana*) in Alaska (Flanagan & Van Cleve 1977), but more than 100 per cent for some nutrients in the litter of *Liriodendron tulipifera* forest in Tennessee (Ausmus, Edwards & Witkamp 1976). Methodological problems make accurate measurements very difficult, but these two studies show that nutrients are rapidly circulated through the microbial population which has generation times in days. Death and decomposition may be balanced by growth to give a fairly constant standing crop, but the nutrients are being circulated through inorganic pools which are capable of being utilized by fine plant roots permeating the litter. Both studies also show marked growth in microbial populations and immobilization of nutrients in spring and early summer, with a decline and presumably a release of nutrients in late summer. The extent to which nutrients are retained in dead microbial cells and mycelium is unknown and the presence of dark, apparently empty hyphae in acid organic soils argues for slow decomposition of at least the chitinous cell walls which have a high nitrogen content. However, Flanagan & Van Cleve (1977) estimated that as a result of a decrease in microbial biomass, 90 per cent of which was fungal, there was a net release of 0.24 g N/sq.m and 0.025 g P/sq.m. within the forest floor in an eleven day period in summer. Ausmus, Edwards & Witkamp (1976) showed similar fluctuations in the L, F and H layers.

The immobilization of nutrients by the microflora and possibly the mechanism of release is shown in the analysis of wood decomposition, for example (Ausmus (1977) and Swift (1977)). Most nutrients in wood are gradually concentrated by fungi until 30-50 per cent of the total calcium, magnesium and potassium, and 90-100 per cent of the nitrogen and phosphorus are contained in mycelium (Fig. 6). Potassium, unlike other elements, shows a large initial decrease in concentration in wood as in other litters through leaching, while other elements are retained by the microflora. An increase in quantity of nutrient may result from nitrogen fixation or from import by fungi. Colonization by a sequence of fauna occurs after there has been considerable decomposition by fungi and is probably influenced by the concentration of nutrients in the microflora, which provide a more accessible nutrient source than the wood itself. Feeding by fauna then results in a net loss of nutrients from the wood, probably by a combination of leaching, movement of animals and comminution, which causes loss of fragments which are rich in nutrients. During the feeding by animals nutrients are ingested,

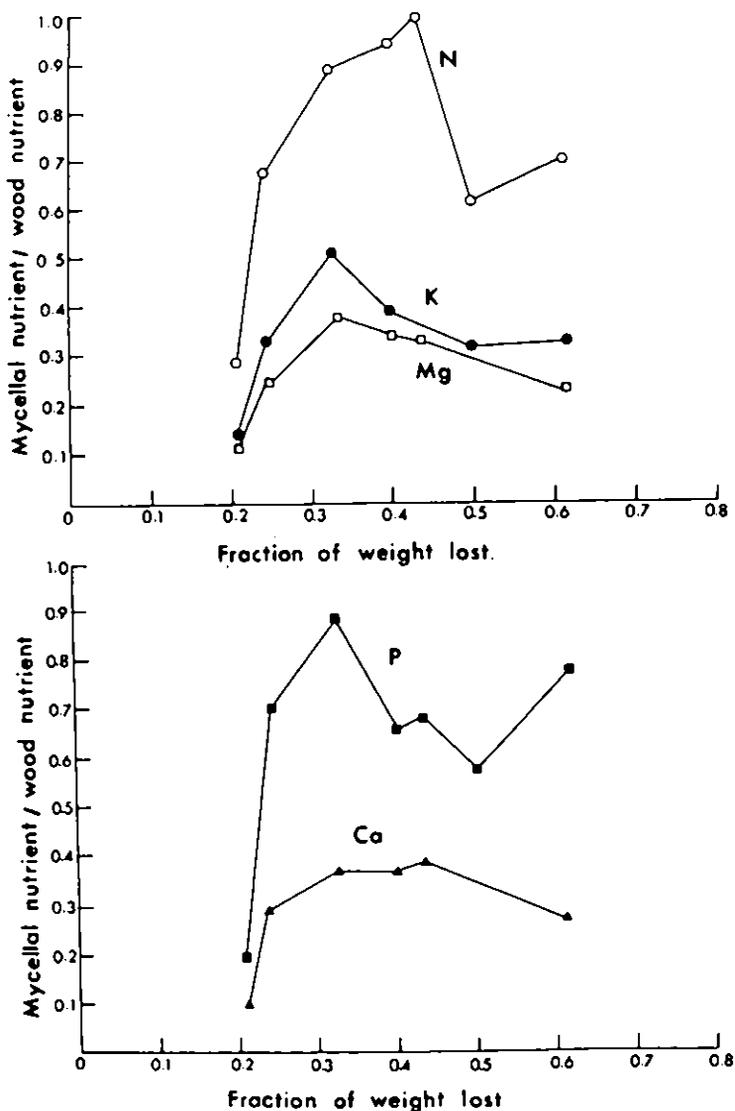


Fig. 6. The pattern of immobilisation of branch-wood nutrients by mycelium of the white rot basidiomycete *Stereum hirsutum* in relation to state of decomposition. Mycelial nutrient is calculated from mycelial standing crop multiplied by mycelium nutrient concentration and is expressed as a proportion of the branch-wood nutrient. (From Swift 1977.)

mineralized and excreted as well as being incorporated into tissue. Thus, there is a continual turnover of the inorganic and organic nutrient pools within the wood. The presence of plant roots within wood after faunal colonization, indicates that the nutrients are utilized by the vegetation and probably contribute to their net loss - at a time when the nitrogen concentration is about 0.5 per cent (C:N 100:1).

The release of nutrients from microflora results from excretion, autolysis, decomposition by other microflora and grazing by fauna on both live and dead cells and hyphae. There is considerable evidence that suppression or elimination of fauna retards the rate of decomposition, directly through consumption and respiration and indirectly through reduced microbial activity (Edwards, Reichle & Crossley 1970; Dickinson & Pugh 1974). Grazing on the microflora by protozoa and by nematodes decreases the microbial biomass but increases the rate of organic matter decomposition and the release of phosphorus and nitrogen in terrestrial and aquatic systems (Johannes 1965; Barsdate, Fenchel & Prentki 1974; Fenchel & Harrison 1976; Coleman et al. 1977), although interpretation of experimental results on phosphorus release may be conflicting (Fenchel & Harrison 1976).

Within an even-aged plantation, especially with conifers, changes in the physico-chemical conditions and in resource quality will influence faunal populations. Increase in acidity and of input of conifer litter will reduce earthworm populations if they were present initially, and the forest floor decomposition is usually dominated by micro-arthropods and enchytraeids and by fungi. The reduction in moisture level is likely to encourage faunal activity by increasing aeration on wet sites, but if waterlogging occurs as a result of felling, anaerobic conditions will again reduce the fauna. Although protozoa can modify bacterial populations and processes, their influence on fungi is probably much more limited as few species are known to be fungivorous (Stout 1974) and their participation in nutrient cycling is likely to decline during the development of a conifer plantation. Interaction within the microflora occurs and the most relevant aspect is the inhibition of litter decomposition by mycorrhizae. Gadgil & Gadgil (1975) showed that the weight loss of Pinus radiata needles without plants or with non-mycorrhizal plants was significantly higher (44 per cent after six months) than in the presence of mycorrhizal plants (39 per cent). The difference is difficult to interpret but may result from the production of antibiotics which inhibit the growth of saprophytes or the greater competitive ability of mycorrhizal fungi, whose nutrient uptake is not dependent on an associated energy source. Thus, organic matter decomposition may be retarded by the spread of mycorrhizas in the development of a plantation, while the mobilization of

nutrients is maintained by the mycorrhizas.

PATTERN AND IMPLICATIONS

Decomposition and nutrient release comprise a complex series of interacting processes controlled by the physico-chemical environment and resource quality and quantity. The balance between these processes and the input of organic matter determines the rates of accumulation of organic matter and nutrients in and beneath the forest floor. In most ecosystems there are a series of trends occurring over different time scales - a pedogenic trend over millenia, on which is superimposed a successional sequence which may be repeated over decades or centuries, and a seasonal and even diurnal rhythm. In even-aged plantations the successional sequence is much more distinct than in mixed-aged situations, with the additional effect of distinct pulses introduced by management activities like brashing, thinning and felling.

The hypothesis, based on the review given in this paper, is that the general sequence of decomposition in conifer plantations will be:

- (1) an initial pulse as a result of death of ground vegetation and site preparation;
- (2) a gradual decline as input from ground vegetation declines and conifer litter increases, and as soil temperature variation and moisture content decline as the canopy closes;
- (3) a pulse as a result of input of green needles, fresh wood and roots at thinning with associated short-term increases in temperature variation and moisture;
- (4) a further decline as the proportion of wood input increases with stand age;
- (5) a final pulse, greater than that at thinning, when felling provides a major input of fresh material and there is increased temperature and moisture response;
- (6) the effect of the final pulse may be sustained by input from regrowth of ground vegetation into a favourable microclimate, until forest cover redevelops in a subsequent generation of trees.

Such a sequence is described in relation to specific management practices by Bunn & Will (1974) and Wollum & Davey (1975). However, there is no direct evidence for or against the suggested sequence of events in terms of measured rates of decomposition and nutrient release over a rotation. The main corroborative evidence comes from the observed amounts of organic matter and nutrients accumulated over time or in response to particular practices. This evidence allows some inferences of rates of decomposition processes, particularly loss of carbon, but gives little indication of the actual pattern of mineralization or of supply of nutrients to the trees.

The studies on effects of clearfelling appear to provide direct evidence with marked increases in nitrate output in stream water from felled, compared with unfelled, areas, additional variation being related to management of the forest waste and forestry practice (Pierce et al. 1972; Verry 1972; Brown, Gahler & Marston 1973; Likens & Bormann 1974; Wiklander 1974; Fredriksen, Moore & Norris 1975; Snyder, Haupt & Belt 1975; Neary 1977). Although there are major variations in concentration, many of these studies show an increase in nitrate output of about an order of magnitude after felling, with a return to base-line concentrations when ground vegetation is redeveloped. Actual changes within the forest floor and soil have received little attention, but Popovic (1974) showed an increased nitrification in soils as a result of felling, the rate being greatest in soils with pH above about 4.3 and C:N below about 30:1. Tamm et al. (1974) point out that the change in nitrogen release is the result of loss of nutrient uptake by the trees which allows temporary accumulation of ammonia, providing the necessary substrate for nitrification. Unless inhibited by soil conditions, there will be an increase in nitrification and, in the absence of uptake by vegetation, the nitrate produced will be readily leached. Thus, there is a change in the product of nitrogen mineralization rather than a change in rate. The amount which is available for mineralization will, however, depend on the amount of organic residues from felling.

Loss of nitrate, and to a lesser extent phosphate, after felling is related to the change in demand, analogous to nutrient leaching under fallow conditions in agriculture. This raises the question of the synchronization of nutrient release from the forest floor and the nutrient demand by the growing crop. The apparent pattern of increasing accumulation of organic matter and nutrients in the forest floor as the forest develops, implies decreasing release of nutrients, although some of the change is probably a redistribution of material within the soil profile rather than a change in absolute amount. The sequence of management practices from site preparation to felling results in a series of pulses of nutrient release. The initial pulse coincides with a small, localized demand by the establishing forest; at thinning the pulse of nutrients from the forest floor probably accounts for some of the increased crop growth at a time when nutrient demand is maximal; at felling there is a release which does not coincide with forest demand. Thus, in even-aged plantations, both supply and demand are phased, but these two major cogs in the nutrient cycle are apparently not fully synchronized. In contrast, the mixed-aged forest has a spatial mosaic which allows greater opportunity for trees and other vegetation to benefit from phases of nutrient input and release associated with individual trees. The mosaic in a

mixed-aged forest will include seasonal variation in input and release when a range of species are involved.

The importance of synchrony of nutrient supply and demand is only theoretical, and probably varies in different climatic regimes. In tropical regions a major proportion of the nutrient capital is maintained in the forest biomass, with a small proportion in the forest floor which has a very short turnover time. With increasing latitude the balance changes, and an increasing proportion of the ecosystem nutrients are retained in the forest floor, until in boreal forests there is a long turnover time (Olsen 1963; Duvigneaud & Denayer-DeSmet 1969; Witkamp & Ausmus 1976). The forest floor, acting as both nutrient sink and source, provides a stability in high latitude forests which makes them less liable than tropical forests to suffer nutrient loss through man's activity. However, while acting as a stabilizing influence, the forest floor reduces the flow of nutrients to the trees, and any increase in the rate of nutrient turnover is expected to increase primary production. Fertilizers give some increase in growth, but efficiency of uptake is low compared with agricultural systems, partly because of the slow response rate of trees. Grazing is an alternative practice which has the potential to increase the rate of nutrient turnover in the forest floor, and by maintaining a vegetation cover can retain nutrients during management disturbances. Some of the positive responses of trees to experimental grazing (Hedrick & Keniston 1966) may result from increased nutrient availability despite potential competition between trees and ground flora. Although current evidence of the value of grazing in forests is inconclusive (Adams 1975), there are logical reasons for examining this, and other alternatives to current management practices, which can increase and control nutrient circulation through the forest floor.

REFERENCES

- Adams, S.N. (1975). Sheep and cattle grazing in forests: a review. *Journal of Applied Ecology*, 12, 143-152.
- Allen, S.E., Grimshaw, H.M., Parkinson, J.A. & Quarmby, C. (1974). *Chemical analysis of ecological materials*. Blackwell, Oxford.
- Alexander, M. (1977). *Introduction to soil microbiology*. Wiley, New York.
- Attwell, P.M. (1968). The loss of elements from decomposing litter. *Ecology*, 49, 142-145.
- Ausmus, B.S. (1977). Regulation of wood decomposition rates by arthropod and annelid populations. "Soil organisms as components of ecosystems." (Ed. by U. Lohm and T. Persson), pp. 180-192. *Ecological Bulletin*, Swedish Natural Science Research Council, 25.

- Ausmus, B.S., Edwards, N.T. & Witkamp, M. (1976). Microbial immobilization of carbon, nitrogen, phosphorus and potassium: implications for forest ecosystems processes. "The role of terrestrial and aquatic organisms in decomposition processes." (Ed. by J.M. Anderson and A. Macfadyen), pp.397-416. Blackwell, Oxford.
- Barsdate, R.J., Fenchel, T. & Prentki, R.T. (1974). Phosphorus cycle of model ecosystems: significance for decomposer food chains and effect of bacterial grazers. *Oikos*, 25, 239-251.
- Bauzon, D., Van den Driessche, R. & Dommergues, Y. (1969). L'effet litière. I. Influence en situ des litières forestières sur quelques caractéristiques biologiques de sols. *Oecologia plantarum*, 4, 99-122.
- Beek, J. & Frissel, M.J. (1973). Simulation of nitrogen behaviour in soils. Pudoc, Wageningen.
- Binns, W.O. (1968). Some effects of tree growth on peat. Proceedings 3rd International Peat Congress, Quebec 1968.
- Birch, H.F. (1964). Mineralization of plant nitrogen following alternate wet and dry conditions. *Plant and Soil*, 20, 43-50.
- Bocock, K.L. (1964). Changes in the amounts of dry matter, nitrogen, carbon and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. *Journal of Ecology*, 52, 273-284.
- Bocock, K.L. & Gilbert, O.J.W. (1957). The disappearance of leaf litter under different woodland conditions. *Plant and Soil*, 9, 179-185.
- Bray, J.R. & Gorham, E. (1964). Litter production in forests of the world. *Advances in Ecological Research*, 2, 101-157.
- Brown, C.W., Gahler, A.R. & Marston, R.B. (1973). Nutrient losses after clearcut logging and slash burning in the Oregon Coast Range. *Water Resources Research*, 9, 1450-1453.
- Brown, J.M. (1976). Peat temperature regime of a Minnesota bog and the effect of canopy removal. *Journal of Applied Ecology*, 13, 189-194.
- Bunn, E.H. & Will, C.M. (1974). Management operations affecting nutrient cycling and fertilizer response in forest stands. Proceedings F.A.O./ I.U.F.R.O. International Symposium on Forest Fertilization, Paris. pp.33-53.
- Bunnell, F.L. & Tait, D.E.N. (1975). Mathematical simulation models of decomposition processes. "Soil organisms and decomposition in tundra." (Ed. by A.J. Holding, O.W. Heal, S.F. MacLean and P.W. Flanagan), pp.207-225. Tundra Biome Steering Committee, Stockholm.
- Bunnell, F.L., Tait, D.E.N. & Flanagan, P.W. (1977). Microbial respiration and substrate weight loss. II. A model of the influences of chemical composition. *Soil Biology and Biochemistry*, 9, 41-47.
- Bunnell, F.L., Tait, D.E.N., Flanagan, P.W. & Van Cleve, K. (1977).

- Microbial respiration and substrate weight loss. I. A general model of the influences of abiotic variables. *Soil Biology & Biochemistry*, 9, 33-40.
- Campbell, C.A., Paul, E.A., Rennie, D.A. & McCallum, K.J. (1967). Applicability of the carbon-dating method of analysis to soil humus studies. *Soil Science*, 104, 217-224.
- Carey, M.L. & Farrell, E.P. (1978). Production, accumulation and nutrient content of Sitka spruce litterfall. *Irish Forestry*, 35, 35-44.
- Coleman, D.C., Cole, C.V., Anderson, R.V., Campion, M.K., Clarholm, M., Elliot, E.T., Hunt, H.W., Schaefer, B. & Sinclair, J. (1977). An analysis of rhizosphere - saprophage interactions in terrestrial ecosystems. "Soil organisms as components of ecosystems." (Ed. by U. Lohm and T. Persson), pp. 299-309. *Ecological Bulletin, Swedish Natural Science Research Council*, 25.
- Cromack, K., Sollins, P., Todd, R.L., Fogel, R., Todd, A.W., Fender, W.M., Crossley, M.E. & Crossley, D.A. (1977). The role of oxalic acid and bicarbonate in calcium cycling by fungi and bacteria: some possible implications for soil animals. "Soil organisms as components of ecosystems." (Ed. by U. Lohm and T. Persson), pp. 246-252. *Ecological Bulletin, Swedish Natural Science Research Council*, 25.
- Daubenmire, R. & Prusso, D.C. (1963). Studies of the decomposition rates of tree litter. *Ecology*, 44, 589-592.
- Dickinson, C.H. (1974). Decomposition of litter in soil. "Biology of plant litter decomposition." (Ed. by C.H. Dickinson and G.J.F. Pugh), pp. 633-658. Academic Press, London.
- Dickinson, C.H. & Pugh, G.J.F. (1974). Biology of plant litter decomposition. Academic Press, London.
- Dowling, P. (1974). Nutrient losses from litter on I.B.P. tundra sites. "Soil organisms and decomposition in tundra." (Ed. by A.J. Holding, O.W. Heal, S.F. MacLean and P.W. Flanagan), pp. 363-373. Tundra Biome Steering Committee, Stockholm.
- Duvigneaud, P. & Denayer-DeSmet, S. (1969). Biological cycling of minerals in temperate deciduous forest. "Analysis of temperate forest ecosystems" (Ed. by D.E. Reichle), pp. 199-225. Springer Verlag, New York.
- Edgerton, P.J. & McConnell (1976). Diurnal temperature regimes of logged and unlogged mixed conifer stands on elk summer range. U.S. Department of Agriculture Forest Service Research Note, PNW-277.
- Edwards, C.A., Reichle, D.E. & Crossley, D.A. (1970). The role of soil invertebrates in turnover of organic matter and nutrients. "Analysis of temperate forest ecosystems." (Ed. by D.E. Reichle), pp. 147-172. Springer Verlag, New York.
- Fenchel, T. & Harrison, P. (1976). The significance of bacterial grazing and mineral cycling for the decomposition of

- particulate detritus. "The role of terrestrial and aquatic organisms in decomposition processes." (Ed. by J.M.Anderson and A.Macfadyen), pp.285-299. Blackwell, Oxford.
- Flanagan,P.W. & Van Cleve,K.(1977). Microbial biomass, respiration and nutrient cycling in a black spruce taiga ecosystem. "Soil organisms as components of ecosystems." (Ed. by U.Lohm and T.Persson), pp.261-273. Ecological Bulletin, Swedish Natural Science Research Council, 25.
- Florence,R.G., & Lamb,D.(1974). Influence of stand and site on radiata pine litter in South Australia. New Zealand Journal of Forestry Science, 4, 502-510.
- Frankland,J.C.(1966). Succession of fungi on decaying petioles of Pteridium aquilinum. Journal of Ecology, 54, 41-63.
- Fredriksen,R.L., Moore,D.G. & Norris,L.A.(1975). The impact of timber harvest, fertilization and herbicide treatment on streamwater quality in western Oregon and Washington. "Forest soils and forest land management." Proceedings 4th North American Forestry Soils Conference, Quebec. (Ed. by B.Bernier and E.H.Winget), pp.283-313. University of Laval Press, Quebec.
- Frissel,M.J. & Damen,J.P.N.(1977)(Eds) Cycling of mineral nutrients in agricultural ecosystems. Agro-Ecosystems, 1 and 2.
- Gadgil,R.L. & Gadgil,P.D.(1975). Suppression of litter decomposition by mycorrhizal roots of Pinus radiata. New Zealand Journal of Forestry Science, 5, 33-41.
- Gosz,J.R., Likens,G.E. & Bormann,F.H.(1973). Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. Ecological Monographs, 43, 173-191.
- Greenwood,D.J.(1968). Measurement of microbial metabolism in soil. "Ecology of soil bacteria." (Ed. by T.R.Gray and O.Parkinson), pp.138-151. Liverpool University Press, Liverpool.
- Grieve,I.C.(1978). Some effects of the plantation of conifers on a freely drained lowland soil, Forest of Dean, U.K. Forestry, 51, 21-28.
- Haberland,F.P. & Wilde,S.W.(1961). Influence of thinning of red pine plantation on soil. Ecology, 42, 584-586.
- Hamilton,C.D.(1965). Changes in the soil under Pinus radiata. Australian Forestry, 29, 275-289.
- Handley,W.R.C.(1954). Mull and mor formation in relation to forest soils. Forestry Commission Bulletin #23.
- Hansen,T.S.(1937). Ecological changes due to thinning jack pine. University of Minnesota, Technical Bulletin, 124, 1-77.
- Heal,O.W. & French,D.D.(1974). Decomposition of organic matter in tundra. "Soil organisms and decomposition in tundra." (Ed. by A.J.Holding, O.W.Heal, S.F.MacLean and

- P.W.Flanagan), pp.279-309. Tundra Biome Steering Committee, Stockholm.
- Heal, O.W., Latter, P.M. & Howson, G. (1978). A study of the rates of decomposition of organic matter. "Production ecology of British moors and montane grasslands." (Ed. by O.W.Heal and D.F.Perkins), pp.136-159. Springer Verlag, Berlin.
- Hedrick, D.M. & Keniston, R.F. (1966). Grazing and Douglas fir growth in the Oregon white oak type forest. *Journal of Forestry*, 64, 735-738.
- Helvey, J.D. (1975). Soil moisture depletion and growth rates after thinning ponderosa pine. U.S. Department of Agriculture Forest Service Research Note, PNW-243.
- Innis, G.S. (1978). Grassland simulation model. Springer Verlag, Berlin.
- Jenkinson, D.S. (1965). Studies on the decomposition of plant material in soil. I. Losses of carbon from ^{14}C labelled ryegrass incubated with soil in the field. *Journal of Soil Science*, 16, 104-115.
- Jenkinson, D.S. & Rayner, J.H. (1977). The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Science*, 123, 298-305.
- Jensen, V. (1974). Decomposition of angiosperm tree leaf litter. "Biology of plant litter decomposition." (Ed. by C.H.Dickinson and G.J.F.Pugh), pp.69-104. Academic Press, London.
- Johannes, R.E. (1965). Influence of marine protozoa on nutrient regeneration. *Limnology and Oceanography*, 10, 434-442.
- Jorgensen, J.R., Wells, C.G. & Metz, L.J. (1975). The nutrient cycle: key to continuous forest production. *Journal of Forestry*, 73, 400-403.
- Kaarik, A.A. (1974). Decomposition of wood. "Biology of plant litter decomposition." (Ed. by C.H. Dickinson and G.J.F.Pugh), pp.129-174. Academic Press, London.
- Kholopova, L.B. (1972). Variation in some physical and chemical soil properties with age of pine plantations. *Lesovadenie* 1972, pp.38-48.
- King, H.G.C. & Heath, G.W. (1967). The chemical analysis of small samples of leaf material and the relationship between the disappearance and composition of leaves. *Pedobiologia*, 7, 192-197.
- Kira, T. & Shidei, T. (1967). Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. *Japanese Journal of Ecology*, 17, 70-87.
- Kolenbrander, G.J. (1971). Contribution of agriculture to eutrophication of surface waters with nitrogen and phosphorus in the Netherlands. Institute of Soil Fertility, Haren, Groningen.
- Lamb, D. (1976). Decomposition of organic matter on the forest floor of Pinus radiata plantations. *Journal of Soil*

- Science, 27, 206-217.
- Likens, G.E. & Bormann, F.H. (1974). Effects of forest clearing on the northern hardwood forest ecosystem and its biogeochemistry. Proceedings 1st International Congress on Ecology, The Hague, Netherlands. pp.330-335.
- Lull, H.W. & Axley, J.H. (1958). Forest soil moisture relations in the coastal plain sands of southern New Jersey. *Forest Science*, 4, 2-19.
- McBrayer, J.F., Reichle, D.E. & Witkamp, M. (1974). Energy flow and nutrient cycling in a cryptozoan foodweb. Oak Ridge National Laboratory, Oak Ridge.
- Malone, C.R. & Reichle, D.E. (1973). Chemical manipulation of soil biota in a fescue meadow. *Soil Biology and Biochemistry*, 5, 629-639.
- Melin, E. (1930). Biological decomposition of some types of litter from North American forests. *Ecology*, 11, 72-101.
- Mikola, P. (1955). Experiments on the rate of decomposition of forest litter. *Communicationes Instituti Forestalis Fenniae*, 43, 1-50.
- Miller, H.G., Cooper, J.M. & Miller, J.D. (1976). Effect of nitrogen supply on nutrients in litter fall and crown leaching in a stand of Corsican pine. *Journal of Applied Ecology*, 13, 233-248.
- Minderman, G. (1968). Addition, decomposition and accumulation of organic matter in forests. *Journal of Ecology*, 56, 355-362.
- Mommaerts-Billiet, F. (1971). Aspects dynamiques de la disparition de la litière de feuilles. *Bulletin Société royale de botanique de Belgique*, 104, 181-195.
- Neary, D.A. (1977). Impact of timber harvesting on nutrient losses in stream flow. *New Zealand Journal of Forestry*, 22, 53-63.
- Nihlgård, B. (1971). Pedological influence of spruce planted on former beech forest soils in Scania, South Sweden. *Oikos*, 22, 302-314.
- Nye, P.H. & Tinker, P.B. (1977). Solute movement in the soil-root system. Blackwell, Oxford.
- Nykvist, N. (1963). Leaching and decomposition of water-soluble organic substances from different types of leaf and needle litter. *Studia Forestalia Suecica*, 3, 1-31.
- Odin, M. (1974). Some meteorological effects of clearfelling. *Sveriges Skogsvårdsförbunds Tidskrift*, 1, 60-65.
- Olson, J.S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, 44, 322-331.
- Ovington, J.D. (1953). Studies of the development of woodland conditions under different trees. I. Soil pH. *Journal of Ecology*, 41, 31-34.
- Ovington, J.D. (1954). Studies of the development of woodland conditions under different trees. II. The forest floor.

- Journal of Ecology, 42, 71-80.
- Ovington, J.D. (1959). The circulation of minerals in plantations of Pinus sylvestris L. Annals of Botany, 23, 229-239.
- Page, G. (1968). The effects of conifer crops on soil properties. Commonwealth Forestry Review, 47, 52-62.
- Page, G. (1974). The effect of forest cover on the properties of some Newfoundland forest soils. Canadian Forest Service Publication #1332.
- Patrick, W.H. (1978). Measurement and predication of anaerobiosis in soils. "Nitrogen in the environment. I. Nitrogen behaviour in field soil." Academic Press, London.
- Pienc, H. & Van Cleve, K. (1978). Weight loss of litter and cellulose bags in a thinned white spruce forest in interior Alaska. Canadian Journal of Forest Research, 8, 42-46.
- Pierce, R.S., Martin, C.W., Reeves, C.C., Likens, G.E. & Bormann, F.H. (1972). Nutrient loss from clearcuttings in New Hampshire. Proceedings of the symposium on watersheds in transition. American Water Resources Association, Urbana. pp.285-295.
- Popovic, B. (1974). The effect of clearfelling on soil nitrogen transformation. Sveriges Skogsvarvsforbunds Tidskrift, 1, 80-85.
- Pyatt, G. (1973). Physical and mechanical properties of soil types. Report on Forest Research, London. 1973. pp.62-66.
- Read, D.J., Armstrong, W. & Weatherall, J. (1973). The effects of cultivation treatment on water potential and soil aeration in wet heathland with special reference to afforestation. Journal of Applied Ecology, 10, 479-487.
- Salter, P.J., Berry, G. & Williams, J.B. (1966). The influence of texture on the moisture characteristics of soils. III. Quantitative relationships between particle size, composition and available water capacity. Journal of Soil Science, 17, 93-98.
- Satchell, J.E. & Lowe, D.G. (1967). Selection of leaf litter by Lumbricus terrestris. "Progress in soil biology." (Ed. by O. Graff and J.E. Satchell), pp.102-118. North Holland Publishing Co., Amsterdam.
- Scheffer, T.C. & Cowling, E.B. (1966). Natural resistance of wood to microbial deterioration. Annual Review of Phytopathology, 4, 147-170.
- Sinha, M.K. (1972). Organic matter transformation in soils. I. Humification of C¹⁴-tagged oat roots. Plant and Soil, 36, 283-293.
- Smith, J.H. (1966). The use of isotopes in soil organic matter studies. Pergamon Press, Oxford. pp.223-224.
- Smith, W.H. (1969). Release of organic materials from the roots of tree seedlings. Forest Science, 15, 138-143.

- Smith, W.H. (1970). Root exudates of seedling and mature sugar maple. *Phytopathology*, 60, 701-703.
- Snyder, G.G., Haupt, H.F. & Belt, G.H. (1975). Clearcutting and burning slash alter quality of stream water in northern Idaho. U.S. Department of Agriculture Forest Service Research Paper INT-168. Intermountain Forest Range Experimental Station.
- Stone, E.L. (1975). Effects of species on nutrient cycles and soil change. *Philosophical Transactions of the Royal Society, London B*, 271, 149-162.
- Stout, J.D. (1964). Protozoa. "Biology of plant litter decomposition". (Ed. by C.H. Dickinson and G.J.F. Pugh), pp.385-420. Academic Press, London.
- Swift, M.J. (1977). The roles of fungi and animals in the immobilization and release of nutrient elements from decomposing branchwood. "Soil organisms as components of ecosystems." (Ed. by U.Lohm and T.Persson), pp.193-202. *Ecological Bulletin, Swedish Natural Science Research Council*, 25.
- Swift, M.J., Heal, O.W. & Anderson, J.M. (in press). Decomposition in terrestrial ecosystems. Blackwell, Oxford.
- Swift, M.J., Healey, I.N., Hibberd, J.K., Sykes, J.M., Bamcoe, V. & Nesbitt, M.E. (1976). The decomposition of branchwood in the canopy and floor of a mixed deciduous woodland. *Oecologia*, 26, 139-149.
- Tamm, C.O., Holmen, H., Popovic, B. & Wiklander, G. (1974). Leaching of plant nutrients from soils as a consequence of forestry operations. *Ambio*, 3, 211-221.
- Tanji, K.K. & Gupta, S.K. (1978). Computer simulation modelling for nitrogen in irrigated croplands. "Nitrogen in the environment. I. Nitrogen behaviour in field soils." (Ed. by D.R. Nielsen and J.G. MacDonald), pp.79-130. Academic Press, New York.
- Tappeiner, J.C. & Alm, A.A. (1975). Undergrowth vegetation effects on the nutrient content of litterfall and soils in red pine and birch stands in northern Minnesota. *Ecology*, 56, 1193-1200.
- Toth, J.A., Papp, L.B. & Lenkey, B. (1975). Litter decomposition in an oak forest ecosystem (*Quercetum petraeae cerris*) of northern Hungary studied in the framework of the 'Sikfokut project'. "Biodégradation et Humification." (Ed. by G.Kilbertus, O.Reisinger, A.Mourey and J.A.Cancela Da Fonseca), pp.41-58. Université de Nancy.
- Turner, J. (1975). Nutrient cycling in a Douglas fir ecosystem with respect to age and nutrient status. *Forestry Abstracts*, 37, 6003.
- Van Cleve, K. (1974). Organic matter quality in relation to decomposition. "Soil organisms and decomposition in tundra." (Ed. by A.J.Holding, O.W.Heal, S.F.MacLean and

- P.W.Flanagan), pp.311-324. Tundra Biome Steering Committee, Stockholm.
- Van Cleve, K. & Sprague, O. (1971). Respiration rates in the forest floor of birch and aspen stands in interior Alaska. *Arctic and Alpine Research*, 3, 17-26.
- Verry, E.S. (1972). Effect of an aspen clearcutting on water yield and quality in northern Minnesota. Proceedings Symposium on Watersheds in Transition, Fort Collins. American Water Resources Association, Urbana.
- Voigt, G.K. (1965). Nitrogen recovery from decomposing tree leaf tissue and forest humus. Soil Science Society of America Proceedings, 29, 756-759.
- Waid, J.S. (1974). Decomposition of roots. "Biology of plant litter decomposition." (Ed. by C.H.Dickinson and G.J.F.Pugh), pp.175-211. Academic Press, London.
- Wiklander, G. (1974). Effect of clearfelling on the content of nutrients in surface and ground water. *Sveriges Skogsvarvsforbunds Tidskrift*, 1, 86-90.
- Wilde, S.A. (1964). Changes in soil productivity induced by pine plantations. *Soil Science*, 97, 276-278.
- Will, G.M. (1964). Dry matter production and nutrient uptake by Pinus radiata in New Zealand. *Commonwealth Forestry Review*, 43, 57-70.
- Will, G.M. (1967). Decomposition of Pinus radiata litter on the forest floor. I. Changes in dry matter and nutrient content. *New Zealand Journal of Forestry Science*, 10, 1030-1044.
- Williams, B.L., Cooper, J.M. & Pyatt, D.G. (1978). Effects of afforestation with Pinus contorta on nutrient content, acidity and exchangeable cations in peat. *Forestry*, 51, 29-35.
- Williams, S.T. & Gray, T.R.G. (1974). Decomposition of litter on the soil surface. "Biology of plant litter decomposition." (Ed. by C.H.Dickinson and G.J.F.Pugh), pp.611-632. Academic Press, London.
- Witkamp, M. (1966). Decomposition of leaf litter in relation to environment, microflora and microbial respiration. *Ecology*, 47, 194-201.
- Witkamp, M. (1969). Environmental effects on microbial turnover of some mineral elements. I. Abiotic factors. *Soil Biology and Biochemistry*, 1, 167-176.
- Witkamp, M. & Ausmus, B.S. (1976). Processes in decomposition and nutrient transfer in forest systems. "The role of terrestrial and aquatic organisms in decomposition processes." (Ed. by J.M.Anderson and A.Macfadyen), pp.375-396. Blackwell, Oxford.
- Witkamp, M. & Drift, J.van der (1961). Breakdown of forest litter in relation to environmental factors. *Plant and Soil*, 15, 295-311.
- Wollum, A.G. & Davey, C.B. (1975). Nitrogen accumulation,

transformation and transport in forest soils. "Forest soils and land management." (Ed. by B. Bernier and C.H. Winget), pp.67-106. Université de Laval Press, Quebec.

Wood, T.G. (1974). Field investigations on the decomposition of leaves of Eucalyptus delegatensis in relation to environmental factors. Pedobiologia, 14, 343-371.