STUDIES ON THE MICROBIAL ECOLOGY OF SOILS FROM *PINUS RADIATA* (D.DON) FORESTS

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PART I

INTRODUCTION AND REVIEW OF LITERATURE

CHAPTER 1

GENERAL INTRODUCTION

Early in 1962 the Forest Research Institute of the New Zealand Forest Service became aware that stands of second crop Pinus radiata (D.Don) on some areas of the Moutere Gravel formation were showing slow growth and had a chlorotic appearance (Fig. 1.1). The second crop followed clear felling of mature P.radiata trees and were aged from 0 to 15 years (Stone and Will, 1965). It was felt that the apparent reduced growth of the second generation had much in common with similar productivity decline reported especially in European forestry literature. Stone and Will (1965) postulated that the immediate cause of the decline was a deficiency of nitrogen highlighted by the low levels of nitrogen in the leaves of the second crop trees, especially those growing on ridge sites.

Numerous field trials have been laid out but many of the trials were poorly designed and consequently could not provide statistically sound results. However, some indication of nutrient deficiencies which occur on the Moutere Gravels were obtained. Even before these trials were laid

down nutrient deficiencies had been highlighted by early attempts at farming. It was the partial failure of these crops that initially led to the planting of exotic pines, in the belief that these trees thrived on a limited supply of nutrients. The first crop of pines generally fulfilled expectations but nutrient deficiencies started to appear in extensive areas of the second crop. Accordingly, the Forest Research Institute made available three scholarships to study different aspects of the problem.

Work was started on a study of the soil sequence across the Moutere Gravels to determine if there was a general decline in fertility of the soil with the age of the soil and the environmental factors, such as climate which differs in the high inland areas and the low seaside areas of the Moutere Gravels, rather than a particular decline in fertility induced by the first crop of P.radiata.

In another study the major weed species Ulex europaeus and Cytisus scoparius was studied to see if its value as a nitrogen fixer would outweigh its disadvantages as a silvicultural weed. Thirdly, a study of the microbial ecology of the soils was undertaken. Whyte (1966) reported that the second rotation trees started to increase their growth rate after approximately five years to a level paralleling the estimated growth rate of the first crop. It was postulated that the residues (needles, roots and branches) remaining after clear felling could cause an increase in microbial numbers and activity with a consequent immobilization of

Fig.1.1 Aerial view of Machine Gully showing chlorotic appearance of young second regeneration *P.radiata*.

mineral nutrients which were not initially very plentiful. For this reason an area in Tasman Forest was selected in which mature trees and regeneration up to nine years old were found together to study microbial activity and numbers, energy dissipation and nitrogen dynamics to determine if immobilization of nutrients was causing the apparent declines.

THE PROBLEM AS A STUDY IN ECOSYSTEM ECOLOGY

In recent years there has been a growing emphasis on investigations into energy and mineral nutrient flow in natural ecosystems (Odum and Odum, 1957; Golley, 1960; Bliss, 1962, 1964, and 1966; Ovington, 1957, and 1959; Bray, 1962; Satoo, 1966; Botkin and Malone, 1968; Warren Wilson, 1967; Menhinick, 1967; Marples, 1966; Ovington and Lawrence, 1967; Kucera et al. 1967; and Tilly, 1968, etc.).

Park (1946) stated "that probably the most important ultimate objective of ecology is an understanding of community structure and function from the viewpoint of its metabolism and energy relationships". Aquatic biologists were first to take the initiative in the study of community energetics, and once this work became generally known studies of terrestrial communities increased. Now this wide concept of ecology is found in most fields including microbiology (Brock, 1967). "Soil microbiology arose in an attempt to account for the chemical processes such as the oxidation of ammonia and the fixation of nitrogen, already shown by chemists to take place in the soil. Towards the close of the nineteenth century

the work of such pioneers as Winogradsky and Beijerinck had demonstrated that some of the most important chemical processes in soil were brought about by specific organisms." (Thornton, 1956).

Russell and Hutchinson (1909) emphasised the complex interrelationships between the components of the micropopulation. Waksman (1931) and Russell (1912) continued this line of investigation, emphasising gross microbiological processes in the soil. Later there was a trend towards the study of more specific processes which were thought to control soil fertility more directly (Clark (1954). Processes of mineral nutrient flow, although attempted by early workers, have proved more amenable to study with the advent of tracer methods but, as yet, no system of 'labelling' energy has been developed. The trend towards an ecosystem approach has again focussed attention on the major energy processes in the soil (International Biological Programmes in England and America).

In the particular ecosystem studied in this investigation energy flow via the detritus pathway predominates and the forest floor is the major area of heterotroph activity. Tracing energy flow through the myriad populations inhabiting the forest floor in an exceedingly difficult task (Birch and Clark, 1953) and a thorough assessment of energy release and transfer by these populations may not be achieved for many years. This difficulty is offset, in part, by the fact that heterotroph metabolism is centralized in the forest floor and the sum of energy release by all populations may be measured

by monitoring some by-product of energy dissipation (Reiners, 1968).

Once these general processes have been elucidated there may well be a more detailed analysis and the organisms responsible for decomposition, which are at present lumped into a single large diffuse trophic level, may be divided into more sharply defined levels. At this stage the intensively studied aspects of soil microbiology should become incorporated into the overall scheme of energy flow.

OUTLINE OF PRESENT WORK

The work described here is an attempt to amalgamate two lines of thought. Firstly, there is the academic enquiry into the control and dynamics of ecosystems. Secondly, there is the practical problem of finding ways of producing better pine trees. These two objectives are often not strictly compatible because academic investigations are not limited by the need to reduce practical difficulties, but an attempt has been made to keep a balance between the two.

CHAPTER 2

REVIEW OF WORLD LITERATURE

2.1 DECLINE IN PRODUCTIVITY OF SECOND AND SUBSEQUENT ROTATIONS

The productivity decline of second and subsequent rotations of coniferous species has caused concern in a number of parts of the world, but the cause or causes of decline seem to vary in different regions. As the concept of productivity can be variously interpreted, depending on the outlook of the observer, different standards may have caused some of the lack of agreement found in the literature as many workers have used the term without adequate definition.

Reports of a productivity decline have come from many parts of the world. This phenomenon has been described from Switzerland, Norway, Denmark, England, Australia and New Zealand and, to a limited extent, in America. Since the conditions under which the trees showing reduced productivity were so different in the various countries the literature from each region has been reviewed separately.

Europe

Human interference in natural ecosystems has been a cause for concern because often undesired changes may occur as a result. For this reason doubts have been expressed, mainly by those concerned with highly productive forests, about the desirability of planting monospecific coniferous forests. The first report of decline in productivity was made by Wiedemann (1923) who studied spruce stands in Saxony. Since that time speculation as to the cause of the phenomenon has exceeded the amount of work on its elucidation.

Thomas (1957) pointed out that the condemnation by European foresters of single species conifer plantations was based primarily on observations made on plantations of Norway spruce (Picea excelsa) established 100 to 150 years ago on the plains of Switzerland and in parts of Denmark and Saxony where there has been a falling off in growth and health of successive rotations. If a decline in productivity was related to the number of generations rather than the absolute time under coniferous plantations then the long generation (60 - 120 years for Picea excelsa) times would mean that the plantations in Europe reported in the literature (Thomas, 1957) would be at a similar stage to those in Australia and New Zealand where second generation stands are now growing.

The drop in productivity seems strange because it would appear beneficial to the expansion of the species if one rotation made conditions more favourable for the growth of their offspring. It is usually thought that plants in

natural situations, for example Sphagnum spp. succession in bogs (Oswald, 1952), change their environment and those which change it to their advantage may increase their activity as a result of the change. Often a change in conditions allows the invasion of a competitor better adapted to the new conditions. In the Sphagnum spp. succession the surface of an actively growing bog may be covered by hummocks and shallow water-logged hollows. Growth of the bog proceeded as a continuous cycle from hummock to hollow and vice versa. Some species thrived better under different moisture conditions from others. Thus Sphagnum magellanicum and S. cuspidatum were the first to appear in a hollow since they could survive under wet conditions. As they built themselves up from the surface S. rubellum became dominant in the slightly drier conditions only to be superseded by S. fuscum as conditions became still drier. Another conclusion which can be drawn from this example, which would explain the phenomenon of second growth decline better, is the speculation that the evolutionary advantage to a species of forming itself into monospecific communities may be surpassed by the advantage gained by allowing species diversity in a community because this diversity is now thought to explain some of the stability in highly polyspecific communities. This hypothesis may help to explain why some tropical tree seedlings will not survive under mature trees of the same species. On the other hand the existence of numerous monospecific communities e.g. Nothofagus spp. and Typha spp. demonstrate

that monospecific communities are possible in nature. Planted monospecific coniferous forests are reported to produce conditions which reduce their growth rates in terms of merchantable timber. Again, perhaps management may lead to self restriction of the trees. The monospecific coniferous system may be more nearly comparable to the closed system of a single fungus growing on agar in a container where waste products tend to accumulate to the detriment of growth.

In Europe decline has been attributed to the type of humus formed by coniferous litter (Thomas, 1957). In so-called deteriorating forests Thomas reported seeing a very prominent raw humus layer which he thought apparently acted in two ways. Firstly, it acted as a sponge which, in periods of drought, dried out. This caused desiccation of the spruce roots which tended to congregate in the surface layer. The problem was only apparent in areas where summer drought produced conditions which were marginal for the species. This observation seemed to be hardly related to declining productivity or soil deterioration, and may be merely a consequence of growing a tree under a climate to which it was not adequately adapted.

Secondly, Thomas (1957) contended that large amounts of litter at any one time tended to increase rapidly the rate of podzolization. Under some of these stands the profile was most "unhealthy" consisting of a thoroughly leached A horizon, often up to several feet deep, followed by an indurated layer frequently impermeable to tree roots. He

also pointed out that the rate of podzolization was not always the same, which suggested the influence of other factors. On the other hand Wilde and Lafond (1954) reported that a forest grown on grassland in the Great Lakes district in North America added to the black earth profile a leached A_2 horizon. The more intensive the leaching the better was the forest growth. If podzolization in both countries was essentially the same process then it is reasonable to say that it was not podzolization per se which was causing the decline. Even the extremely leached sandy podzols with a thick rock-like hard pan at times supported stands of white pine yielding up to 400 solid cu metres/ha (Wilde and Lafond, 1954). Wilde and Lafond (1954) contended that the deterioration of forest stands on podzols of Germany and other European countries was caused by biological or nutritional deficiencies rather than by the adverse influence of the ortstein horizon. The same authors have theorized that the removal of biomass from the forest had started a nutrition deficiency in European forest.

If the ratio of the rate of decomposition of a unit weight of litter to the production of new nett plant material per unit of ground surface area differed under different climates then the amount of litter on a unit surface area of ground may differ under various climates. This assumes that the total rate of decay per unit of substrate was determined largely by climate and was probably not related to the amount of standing crop of litter per unit ground surface at any

one time.

In cold temperate climates Thomas (1957) observed the "unhealthy" accumulation of a large amount of litter. This accumulation may be a natural consequence of the change in the ratio mentioned above. In other words, because there was slower decomposition of litter per unit weight more had to accumulate before that total rate per unit area of ground surface could increase. This accumulation may cause secondary problems which gave the appearance of being a decline in productivity which had been attributed to monocultural practices but which may in reality have been a consequence of growing a plant in a climate to which it was not adequately suited.

To illustrate the satisfactory growth of mixed forests Thomas (1957) describes P. pinaster forests of Landes region of France and the Iberia plantations of Portugal where dominant conifers and subdominant broadleaf trees and herbs have been successfully grown for hundreds of years. However, this could have been due to the influence of the broadleaf trees or a different climate.

Rennis (1962) supported Wilde and Lafond's (1954) conclusions and stressed the importance of removal of nutrients from the forest in the timber, especially where soil nutrients were scarce initially. Rennie's (1957) studies demonstrated the fundamental difference in nutrient requirement between virgin and timber-exploited forests.

Many workers have investigated in detail the changes which occur when mull changes to mor and vice versa, and have suggested that it was usually associated with vegetation changes. This work has been reviewed by Dimbleby (1962). Usually the changes were reversible but Dimbleby quotes an example from Denmark where heathland was sometimes developed by overstocking beech on poor soils. This gave a mor upon which the beech would not regenerate. Under conditions of natural stocking this may not have happened.

Most authors have reported that conifers produce a greater podzolization, humus accumulation, porosity, infiltration capacity, acidity and lower bulk density (Page, 1968) than other types of forest and grassland vegetation, but Lull and Axley (1958) reported no difference in the moisture content of sandy soils in New Jersey under pine and oak while Caud and Abuturov (1961) and Tikhonov (1963) noted lower humus contents and shallower A soil horizons under pine than under larch or beech in U.S.S.R. The results of Holmsgaard and Holstener-Jorgensen (1961) also showed no significant differences in soil properties under 1st, 2nd and 3rd rotation crops of Norway spruce in Denmark. Soil factors which can be attributed to the influence of greater biomass per unit area of conifer litter, such as decreased pH, increased depth or organic matter, and moisture changes tended to return to their original values when the crop reached 90 - 110 m in height and produced a different microclimate on the floor. Page (1968) concluded that under these management conditions

there was little basis for suggesting deterioration due to the first generation of conifers in England.

Australia

In Australia conditions were different. There the native vegetation has been removed and replaced by an even-aged monospecific coniferous forest but differences in productivity between the first crop and subsequent generations have been claimed. Australian literature (Lewis and Harding, 1963; and Keeves, 1966) seems to point to a relationship between second generation decline and clear fell slash burning but no change has been reported if clear felling was not preceded by burning.

For example Lewis and Harding (1963) studied South Australian plantations on three main areas :

1. podzolized sands and associated calcimorphic soils of dune regions of South East;
2. Adelaide Hills complexes of laterized relief, sedentary and alluvial soils;
3. northern dry country red-brown earths and alluvials.

Lewis and Harding have reported an average drop of 25% in yield between the first and second crop on 80% of the areas which were felled and burnt. In a compartment designated site quality V (as defined in S. Australia on a I - VII scale) a permanent sample plot which was felled and regenerated without burning showed no drop in tree growth rates. Thomas (1957) working from estimated second crop growth rates has suggested a decline was evident. He quoted the Mt. Burn

area where the first rotation at nine years predicted 6,000 cu.ft/acre at 28 years. The predication of growth rates may not be strictly valid in this instance (Thomas,1957) because there was a rich volcanic ash layer at depth under the plantation which may not yet have been reached. Secondly, a fire at the end of the first rotation may have destroyed organic nitrogen in the upper A horizon and this had not yet been replaced. Thomas' second statement supports the theory that the degeneration was due to burning while his first observation invites caution in applying growth curves from one area to another.

Keeves (1966) has presented a detailed account of the growth of a number of stands of P.radiata in South-west Australia. His evidence for productivity decline was based on evidence from large areas and detailed evidence from particular sites both burned and unburned and also natural and artificial regeneration. Extra stocking which has been taken into correlation of different age groups, was accomplished by yield tables.

Keeves has contended that there was evidence to show that with burning there was a loss in productivity of between 2,000 and 4,000 cu.ft/acre in all areas whether of high, medium or low site quality, while there was very limited evidence suggessting that without burning losses were not present.

Changes in soil properties between semi-natural Eucalyptus dominated communities and P.radiata plantations were observed by Hamilton (1965). Changes in soil colour, loss on ignition, bulk density, total carbon and total

nitrogen and other properties were more in the less fertile dry sclerophyll woodland. He found that the C:N ratio increased in all sites, as gauged by height, growth and shoot weight of both Eucalyptus sp. and P. radiata and that all soils showed a decline in ability to grow these species after supporting pure pine stands.

The coarse textured strongly podzolized soil on a granite area showed overall the greatest loss in fertility. Growth was reduced by from 72% to 45% of the original in seven out of eight of the dry sclerophyll sites.

If the total amount of nutrients in the soil was low initially the nutrients volatilized on burning would have a marked effect on the nutrient status especially if the rate of supply of nutrients in rainwater were slow. In a simulated study in the laboratory Knight (1965) found that temperature likely to be experienced in a fire caused a marked loss of nitrogen which was proportional to the temperature.

North America

Site decline has been reported in America by McComb and Riechen (1959) working in Iowa, but few details were mentioned. The drop in productivity on occupied sites was said to be demonstrated by less growth. The soil properties showing the most marked changes in conjunction with this decline were :

1. concentration of clay in the B horizon
2. higher acidity
3. lower organic matter in the A and B horizons
4. decreased permeability of the B horizon.

The height of dominant trees dropped three meters for every 10% increase in clay in the B horizon.

Wilde (1959), on the other hand, reported a soil ameliorating effect by P. banksiana and P.resinosa in Wisconsin in a 32-year old plantation growing on an area which had been deforested 60 years previously. There was a slight but significant difference in the state of several fertility indicators in favour of soil supporting P.resinosa, namely the content of organic matter, total nitrogen, available phosphorus, and available potassium.

Forests in the Canadian boreal region showed similarities to those in North Sweden (Weetman and Nykvist, 1963). In both these regions total nitrogen reserves were lower than in regions closer to the tropics and a greater percentage of this nitrogen was incorporated into the thick litter layer. This resulted in a nitrogen shortage for the plants even though the amount of total nitrogen increased during one generation. A soil productivity "decline" can therefore occur in these regions in less than the time taken for one generation.

New Zealand

Second rotation productivity decline of P.radiata growing in Mapua, Granitic Kaiteriteri and Rosedale soils of

the Moutere Gravel formation in the Nelson Province of New Zealand was reported by Chittenden (1965). Stands in the province were natural regeneration after clear felling. Elsewhere in New Zealand this decline had not been observed (Stone and Will, 1965). Forestry practice in New Zealand differed from that in Europe in that the climate allows faster growth rates in New Zealand which result in shorter generation times. In Europe the canopy may open more and subsequent change in micro-climate on the ground floor results. Burning after clear felling was not usually necessary in New Zealand and in this New Zealand forestry practice differs from that of Australia. A comparison of the growth rings of the first and second rotations on the same sites shows an average decrease of approximately 15% to 20% (Whyte, 1966) in the second generation in some areas, but comparisons have been complicated by the fact that first rotation trees were regularly spaced while natural regeneration has resulted in a high density of second rotation trees and averages of 20,000 to 39,000 seedlings per acre result.

How much of the apparent productivity decline of the 12 crop trees on each one-tenth acre plot can be ascribed to overcrowding (Macarthur, 1952; Lysaght, 1942; and Ure, 1949) and whether or not there was any greater overcrowding on the less productive sites has not yet been fully investigated. Appleton and Slow (1966) suggested that despite overcrowding there was a significant decrease in the site productivity.

There is evidence that this phenomenon should not be strictly included in productivity decline within the last two generations for, as early as 1925, Dr. J.P.S. Jamieson (Appleton and Slow, 1966), a former Nelson medical practitioner and plantation owner, recorded decreased vigour and the occurrence of chlorotic foliage on one ridge of his evenly spaced 8-year old P. radiata plantations at Braeburn. Agricultural development in Waimea district was hampered by low soil fertility early in this century. These observations have indicated that the problem was one of low soil fertility brought about by gradual loss of nutrients throughout the long history of this soil or some other factor such as moisture deficiency and aggravated by erosion moving the top soil from ridge tops. If agriculture in this area was hampered by low fertility of the soil then the production of high yield P. radiata would also be affected (Humphreys, 1964) because P. radiata responds to a reasonably fertile soil (Van den Driessche and Waring, 1965). If the productivity decline was real then the suggestion of Raupach (1967) may be applicable to this situation. Raupach (1967) postulated that nutrients becoming available from clearing slash, for example, gorse and manuka, may exceed those from clear felled pine slash from the first rotation and may apparently cause a second rotation decline in some instances.

CONCLUSIONS

Because the parameters used for the measurement of production have often been those used for the measurement of merchantable timber production there may be a real decline in second and subsequent crop productivities in some cases if productivity is defined in economic terms, but if measured as total biomass production the decline may not be so real.

Differences in growth rates in various regions may be explained by different soil and climatic conditions in the areas studied and in the methods of management. For example, in Australia sites showing deterioration had been burnt after clear felling, or in cold temperate climates where litter accumulation (Thomas, 1957) caused problems not found in regions where the litter is more readily decomposed.

Some factors such as a decline in nutrient levels due to removal of tree parts or a build up of toxic factors in pure plantations (Raupach, 1967) probably have a more universal occurrence.

Because of the different environmental conditions in other parts of the world the merchantable timber production decline at Nelson may not be comparable, but a knowledge of some features of the overseas problem may be useful in suggesting reasons for the decline at Nelson.

2.2 FACTORS GOVERNING THE LEVEL OF ORGANIC MATTER AND NITROGEN IN SOIL

Stevenson (1965) reviewed the literature dealing with levels of nitrogen in the soil and concluded that the equilibrium value is a function of vegetation type, climate, nature of terrain, physical characteristics of the soil activities of the microflora and fauna. Jenny (in Stevenson, 1965) ranked these factors in decreasing order of importance as: climate, vegetation, topography, parent material and age. When the soil environment is changed new rates of addition and decomposition of O.M. are likely and ultimately a new balance between losses and gains will be reached with the O.M. in the soil at a new level (Jenkinson, 1966).

A more general approach was adapted by Olson (1963) who combined the abovementioned factors and postulated a model to explain the balance between decomposition and production of O.M.

Vegetation

Each type of vegetation tends to be associated with a soil containing a particular level of nutrients and organic matter. Cause and effect are hard to distinguish. On the one hand successions on glacial moraines show a build up of nitrogen and a subsequent decline after legume stages are replaced by other types of vegetation (Crocker and Major, 1955; and Stevens, 1968).

Perhaps inefficiency of cycling causes losses which the vegetation tolerates until a certain minimum level is reached at which time a succession by species better adapted to the lower nutrient level takes place. This explanation is obviously incomplete because other factors must exist which inhibit later vegetational stages from entering the succession before N build up in the legume stages has been completed.

Evidence that the vegetation is to some extent the cause and not the effect is demonstrated by the rapid decline in nitrogen levels immediately following legume vegetation.

For example, Equnjobi (1969) found a decrease from 5,000 kgN/ha to 3,000 kgN/ha after the succession from Ulex europeus to Leptospermum scoparium and then a form of stabilization at this level.

Similar trends have been reported as being due to the change from virgin vegetation to annual crops (Shutt, 1910; Bracken and Greaves, 1941; Haas et al 1957; and many others). The rate of loss of O.M. from soils during the first year of cultivation after a pasture period or when virgin land is cleared is greater than in subsequent years (Greenland and Ford, 1964).

The level of N continues to decline rapidly for the first 10 - 20 years until a quasi-equilibrium value is reached. Not all the losses of N can be attributed to its removal by crops. Synder (1905) found a 27% loss of N from the top 25 cm of soil in 12 years. Crop removal accounted for only

22% of this loss. Shutt (1910) found that crop removal accounted for only half of the 33% decline in 25 years.

Brown et al. (1942) reported a loss of 17-22% in the top 12 cm of some alberta soils. Numerous other workers have reported losses of the same order (Crolter, 1947; Jenny, 1933; and Salter and Green, 1933). Ensminger and Pearson (1950) cite evidence for the depletion of N by numerous agencies. The importance of each factor will depend on the conditions in the particular area. Thus cultivation involves soil disturbance which may act as an independent factor in determing the ultimate level, although the development of an equilibrium level of soil N suggests that the phenomenon is the same as in undisturbed communities but that the rate of formation of an equilibrium is increased by soil disturbance.

The way in which N is distributed in the ecosystem and the rate and efficiency of cycling under a particular type of vegetation may influence the amount present at any one time. The reduction in productivity with a possible lowering of soil N content after a change in vegetation may be a natural phenomenon occurring even in undisturbed communities and may be of survival value to the community.

These phenomena may help to explain observed declines in productivity occurring when virgin vegetation is replaced by the introduced species, e.g. conifers, when the high equilibrium value is reduced. If this occurs then only the continual addition of fertilizers will keep the level at a

value. Also if cultivation has an effect on the level of soil N and the rate of attainment of this level the very considerable soil disturbance during clearing, planting and logging operations (see Fig. 2.2.1) should have a marked effect.

Climate

According to Stevenson (1965) "climate is the most important single factor which determines the array of plant species available at any given location, the quantity of plant material produced, and the intensity of microbial activity in the soil; consequently this factor plays a prominent role in determing the nitrogen and organic matter levels in the soil".

Stevenson (1965) has summarised the work of Jenny who found a correlation between soil nitrogen content and components of climate. For instance Jenny (Stevenson, 1965) proposed that effect of temperature on total N content could be described by

$$N = \frac{a}{1 + ce^{-Kt}}$$

where N = nitrogen content

t = temperature in ^{o} F

a, c, K = constants.

He used this equation in a study of a North-South transect of a semi-arid region in Central U.S.A. and showed how the constants varied with vegetational type. Using the results of data collected from Central U.S.A. by Jenny, Tasman Forest soil should contain 0.1% N. Hanmer and Balmoral Forests

Fig.2.2.1

Soil disturbance after clear felling in Tasman Forest.

should contain slightly more nitrogen since they have a lower mean temperature. The comparison in this instance is not really valid because the N.Z. *Pinus sp.* forests have been planted and have been in existence for only one or two generations.

Nitrogen content also varies with moisture if the ratio of precipitation to absolute saturation deficient of the air is used to describe the moisture content. Leeper (1938) found that Australian soil data fitted the proposed relationship.

These two components probably do not exhaust the list of climatic factors which are related to soil nitrogen levels and further correlations will probably soon be discovered.

Organisms

Senstius (1958) concluded that the increase in soil organic matter, and consequently nitrogen, with decreasing temperature in an aerobic environment occurs because at lower temperatures the activities of micro-organisms decrease more rapidly than do the photosynthetic processes of plants.

Senstius (1958) contended that at temperatures from 0-25° C organic matter should accumulate in the soil. Waksman and Gerretsen (1931) found that in temperature range of from 5-30° C the lower the temperature the lower the rate of decomposition of organic residues, and the higher the nitrogen content. Jensen (1939) contended that with

decreasing temperature a greater percentage of organic matter was converted into microbial content than released as CO_2.

Conclusion

The level of nitrogen in Tasman Forest soil may be controlled to some extent by climate, vegetation or micro-organisms but age of the soil and the processes of leaching of mineral nutrients probably is the greatest single factor controlling the level of nitrogen in this soil. The general low levels of nutrients probably does not allow the accumulation of any greater amounts of O.M.

CHAPTER 3

NELSON AREA

3.1 HISTORY

In February, 1842, five vessels, sponsored by the New Zealand Company, arrived in Nelson Haven bringing 764 new colonists for the Second Settlement under the Wakefield Scheme. Unfortunately the New Zealand Company's officers in London were unaware of the hilly nature of Nelson and the preponderance of soils of low fertility, and, because of difficulties with the Maoris over land purchases, many of the promised allotments were either unsuitable or not available for these inexperienced pioneers. In consequence, little employment was offering, which caused widespread hardship; but within a year cottage farms had been introduced in the Waimea and these later developed into efficient holdings for mixed farming (Barnicoat, 1967).

The first farmers on the Moutere Gravels were German colonists who arrived at Upper Moutere in 1844-45. Progress was slow because of the poor soil. The seaward end of Moutere Gravel was probably used by the settlers on the adjoining lands of the Waimea Plains for rough grazing but no

success was obtained in early years in establishing English grasses and clovers. After clearing the forest area of Moutere Gravels English grasses and clovers were sown on the burn after felling the Nothofagus spp. forests. For several years good sheep grazing was experienced, but then deterioration set in.

Orchards were planted by the early settlers to provide apples for the diggers in the gold rushes of the 1860's. Following a successful shipment of Nelson apples to England in 1910 there were several boom years of planting.

3.2 GEOLOGY

According to Stevens (1967) the origin of the Moutere Gravel region is not known. It is possible that it is a complicated fault angle depression, marking an old line of the Alpine Fault. The depression is bounded on the east by a strip of Triassic rocks, forming the low foothills, and by Permian rocks forming the high hills behind. The first series of hills bounding the western side of the Moutere Depression consists of Separation Point Granite, but the high mountains behind are of Mount Arthur marble and associated shales and argillites of middle Ordovician age (445 million years).

In the earliest Pleistocene (1½ or 2 million years ago) glaciers developed in the Spenser Mountains and St.Arnaud Range. During this time the rivers draining the glaciated

region carried vast quantities of coarse rock debris out into the Moutere Depression. This debris, deposited as gravels and sands, was spread as an alluvial plain across the entire depression and also extended out into Tasman Bay and beyond into Cook Strait, down to the glacial sea level, some 300-350 feet below present day sea level. These old fluvio-glacial gravels and sands are called the Moutere Gravels. Their extreme weathering suggests that they have been subject to a long period of deep weathering in a warm, humid climate, presumably during the interglacial periods of the Pleistocene.

During the interglacial periods, and since the end of the Pleistocene, some 10,000 years ago - when the sea returned to about the present level, or slightly higher - the coastal edge of the old alluvial plain of the Moutere Gravels was trimmed back to the present shore line and, in the vicinity of the large rivers, cut even further back.

Inland, the rivers of the region have cut into the surface of the old alluvial plain to produce a topography of low hills which, however, all rise to a uniform summit level (representing the old alluvial plain) sloping gently northwards from the St. Arnaud Range and Spenser Mountains.

3.3 SOILS

The soils of the region are of generally low to very low fertility. All crops require liberal applications of fertilisers, and many trace element deficiencies have been

identified in these soils.

Six soils are mapped on the gravels, differences being due to variations in climate, original vegetation, topography and parent material. Mapua soils are found in the area of study. They are a transitional yellow-brown to yellow grey earth; strongly leached, deeply and strongly weathered soils with weak structured sandy loam topsoils and heavy clay subsoils (Chittenden, 1967).

Most of Tasman Forest soil has been classified as Mapua Hill Soil (Fig. 3.3.1). These soils are present on steeper slopes and are associated with Mapua sandy loam, but are shallower. They have a similar fertility to Mapua sandy loam. The gravels underlying Mapua soils are more strongly weathered than gravels further inland, and are more strongly leached and have a deeper and heavier clay subsoil. The topsoil is sandy and easily eroded. Cultivated land often has three inches of topsoil in gullies but none on the ridges. On easier slopes there is evidence of impeded drainage with moderately gleyed subsoils, and occasional iron stained pans are formed. The fertility of the soil is very low with calcium, phosphorus and potassium present at particularly low levels (Chittenden, et al. 1966).
Table 3.3.2 shows the amounts of mineral nutrients in Mapua Hill Soils (Adams, 1969, pers.comm.).

Fig.3.3.1 Profile of Mapua Hill Soil showing the poor topsoil and clayey subsoil. Each red division on the scale represents one inch.

Table 3.3.2 Amounts of mineral elements in Mapua Hill Soils

MAPUA HILL SOIL

Values in Kg/ha to 22 inches

	org.C	N	P 2mm	Pt	P available*	Ca	K	Mg	Fe ($x10^3$)
Main Ridge Tops									
M I	42,600	1707	727	1007	133	20,160	76,070	35,540	180
M II	37,500	1845	755	1012	131	23,070	78,340	42,050	175
Ridge Tops									
M III	59,600	2853	1097	1209	148	13,480	65,630	42,400	170
M IV	60,100	2575	756	831	109	14,020	62,690	39,490	147
Gullies									
M V	62,400	2931	1027	1137	205	15,780	71,010	42,930	182
M VI	60,100	2728	939	1046	178	16,360	69,240	37,260	137
Steepland									
M VII	60,200	3311	814	1305	153	27,720	90,680	46,170	166
M VIII	56,800	2716	806	1893	380	43,450	98,450	35,110	158

* P available = surface Al-P + surface Fe-P + Ca-P from P fractionation.

3.4 LAND USE

The country running from Mapua in the north to Glenhope in the south comprises some 300,000 acres of gravel soils at times subjected to drought. Before its requirements were understood, the first grass planted had deteriorated and was replaced by a widespread covering of Leptospermum scoparium Ulex europaeus and Pteridium aquilinum var.esculentum. Attempts were made in the early 1900's to establish orchards but few were successful and many areas were overplanted in pine trees. Pine trees are still being planted on Moutere soils today but mainly on the steeper and less accessible areas. Orchards thrive from Motueka to Appleby and more areas are being regrassed every year. It has only been since the realization that all Moutere type soils are grossly deficient in lime, phosphate and other elements that any real progress has been made in maintaining good pasture on this country (Inch, 1967).

3.5 CLIMATE

Nelson is situated in central New Zealand and has a climate which, to a large extent, is typical of the whole country. Sunny, windy conditions, and a plentiful rainfall evenly distributed throughout the whole year are prevalent. Moderate average temperatures (12.6° C yr mean) are derived from quite high extremes (Mean Max. Jan. 26.2° C, Mean Min. July -1.4° C). The variety of weather events associated

with the easterly passage of anticyclones are also experienced.

Variations in rainfall show a slight winter maximum indicating that the more active fronts and depressions of winter are better providers of rainfall than the convectional activity more characteristic of summer. The wettest month is October with 3.54 inches, with February the driest (2.89 inches). Total rainfall for the year is 38.23 inches. Winter rainfall is more efficient in producing soil moisture, but evapotranspiration figures suggest that there is seldom need for extensive irrigation even in summer, though locally this may be necessary.

On average, Nelson city receives 56% of the total possible sunshine compared with the national average of 47%. The high degree of turbulence of the air in the general Cook Strait area often prohibits the formation of large overcast layers of stratus cloud, which helps account for Nelson's sunshine coupled with the fact that rainstorms tend to be heavy and shortlived.

Winds at the surface are determined mainly by physical features, the most common winds being from the North, North-east or South-west bearings. The lowlands are relatively sheltered.

Upon this general picture is superimposed a host of smaller micro-climates mainly dependent upon aspect and altitude together with other local climatic features. Differences in vegetation between north and south-facing slopes may

be noted. Along the coast a daily reversal of wind is experienced with on-shore breezes during the day (Kissling, 1967).

The climatic data for the Nelson region is compared with that of the Hanmer and Balmoral Forest areas in Table 3.5.1.

3.6 ORIGINAL VEGETATION

In 1842 F. Tuckett, the principal surveyor of the New Zealand Land Company, commented on the poor soil and barren appearance of the Mahana-Tasman area of the Moutere Gravels. He states "the tract between the Moutere and Waimea rivers is almost uniformly sterile, its surface consisting of a mixture of clay, gravel and sand approximately four inches deep on a subsurface of stiff ochre-coloured clay producing only stunted fern and manuka on the high ground and flax (Phormium sp.) and tufts of coarse grass on the swampy land".

Information collected from other sources confirms the sparse growth on the seaward end of the gravel formation. Leptospermum sp., Pteridium sp. with native grasses appear to have been dominant in the area, with a few patches of Nothofagus sp. and Phormium sp. in gullies.

The most outstanding feature of the vegetation cover was the absence of Nothofagus sp. forest on the seaward end of the formation where Tasman Forest is situated today. Although forest fires during the period of Maori occupation

Table 3.5.1 Climate of Hanmer, Balmoral, and Nelson City (Average of 10 years, New Zealand Meteorological Service, 1966).

	Month												
	J	F	M	A	M	J	J	A	S	O	N	D	Average
Appleby Nelson °C	17.2	17.2	15.8	13.3	10.3	7.8	7.2	8.0	10.3	12.2	14.1	16.0	12.5
Hanmer °C	15.6	15.8	13.6	11.1	7.2	4.4	3.3	5.6	8.3	10.5	12.6	13.9	10.2
Balmoral °C	16.1	16.1	14.2	11.4	7.8	5.0	4.3	6.0	8.3	10.9	12.9	15.0	10.7
Appleby Nelson Rainfall in inches	2.6	2.4	2.2	3.3	3.7	3.5	3.2	3.7	3.3	3.5	2.7	2.8	3.1
Hanmer Rainfall in inches	3.5	3.7	3.3	3.4	4.8	3.5	3.7	4.0	4.0	4.3	3.3	3.8	3.8
Balmoral Rainfall in inches	2.1	2.1	1.7	2.1	2.8	2.3	2.1	2.5	2.3	2.5	2.3	2.3	2.3

may have had some influence on the sparse cover recorded by European settlers, climatic and edaphic factors appear likely to have been responsible for the shrub vegetation (Nelson Catchment Board, 1952).

3.7 FORESTRY

Eighty thousand acres of exotic forest lie within a radius of 40 miles of Nelson City. Forty-seven thousand acres of these plantations are owned by the New Zealand Forest Service and 33,000 acres by companies, local authorities and private individuals. Most of the plantations were established between 1917 and 1933, with the bulk in 1927 to 1932. Since that time there has been planting on a smaller scale (Verey and Biggs, 1952).

New planting is increasing the exotic forest estate in the district by about 6,000 acres annually. A large contribution to this annual programme is being made by local farmers under the Forestry Encouragement Loan Scheme.

The forests lie largely on Moutere Gravels between the Hope Saddle in the south and Tasman Bay in the north, but there are also small areas in the eastern hills of Waimea County. Afforestation of granite soils in the north-west of the district is now being carried out.

P.radiata is the major species in local forests, in fact it is virtually the only species in company, local authority and private forests. In State Forests P.radiata occupies about half the area planted, but comprises 80% of present day afforestation programmes. State Forests also contain large areas of P.ponderosa, P.nigra and Pseudotsuga menziesii and smaller areas of some 30 minor coniferous and broadleaved trees. Pseudotsuga menziesii is the only species

other than P.radiata which is still planted on an extensive scale; it comprises 20% of the Forest Service's annual planting acreage.

Nelson's exotic forests show very satisfactory rates of growth and provided they receive timely silvicultural treatment will yield good quality timber. Growth rates compare favourably with those in most other regions in New Zealand. For example, P.radiata will produce an average of 12,500 cu.ft. (total stem volume) in 35 years from unthinned stands. This represents an average annual increment of approximately 350 cu.ft. per acre. Under similar conditions and at the same age Pseudotsuga menziesii yields an average of 11,900 cu.ft. or 340 cu.ft. annually but over a longer period will probably be the higher yielding species (Slow, 1967).

The hill soils with good drainage and with 18 inches or more of free rooting together with a moisture retentive subsoil are well suited to tree growth. Only in localised areas of the Moutere Gravels is rooting restricted by poor drainage or compact gravels lying close to the surface.

Two opposing views have been presented concerning the growth rate of the second rotation P.radiata crop.

Whyte (1968) supports the first group who maintain that there is a drop in the commercial value of the crop from the first to the second generation. This type of parameter is able to be measured by comparing stumps from the first rotation and trees from the second. Whyte considers that there was a

drop in productivity in the early years of establishment and then an increased growth rate comparable to the first rate. Holstener-Jorgensen (1968) who supports the second group has made measurements in other parts of the forests and considers that there is no actual productive decline but that the soils were always infertile and the greater weed growth (Fig.3.7.1) among the second rotation has caused the drop in commercial value of the crop. He has the support of Cockayne (1914) who wrote "there is a widespread belief that Pinus radiata is a great soil exhauster and that the ground once occupied by the tree becomes very infertile. It is evident that the growing of P.radiata instead of weakening soil fertility has the opposite effect".

Both groups are probably right if considered in the following way.

Whyte (1968) has found a decline in commercial value of the P.radiata second rotation in some areas, especially ridges, and Holstener-Jorgensen (1968) has postulated that this may be due to the general infertility of the soil, dense regeneration and the abundance of weeds among the crop.

This leads to many avenues of research. Factors causing the initial retardation in growth, the economics and benefits of fertilizer application and the factors causing differences between sites need to be studied.

Fig.3.7.1

Dense weed competition among P.radiata seedlings in R65-66 site at Tasman Forest.

PART II : EXPERIMENTAL

CHAPTER 4

INTRODUCTION TO EXPERIMENTAL SECTION

4.1 DISCUSSION OF FACTORS WHICH MAY BE RESPONSIBLE FOR THE POSTULATED DECLINE IN PRODUCTIVITY OF P.RADIATA IN TASMAN FOREST.

(a) Carbon:Nitrogen Ratio Changes

The carbon:nitrogen ratio has long been accepted (Windsor, 1958; Cowling and Merrill, 1966) as a major factor governing the rate of decomposition of residues in the soil. It is possible that over a period of years a change in the C:N ratio of the decomposing residues may bring about a change in the nitrogen mineralisation pattern.

Also local variations in soil nitrogen content between contiguous sites may give rise to differences in the nitrogen content of plant material grown on them. The resulting changes in C:N ratios may then affect decomposition rates.

If, for example, in a forest of P.radiata such as Tasman Forest, dry matter production on the ridges were as great as on gully sites while nitrogen supply on ridges was less, then it is possible that the C:N ratios of the residues from the first crop would be higher on ridge sites

than in gully sites. This effect could be self-perpetuating if the decomposition of residues were hampered by the lower C:N ratios. An accumulation of organic matter would result. But, as observations made at Tasman Forest indicate, accumulation on the ridges does not exceed accumulation in the gullies and decomposition rates are sufficient to reduce O.M. to low levels in both places. Heilman (1963) found that the nitrogen content of comparable tissue of P. taeda trees on low nitrogen soils of ridges compared with higher nitrogen soils of gullies was similar. He also demonstrated that the C:N ratio was the same for nearly all sites and age classes. Van den Driessche and Waring (1966a) also found that the efficiency of nutrient utilization was approximately constant with differences in levels of mineral nutrient supply.

The amount of energy available to organisms responsible for decay may change in two ways. Firstly, clear felling of vegetation may cause a sudden increase in energy material which would cause immobilization of nitrogen if the residues were sufficiently susceptible to decay and of a sufficiently high C:N ratio. Secondly, if production of dry matter per unit area increased at any stage energy supply to the decomposers would increase and could result in a temporary nitrogen shortage.

Periods of change of this type are likely to occur at:

(a) clear felling of the original vegetation

(b) period of rapid first crop P. radiata growth;

(c) period of felling of first P. radiata crop;

(d) periods of rapid second crop growth.

Little is known of the amount of organic matter in a Leptospermum scoparium vegetation or of its productivity, but a study on this species in the Hutt Valley, New Zealand, may be applicable. Equnjobi (1969) found an accumulation of 3,000 - 4,000 kg O.M./ha/yr in a L. scoparium community of 10 - 45 years' age. The site was similar to Tasman Forest, in that it contained approximately 2,500 kg N/ha, so that production on the two sites may have been similar.

(b) Availability of Nitrogen from Soil O.M.

It is possible that the 2,600 kg N/ha (Adams, pers. comm.) in Tasman Forest soil is less available than nitrogen in other soils containing a similar amount.

Swaby and Ladd (1962) have proposed a model for humus formation which appears to explain the observed phenomena. They suggest that humus is formed inside recently dead cells by rapid polymerization or condensation of the highly concentrated free radicles present in the cells. The contents of a recently dead cell are usually devoid of microbial influence capable of destroying any available compounds involved in humus formation. The final product is postulated to be a three dimensional polymer containing many different phenol and quinone units without an ordered sequence and irregularly cross-linked by different covalent bonds and

requiring innumerable extra-cellular enzymes from different micro-organisms to dissemble it piece by piece from the outer surface.

If periods when environmental factors likely to kill cells were more prevalent in Tasman Forest than in other forests then the nitrogen in Tasman Forest may be less available because more cell deaths have allowed more stable humus formation in this soil.

While Broadbent and Nakashima (1967), Simpson and Freney (1967), Jansson (1963) and Jansson (1960) have found that applied nitrogen becomes less available the greater the time of application, little is known of the rate of stabilization of nitrogen in different soils. It is possible that some soils stabilize nitrogen faster than others, leading ultimately to a greater percentage of resistant nitrogen.

If it could be shown that environmental conditions in Tasman Forest kill more cells per unit time than in other places or that nitrogen uptake by plants per unit amount of nitrogen from Tasman Forest soil was less than uptake from other soils under the same environmental conditions then it could be postulated that the nitrogen in Tasman Forest is more resistant.

The importance of the first factor would be hard to assess as little is known of the causes and rates of deaths of micro-organisms although Harmsen and Van Schreven (1955) reported evidence of the accumulation of humus by micro-

organisms under unfavourable conditions (e.g. under continental climate and in the top layers of soil).

Information on the second factor is also scarce. Heilman et al. (1963) have found that the growth of P. taeda on soil containing 2,621 kg N/ha had a total uptake of 190 kg/ha in the shoot portion over a period of 30 years. This is lower than estimates for uptake from Tasman Forest soil (approximately 200 kg N/ha, estimated from amounts in Kaingaroa Forest, North Island, Stone and Will, 1965).

The uptake of nitrogen and dry matter production on Heilman's site was related to the nitrogen content of the soil. A gully site with soil containing 5,488 kg N/ha produced trees which absorbed 224 kg/ha in 30 years.

Thus there seems to be little evidence to support the theory that Tasman Forest soil nitrogen is any more resistant than nitrogen in other soils.

(c) Instability of Pine Forest Ecosystems

In an ecosystem when the amount of available nutrients is limited, for example, a pine forest established on infertile soil, the greatest rate of production of dry matter would be obtained from a biomass with the greatest ratio of photosynthetic to non-photosynthetic tissue, and the maximum nutrient turnover between successive autotroph generations. This envisages a system where biomass is immediately decomposed and the released minerals are re-used for further dry matter production.

Obviously this system would not fulfil the requirements of the timber industry. Practical forestry requires the accumulation of large amounts of non-photosynthetic tissue in the form of tree stems. This involves long generation times and dry matter accumulated in the standing crop can be very high.

The ideal ecosystem does not exist in nature but as Florence (1967) has suggested, it would be useful to know how closely this ideal can be approached especially with regard to the amount of dead organic matter present in the ecosystem.

The ease of managing a monotypic forest had led to its widespread adoption. Florence (1967) has suggested that this system, lacking the diversity of species present in other ecosystems, may be unstable. He therefore concludes that "the first line of enquiry might be an examination of concepts concerning species, interactions and dynamics of vegetational processes within natural communities". I feel that this will be the ultimate line of enquiry, in that, once these relationships have been elucidated very little will remain to be solved.

It is possible that the diversity of the heterotrophic species may be sufficient to maintain stability in a community with a single plant species or the stability of these systems is due more to long generation times than to other factors. It is also possible that the stability of monotypic communities such as Nothofagus spp and Typha spp

is maintained by an overriding environmental factor and if management acts in this manner pine forests may be as stable.

Forestry management requires a method of maintaining or increasing productivity without increasing silvicultural problems which arise with the introduction of other major autotrophs.

Initially it was decided to study the factors which affect the decomposition of organic matter and the resultant balance between production and decomposition, and then to investigate the diversity of the micro-organisms present in the forest as a start to the investigation of diversity and stability in a community with a single plant species.

4.21 SITES

A survey of forests on the Moutere gravels was made and a forest area showing typical symptoms of low fertility, together with suitable areas of regeneration, was selected for particular study. The site chosen was a large hollow in Tasman Forest in which regenerating trees ranged from seven years old to areas on which the first crop of mature trees were being felled. Five locations were selected, each with a different regeneration age group. At each, a ridge and a gully site were marked out. The sites were sampled regularly throughout the course of the investigation. The general region is shown in Fig. 4.2.1 and the ages of regeneration in the Machine Gully area are shown in Fig.4.2.2. An aerial photograph of Machine Gully is shown in Fig. 4.2.3.

TASMAN FOREST

UP31	Ridge (= Upper) site in Machine Gully of mature unfelled *P.radiata* planted in 1931.
LP31	Gully (= Lower) site in Machine Gully of mature unfelled *P.radiata* planted in 1931.
P31	Composite of UP31 and LP31.
UPR67	Site clear felled (*P.radiata*) in March, 1967. Half-way between ridge and gully.
UR66-67	Ridge site in area felled November, 1966.

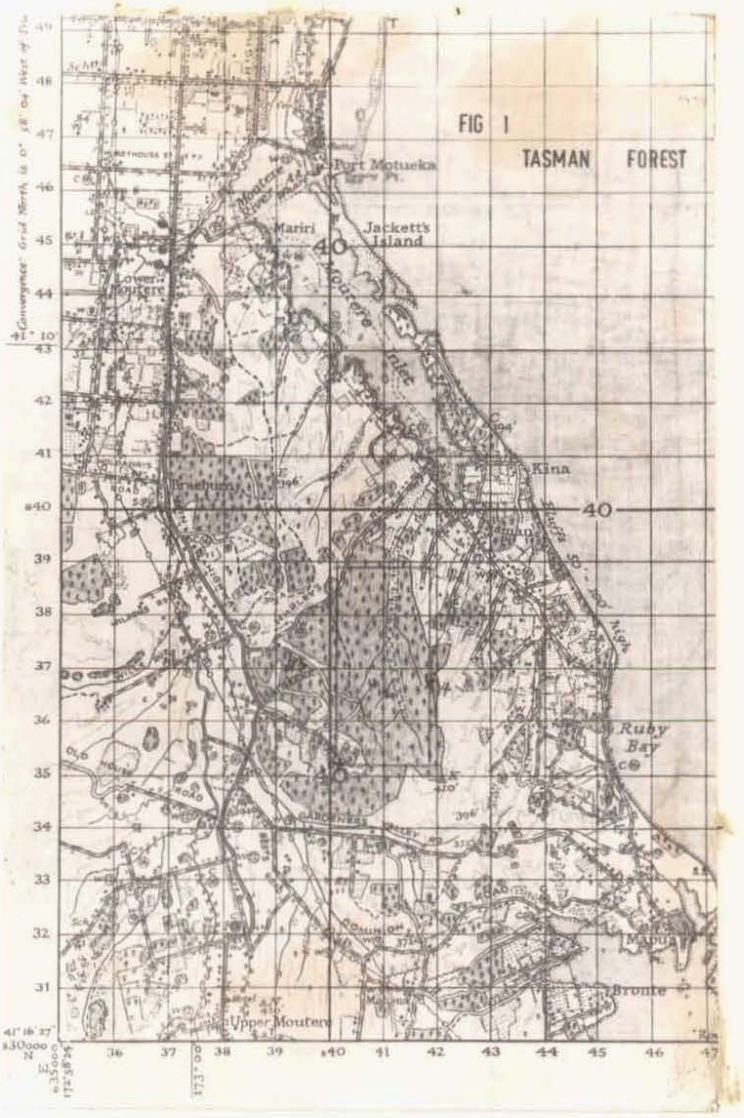


Fig.4.2.1

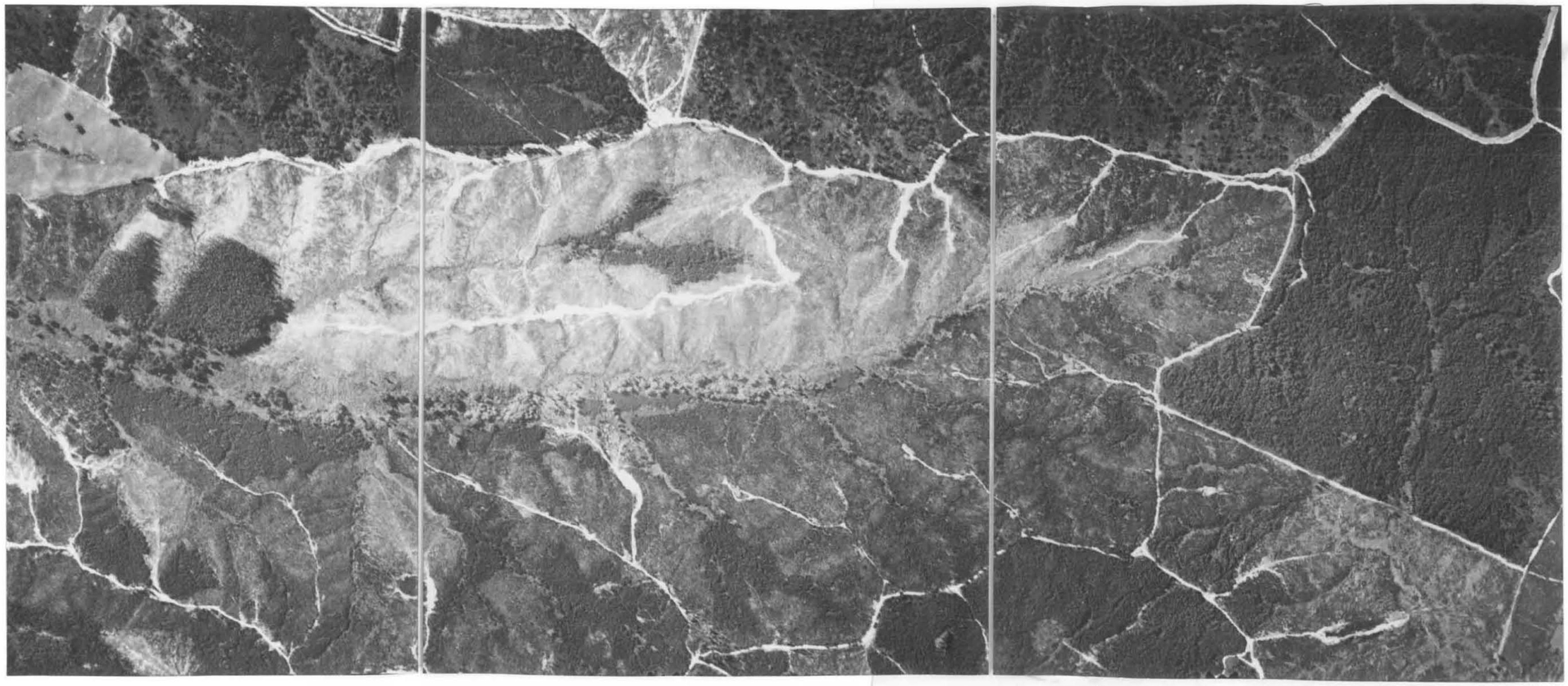
Photograph of a portion of topographical map S14 (approximately 1:126700). Machine Gully contained in the square.

Fig. 4.2.2

Map of Machine Gully showing ages of regeneration of P.radiata. This map represents the situation as it existed in early 1967. By 1969 all P31 areas had been clear felled. Sites sampled are shown by a dot.

LR66-67	Gully site in area felled November, 1966. Site was surrounded by areas with soil disturbed by logging.
R66-67	Composite of UR66-67 and LR66-67.
UR65-66	Ridge site in area felled approximately December, 1965.
LR65-66	Gully site in area felled approximately December, 1965.
R65-66	Composite of UR65-66 and LR65-66.
UR63	Ridge site in area felled in 1963. Thinned in September, 1967.
LR63	Gully site in area felled in 1963. Thinned in September, 1967.
R63	Composite of UR63 and LR63.
UR60	Ridge area felled in 1960.
LR60	Gully area felled in 1960. This site was surrounded by gorse within 10 metres.
R60	Composite of UR60 and LR60.
ULR54	Site half-way between ridge and gully near Harakeke Mill. Felled in 1954. On site of lupin trial reported by Slow and Appleton (1965).
Manuka	Ridge site close to main logging road in Machine Gully. Covered in <u>Leptospermum scoparium</u> approximately 3 metres in height.

Fig. 4.2.3 Aerial photograph of Machine Gully area in Tasman Forest. Rephotographed from prints held by N.Z.Forest Service, Nelson.



HANMER STATE FOREST

H R60	Area felled in 1960. Supporting regeneration.
H R51	Area felled in 1951. Supporting regeneration.
HAN	Composite of H R60 and H R51.

BALMORAL STATE FOREST

BR60	Area felled in 1960.
BR46	Area felled in 1946.
BAL	Composite of BR60 and BR46.

LINCOLN COLLEGE FARM

LIN	Area of Temuka silt loam near shelter belt on Dairy Farm at Lincoln College.

CLIMATE OF A STATION NEAR TASMAN FOREST

The climate of the month of sampling and three months previous to sampling are set out in Table 4.2.4. Figures were taken from the N.Z. Meteorological Service Report (New Zealand Gazette 1966-1969).

Fig.4.2.5

Machine Gully in Tasman Forest showing the R65-66 site with young P.radiata regeneration. Sites R60 and R63 were located in the older generation in the background.

FIG. 4.2.4 Climate of Tasman Forest area. Data for each sampling date and three previous months are included. Months of sampling are underlined.

Month	Year	Mean Maximum Temperature °C	Mean Minimum Temperature °C	Mean of Maximum & Minimum Temperature	Total rainfall in inches	No.of days of rain	Hours of Sunshine
9	68	14.4	5.0	10.0	3.16	13	204
8	68	13.3	4.4	8.9	3.78	11	180
7	68	12.2	1.7	6.7	3.58	7	174
6	68	12.8	3.3	7.8	4.77	16	93
6	68	12.8	3.3	7.2	4.77	16	93
5	68	15.0	6.9	10.8	2.64	13	137
4	68	18.3	9.0	13.6	3.76	10	140
3	68	23.0	13.9	18.4	2.07	7	221
2	68	23.6	11.9	17.8	0.55	4	202
1	68	22.6	12.3	17.4	0.97	6	290
12	67	20.6	11.8	16.2	1.71	12	225
11	67	19.0	9.5	14.3	7.84	17	204
1	68	22.6	12.3	17.4	0.97	6	290
12	67	20.6	11.8	16.2	1.71	12	225
11	67	19.0	9.5	14.3	7.84	17	204
10	67	17.6	7.8	12.6	2.95	10	269
8	67	14.1	5.8	10.0	7.76	20	140
7	67	11.9	1.1	6.5	1.83	10	144
6	67	12.0	1.1	7.0	0.57	4	189
5	67	15.5	5.7	10.6	2.77	10	177
4	67	18.8	9.4	14.0	3.61	9	208
3	67	21.0	11.8	16.3	1.51	9	189
2	67	22.3	11.0	16.7	0.81	4	260
1	67	21.8	12.0	16.9	1.52	9	237
12	66	20.3	11.3	15.8	3.60	15	204
11	66	18.0	8.6	13.3	6.19	15	217
10	66	17.0	6.7	11.9	2.48	8	291
9	66	13.9	5.3	9.4	3.32	14	158
8	66	12.3	1.7	7.0	1.06	6	197

CHAPTER 5

MEASUREMENTS OF THE ENVIRONMENT IN TASMAN FOREST

Environmental factors together with the genotype control the growth of a plant. The environment has a direct influence on the plant as well as an indirect one by also influencing the biotic factors which have an effect on the plant. It has been shown by Stone and Will (1965) and Whyte (1966) that the growth of merchantable *P. radiata* on the Moutere Gravels is retarded on ridge sites compared with gully sites. It was therefore decided to try to assess some of the many variables which could cause these differences. The study of these environmental variables was part of a general investigation of the problem of decline in growth of second generation trees in Tasman Forest.

WATER CONTENT

INTRODUCTION

The primary objective in measuring the water content of the soil was to determine if micro-organism numbers and activity were correlated with the water content. It was also desired to know if the vegetation caused any differences in water content due perhaps to increased transpiration at some stage in the life history of the trees.

METHOD

Soil samples were collected from four depths down to 25 cm in the manner described in Section 10.2. Plastic bags containing the samples were kept at ambient temperature for two days while they were transported to the laboratory where they were cooled to $6 \pm 2^{\circ}$ C until the water content was measured. Soil samples were oven dried at $102 \pm 2^{\circ}$ C for 12 hours, cooled in a desiccator and weighed to the nearest 0.01 g. Water content was expressed as a percentage of the oven dry soil weight. Names given to factors in the analysis of variance are the same as those used in Section 10.2. Regression analysis, using a stepwise Multiple Regression programme, was carried out as described in Section 10.2.

Fig.5.1.1 Water content of soil samples collected on two occasions in summer and winter in Tasman Forest. Samples were transported to the laboratory in plastic bags and oven dried at 102 $\pm$ 2° C for 24 hours. Samples were obtained at four depths under P.radiata regeneration of four ages growing on ridge and in gully.

Fig.5.1.2 Water content of four samples collected at four depths in Tasman Forest under four ages of P.radiata regeneration.

Fig.5.1.3 Water content of soil samples collected from four ages of P.radiata regeneration in Tasman Forest.

Fig.5.1.4 Water content of soil samples collected from four depths on two occasions in summer and winter in Tasman Forest under P.radiata regeneration

Fig.5.1.5 Water content of soil samples collected from ridge and gully sites in Tasman Forest under four ages of P.radiata regeneration.

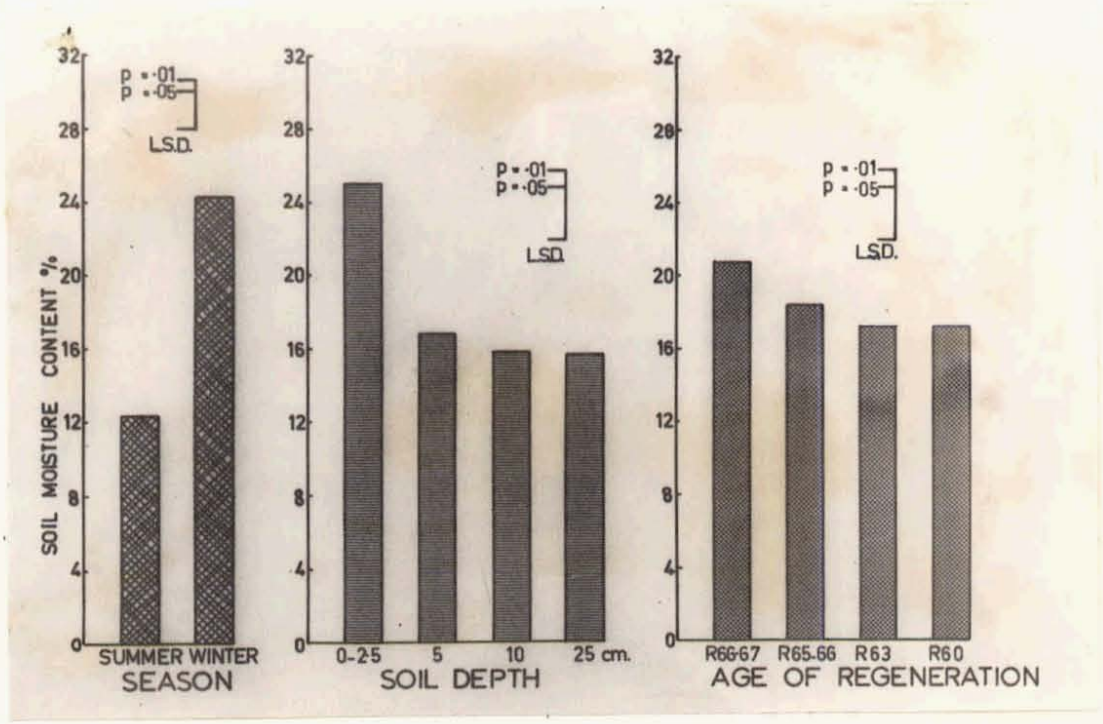


Fig. 5.1.1 Fig. 5.1.2 Fig. 5.1.3

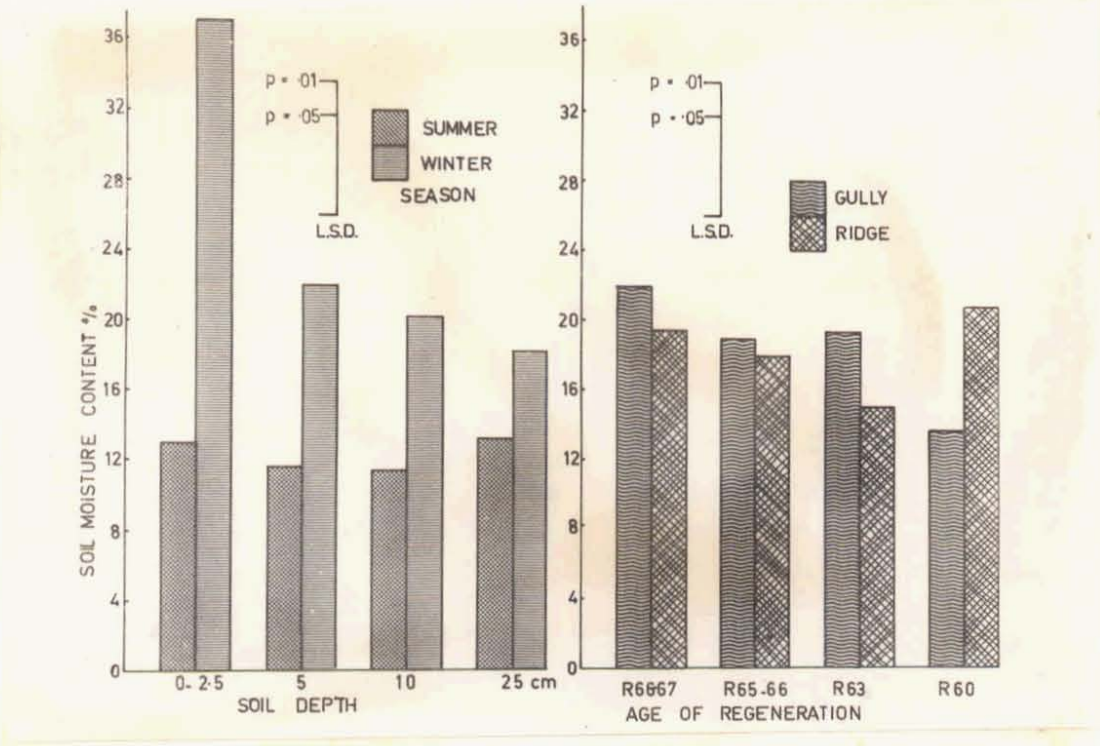


Fig. 5.1.4 Fig. 5.1.5

RESULTS AND DISCUSSION

The analysed results are presented in Appendix 5.1A and details of interactions are presented in Figs. 5.1.1, 5.1.2, 5.1.3 and 5.1.4.

The method of keeping the soil samples in plastic bags and not in sealed tins may have led to some loss of water. Thus values recorded for the water content may not have been exactly equal to those at the time of sampling, but since all soils received the same treatment after the samples were collected differences would be relative.

The water content of Tasman Forest averaged 18.3%. This represents about 40% water holding capacity (W.H.C.) which was found by Gaarder (1957) to be an optimum value for microbial activities. This value is an average of water contents which were both too high and too low for optimum microbial activity, therefore microbial activity had to be measured over a wide range of water contents to gain some idea of the variation. This work is described in Chapter 6.

The effects of age were almost significant. Bare soil (Fig. 5.1.3) on site R66-67 contained 20.7% moisture while soil covered with vegetation contained an average of 18.5% and 17.2%. Faster drying of soil under dense P.resinosa vegetation compared with cleared areas was noted by De Vries and Wilde (1962). The difference may affect the activities of micro-organisms in the soil although the reduced soil water content under vegetation may be compensated for by the more even micro-climate found under vegetation.

The factor season (Fig. 5.1.1) showed that summer values of 12.3% were half the winter value of 24.3%. The mean winter value was slightly less than 60% W.H.C. Measured soil moisture conditions were therefore close to optimum during winter. However, some waterlogging was present in the field in some soil samples, but the interval between collection and measuring allowed some samples to drain.

The effect of depth of the soil from where the sample was taken is shown in Fig. 5.1.2. The 0 - 2.5 cm layer had a higher water content than the other, deeper layers. This was probably due to the greater W.H.C. of the soil in this layer compared with deeper layers, even though the surface layers should have tended to dry more rapidly than the deeper layers.

The season x depth interaction (Fig. 5.1.4) shows that the difference between summer and winter moisture values decreased with increasing soil depth. At the surface there was almost a 300% difference while at 25 cm depth the difference was approximately 40%.

Position x age (Fig. 5.1.5) interaction was interesting, in that the ridge sites under younger regeneration possessed slightly lower soil water contents than gully sites. This trend was, however, reversed at the R60 site. This is contrary to the observation that areas with older vegetation, and presumably more dry matter per unit area, cause the soil to possess lower moisture contents. This

means that ridge sites in the young regeneration areas should possess more biomass than the gully sites. This is contrary to the report of Whyte (1966) unless transpiration of plants on the ridge sites was greater even though the volume of wood in merchantable trees on ridge sites was less. This situation would have to be reversed at R60.

Water content showed a correlation (Fig. 10.2.1) with bacterial numbers at the 0 - 2.5, 5 and 10 cm depths and with pH at the 25 cm depth. Jones (1968) found a correlation of 0.452 between water content and bacterial numbers which was one of the highest correlations found in his study.

5.2 ACIDITY

INTRODUCTION

The measurement of pH was undertaken firstly to determine if it varied in any regular manner in the soil under *P. radiata* regeneration of different ages in Machine Gully, Tasman Forest, and secondly, to see if any other features which were measured in Tasman Forest could be correlated with pH.

Under ordinary conditions the hydrogen ions themselves have little direct effect upon plants, but the degree of acidity of the soil may have a regulatory effect on the chemical processes that influence growth. Increased acidity may reduce the availability of nutrients and cause the release of toxic soluble compounds of aluminium and iron (Oosting, 1958). For this reason it was decided to determine if there were a correlation between soil pH and numbers of the groups of micro-organisms found in the soil.

Most workers (e.g. Hamilton, 1965; Zinke and Colwell, 1965) have not been able to correlate pH with the age or productivity of the conifer tree crop but many workers have found that conifers tended to cause the soil to assume some pH value, usually less than the pH of soil found under the non-coniferous vegetation. Under some conditions, for example, in an area supporting almost pure *Calluna vulgaris* on Sufford Moor, Rennie (1962) found that the original value of

pH 3.3 was reduced to 3.1 by conifers and raised to 3.5 by hard woods. It was thought that after clear felling the pH of the soil may change and therefore analysis of soil under different ages of regeneration was undertaken.

METHOD

Soil samples were collected from Tasman Forest on eight occasions and from Balmoral and Hanmer Forests on one occasion. Ten g of soil were added to 90 ml of distilled water and the resulting suspension was shaken vigorously for two minutes and left overnight. Readings at this degree of dilution were more convenient because this was previously used as the first dilution of a series of dilutions used in the estimation of micro-organism numbers.

Hydrogen ion concentration determinations were made with a glass electrode using a Radiometer 22 pH meter which was calibrated before and at intervals during the taking of readings. The samples collected from Tasman Forest on 28 August, 1967, were wetted with tap water instead of distilled water, as used in other cases. This caused consistently higher values which have been compensated for in the results. The pH of soil samples to January 1968 were obtained by recording the value on the meter while the suspensions were being shaken. Samples analysed after this date were allowed to come to equilibrium before the result was recorded. Results obtained before January 1968 have

been compensated to allow for this and all results are presented as values obtained at equilibrium. It was possible to compensate objectively because values obtained by the two methods differed by 0.4 ± 0.1 pH unit. Terms used to describe factors in the analysis of variance table are explained in Section 10.2.

RESULTS AND DISCUSSION

The analysis of variance of the results is presented in Appendix 5.2A.

The significance of the replication factor casts doubt on the reality of the significance found for the season factor. No importance can therefore be attached to the factor season. The age of regeneration (Fig. 5.2.1) showed a significant effect. High pH values were found at R66-67 and R63 while low values were present at R65-66 and R60. No explanation can be found to explain the high value at R63.

The season x position interaction (Fig. 5.2.2) showed the pH of ridge sites changed from 4.7 to 4.9 from winter to summer while gully sites stayed constant. If this phenomenon was related to water table movement the gully sites would probably show differences in pH rather than the ridge sites. However, it is possible that because ridge sites appear to possess less A horizon soil, that the soil present on the ridge sites was less well buffered and this allowed environmental factors to affect the change in pH.

Fig.5.2.1 The acidity of soil samples taken from under stands of P.radiata regeneration of four ages. Samples were taken from ridge and gully sites at four depths on four occasions.

Fig.5.2.2 The acidity of soil samples collected on two occasions in summer and winter from ridge and gully sites under P.radiata regeneration in Tasman Forest. Samples were obtained from four depths in the soil.

Fig.5.2.3 The acidity of soil samples taken from ridge and gully positions under four age classes of P.radiata. Samples were collected from four depths and were measured in a 1:10 soil:water suspension using a pH meter with glass electrodes.

Fig.5.2.4 The acidity of soil samples collected from four depths under P.radiata of four ages growing in Machine Gully, Tasman Forest.

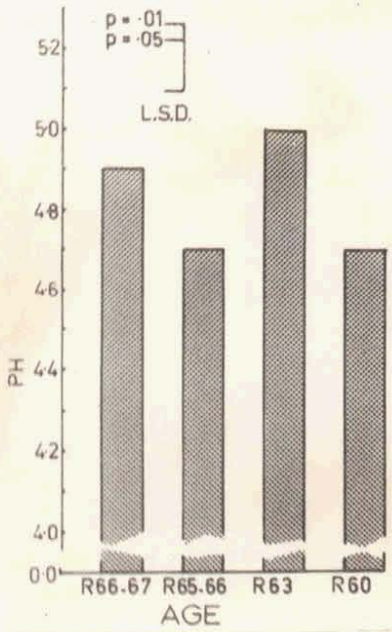


Fig.5.2.1

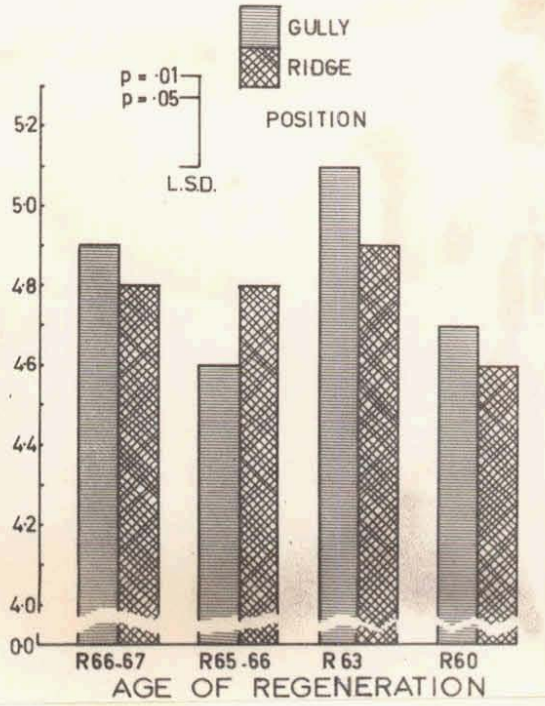


Fig.5.2.3

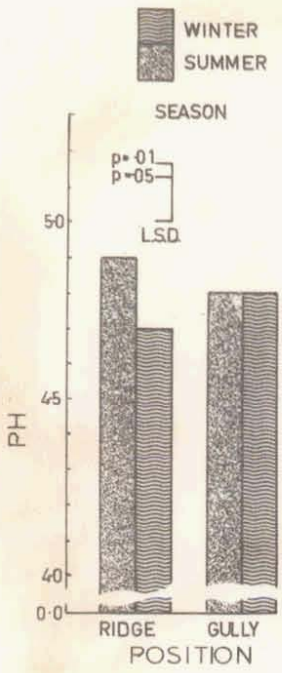


Fig.5.2.2

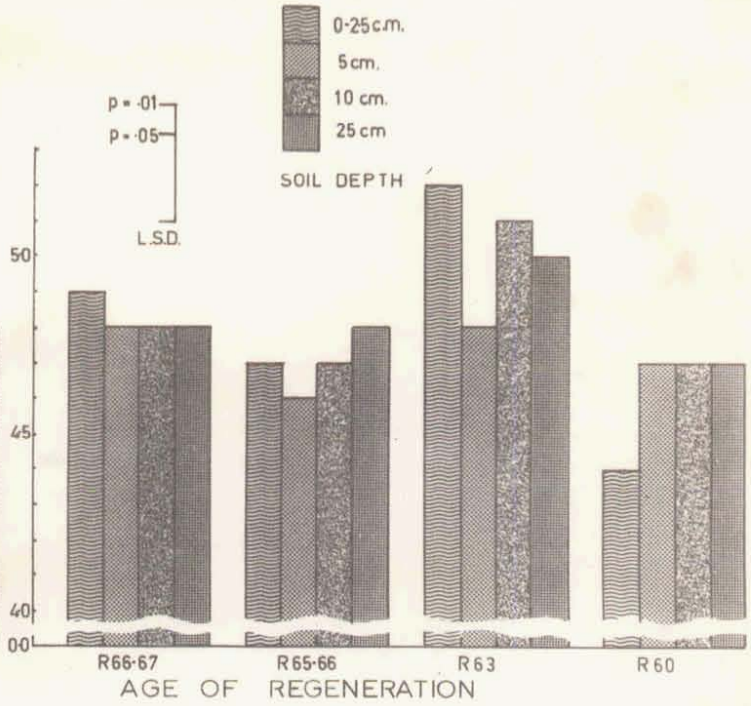


Fig.5.2.4

The position x age interaction is presented in Fig. 5.2.3. As shown by this interaction, values for gully sites were greater than those for the corresponding ridge sites except at R65-66 site. It is difficult to understand why a difference should occur only at the R65-66 site. The age x depth interaction (Fig. 5.2.4) showed a complicated pattern. On some sites pH declined with soil depth while at other age classes the reverse held. The difference in pH values at various sites, different depths, topographical positions and age classes, appears to be too complicated to be explained by a simple explanation. Since pH readings were taken only in an attempt to correlate pH with other factors the factors controlling pH variation are not so important in this study.

An attempt was made to correlate pH values obtained with the numbers of groups of micro-organisms by use of a Multiple Regression Programme, as explained in Section 10.2 (Fig. 10.2.1). The soil pH values had a low correlation with actinomycete numbers at 10 cm depth and a correlation of r= 0.366 with the water content of the soil at 25 cm. The correlation between water content and pH may be explained if it is postulated that the greater water content allowed the micro-organisms to produce more acid conditions by decomposition of residues. However, the presence of residues at this depth would be insignificant. Perhaps there was an interaction between the water molecules and clay components of the soil producing more free $H3O^+$ ions.

The overall variation in pH values explained by numbers of micro-organisms was very low and the complicated pattern of pH values observed make its use in explaining other phenomena difficult.

The average value of 4.8 found for Tasman Forest soil is lower than the pH of 5.7 in R60 and R46 regeneration at Balmoral Forest and 5.5 in R60 and R51 regeneration at Hanmer Forest. These differences in pH suggest that there may be differences in other soil factors between the soils.

5.3 WEIGHT OF ORGANIC MATTER IN LITTER LAYERS

METHOD

Three 30 x 30 cm plots were marked out at random on two ridge sites and one gully site under mature (P31) P.radiata at Tasman Forest. All litter and duff from the plots were collected. An arbitrary decision on the division of components was made. Difficulty in separating soil from well decayed duff layers made estimates of weight unreliable and therefore extensive sampling was not considered worthwhile.

Samples were mixed and sub-samples were oven dried for 24 hours before weighing.

Results: The results are given in the table below (Table 5.3.1)

	Litter	Duff	Total O.M.
Ridge	3,552	23,201	26,753
Ridge	4,929	13,298	18,227
Gully	4,742	9,582	14,324
Average	4,408	15,361	19,768

Table 5.3.1 Amount of O.D. organic matter on soil surface under P31 P.radiata expressed in kg/ha.

Results show that the amount of duff per unit area of ground surface was four times as high as the amount of litter.

5.4 ENERGY

INTRODUCTION

The measurement of the energy content of organic matter (O.M.) in different parts of the biosphere is becoming increasingly important as the study of ecology lays greater emphasis upon energy flow in ecosystems (Gorham and Sanger, 1967). This section presents calorific values for organic matter in surface soils under P.radiata.

METHOD

Soil samples were treated as described in Section 6.25. Soil was dried at 102 ± 1° C and cooled in a desiccator before weighing into crucibles. Energy content was determined using a Gallenkamp Adiabatic Bomb Calorimeter (Model CB110). No nitrogen and sulphur corrections were made since the soil contained very little of these elements. Samples of soil were wrapped in filter paper of known calorific value to facilitate ignition. Appropriate fuse wire corrections were made for each sample and the ash remaining in the colorimeter was weighed after cooling in a desiccator to allow expression of the results on the basis of ash free dry weight. Since the soils did not contain free carbonates the loss of weight was considered to be a reasonable estimate of the amount of organic matter present.

Table 5.4.1 Amount of energy contained in soil and litter samples from *P.radiata* forests

	Replication 1		Replication 2	
Soil	Cal/g	O.M.%	Cal/g	O.M.%
Lincoln	442.8	7.8	408.9	7.2
Hanmer	181.2	2.6	202.3	3.4
Balmoral	269.9	4.7	318.7	3.9
Tasman Forest beneath *L.scoparium*	139.7	0.9	124.6	0.9
Tasman Forest P31	151.7	1.2	163.1	1.1
Tasman Forest R60-63	240.7	2.3	236.5	2.7
Tasman Forest P31 Litter	5781.3	96.3	5691.1	96.8
Tasman Forest P31 Duff	3990.2	69.3	3878.5	66.4

The results are averages of duplicate samples.

The calorimeter was standardized using benzoic acid. Results obtained from standardization were consistent (6327.8 and 6325.9 cal/g) and nearly equal to the standard value of 6319 cal/g. The large amount of mineral matter in the samples probably did not affect the results (Gorham and Sanger, 1967). Differences in calorific value of individual pieces of filter paper were negligible, for example, two pieces tested gave values which differed by 1 cal/g. All filter paper used was taken from the same batch.

RESULTS AND DISCUSSION

The results are presented in Table 5.4.1 and Fig. 5.4.2.

The most unusual feature of Fig. 5.4.2 is the very high calorific values of soils from Tasman Forest. Lincoln, Hanmer and Balmoral soils show values higher than usually associated with biological material but are not higher than reported values of 7000 cal/g in hibernating animals. Even though this work was carried out on a material of low calorific value by means of many control experiments the differences between the results obtained in this thesis and other reported values are too large to be explained by any obvious experimental error.

Using the values obtained Tasman Forest would contain 1.02×10^{10}, 2.42×10^{10} and 5.40×10^{10} cal/acre in the

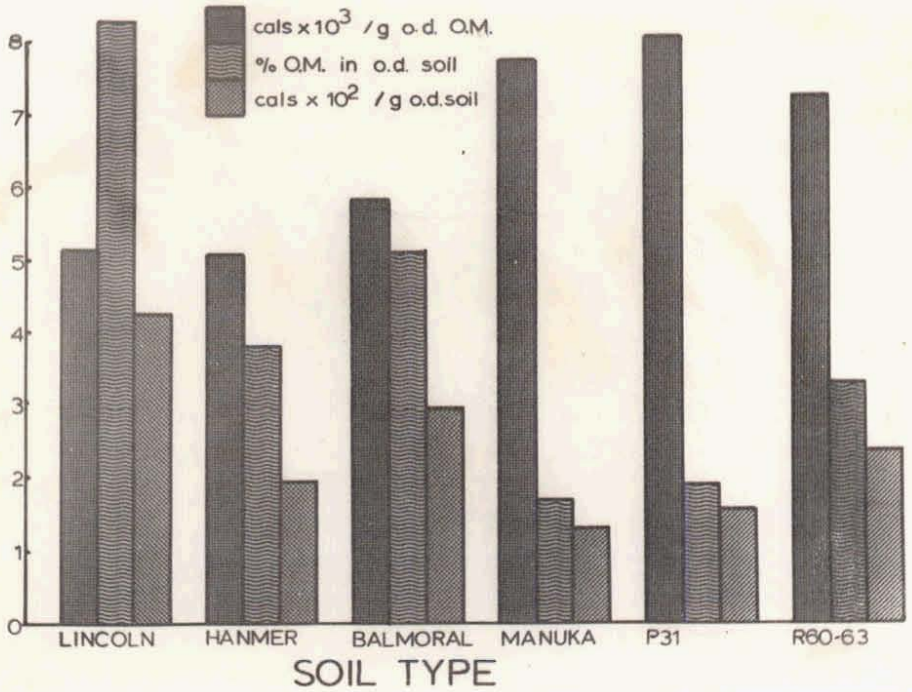


Fig.5.4.2

Energy content, estimated using a Bomb Calorimeter, of soil samples collected from Lincoln College Dairy Farm, Hanmer, Balmoral and Tasman Forests. Soil was collected down to 25 cm depth.

litter, duff and soil fractions respectively.

There is some evidence that the O.M. in soils with low O.M. contents has a high calorific value. Gorham and Sanger (1967) found that samples with less than 50% O.M. averaged 5110 cals/g while samples with more than 60% averaged 4970 cal/g. Salmi (1954) has also reported that the degree of decomposition might also be expected to influence the calorific value of soil O.M. Working with Finnish peat samples he recorded a striking degree of positive correlation between calorific value and the degree of decomposition. Thus, Tasman Forest soil may possess O.M. of a very high degree of decomposition.

CHAPTER 6

ENERGY DISSIPATION UNDER CONTROLLED CONDITIONS

INTRODUCTION

Characterisation of total energy dissipation in the soil is an ideal not yet achievable. The closest approximation available to date involves measuring the rate of absorption of O_2 or the release of CO_2 as a measure of the main energy processes occurring in the soil. Unfortunately not all reactions involving O_2 and CO_2 are biological (Drobinkova and Drobnik, 1965; and Scharpensell and Beckman, 1964).

A very limited amount of research on soil respiration has been undertaken to date. However, a few workers have studied the effects of factors such as temperature, moisture, and the addition of amendments (Chase and Gray, 1957; Gaarder, 1957; Gilmour, Damsky and Bollen, 1958; Gray and Wallace, 1957; Katznelson and Rouatt, 1957; Katznelson and Stevenson, 1957; Rovira, 1953; and Drobnik, 1960.

In this investigation an attempt was made to establish the relationship between environmental factors and the rate

of energy dissipation as measured by O_2 uptake, CO_2 evolution and weight loss.

Estimation was attempted for two reasons.

Firstly, a knowledge of the response curve for energy dissipation for different levels of environmental factors can be used to analyse the whole ecosystem and to predict changes which would occur when organisms or environmental factors are manipulated.

Secondly, a selection of soils was studied to determine if some aspect of the response curve for Tasman Forest soils differed from the soils from other regions. Any significant deviation may help to highlight some of the factors causing a decline in second generation productivity if such a phenomenon exists.

CHAPTER 6

ENERGY DISSIPATION UNDER CONTROLLED CONDITIONS

6.1 CARBON DIOXIDE EVOLUTION

6.111 EFFECT OF TEMPERATURE, MOISTURE AND SOIL TYPE ON RESPIRATION IN SOILS FROM HANMER, BALMORAL AND TASMAN FORESTS.

Method

Carbon mineralisation was studied using soil obtained from Hanmer and Balmoral Forests in Canterbury and Tasman Forest in Nelson. All soils were gathered from areas planted in *P. radiata*.

Balmoral and Hanmer soils were collected at a single site from the 0 - 12 cm layer 18 months before their use in the experiment. Tasman Forest soil was collected from the 0 - 10 cm layer under a mature stand (P31) six months before use. All soils were air dried after collection, finely ground, passed through a sieve with 0.0166 inch apperturee and thoroughly mixed before use.

Ten g of soil on an air dry weight basis were placed in each 8-dram vial (2 cm diam. x 7 cm) and distilled water

was added to bring the soils to the desired water content (10%, 20%, 28.5%, 40% expressed as oven dry weight). Extra vials were filled with Tasman Forest soil so that additional samples with moisture contents of 0%, 15%, 25% and 35% could be included.

A 1-dram vial containing 0.2 g BaO_2 and 1-ml distilled water was placed on the surface of the soil in each 8-dram vial, which was then closed with an airtight cap. The contents of the 1-dram vial absorbed CO_2 produced by microbial respiration and provided an equimolar amount of O_2. (Cornfield, 1961). The experiment, as set up, gave a 4 moisture x 4 temperature x 2 duplicates x 3 soils design with the addition of three extra moistures for Tasman Forest soils.

Vials were incubated at $31^\circ \pm 1^\circ$ C, 24° C $\pm 1^\circ$ C, $18^\circ \pm 1^\circ$ C and 8° C $\pm 2^\circ$ C. The 1-dram vials were removed after approximately 10 days' incubation, and the amount of $BaCO_3$ formed was estimated, using a Collins calcimeter (Collins, 1906).

Carefully weighed amounts of oven dried (102° C $\pm 2^\circ$ C) BaO_2 were reacted with 10-ml aliquots of 2N HCl in the calcimeter to obtain a standard curve. To allow an equilibrium to be established soil respiration was not measured until four weeks after initial wetting.

Two samplings at each temperature were completed. These were designated sampling period one and sampling period two respectively.

The results were subjected to analysis of variance. However, Balmoral and Tasman Forest soils with moisture contents of 10%, 20%, 28.5%, and 40% were analysed and the results were presented in Section 6.112, while Tasman Forest soils with moisture contents of 0%, 10%, 15%, 25%, 28.5%, 35% and 40% were subjected to a separate analysis. The results of this analysis are presented in Section 6.113.

6.112 EFFECTS OF ENVIRONMENTAL FACTORS ON CO_2 PRODUCTION IN SOILS FROM HANMER, BALMORAL AND TASMAN FORESTS

RESULTS AND DISCUSSION

The Analysis of Variance Table of the results of the experiments described above is set out in full in Appendix 6.1A.

Temperature (Fig. 6.1.1)

Carbon dioxide production was significantly different at all temperatures except 24° C and 31° C. The amount produced at 31° C was almost three times that at 8° C.

Moisture (Fig. 6.1.2)

Increases in the moisture content of the samples from 10% to 30% did not cause the same marked response as temperature. The mean of the three soils showed a decline at 40% moisture due to the effect of waterlogging in two of the three soils as shown by the Soil x Moisture interaction.

Fig.6.1.1 Effect of soil temperature on CO_2 evolution from soil samples from Hanmer, Balmoral and Tasman Forests estimated using the method of Cornfield (1961).

Fig.6.1.2 Effect of soil moisture on CO_2 evolution from soil samples from Hanmer, Balmoral and Tasman Forests using the method of Cornfield (1961).

Fig.6.1.3 Effect of temperature on CO_2 production in soil samples collected from Hanmer, Balmoral and Tasman Forests. Carbon dioxide production measured using the method of Cornfield (1961).

Fig.6.1.4 Effect of moisture content on CO_2 production in soil samples collected from Hanmer, Balmoral and Tasman Forests.

Fig.6.1.5 Carbon dioxide evolution in soil samples from Hanmer, Balmoral and Tasman Forests.

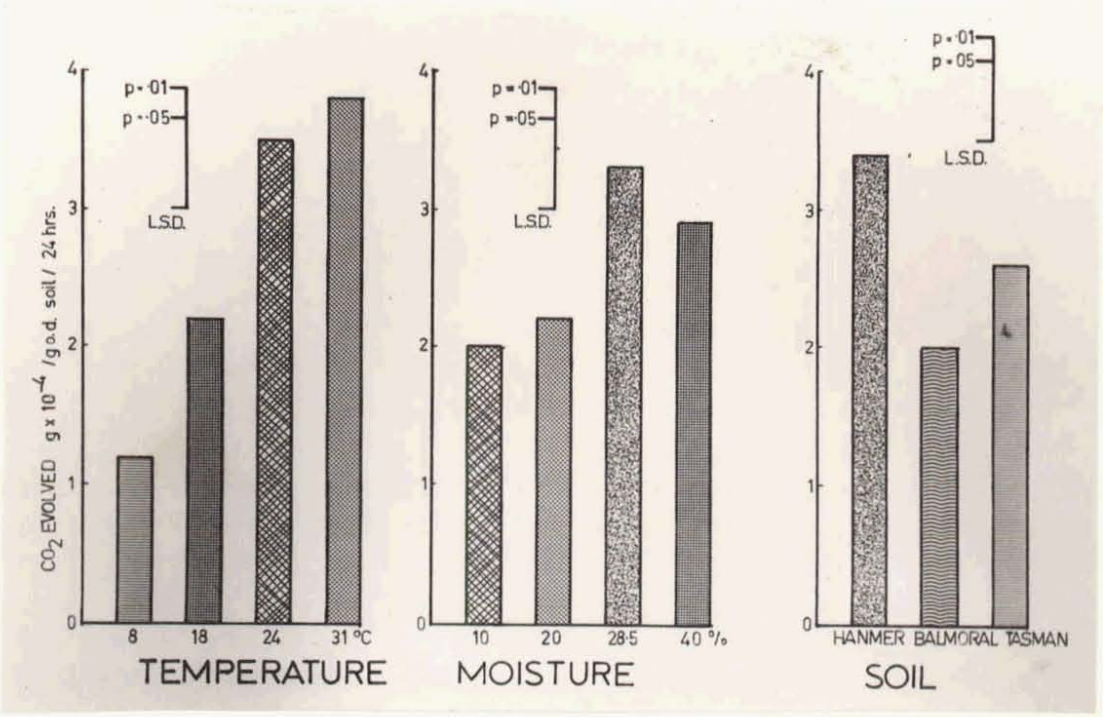


Fig.6.1.1 Fig.6.1.2 Fig.6.1.5

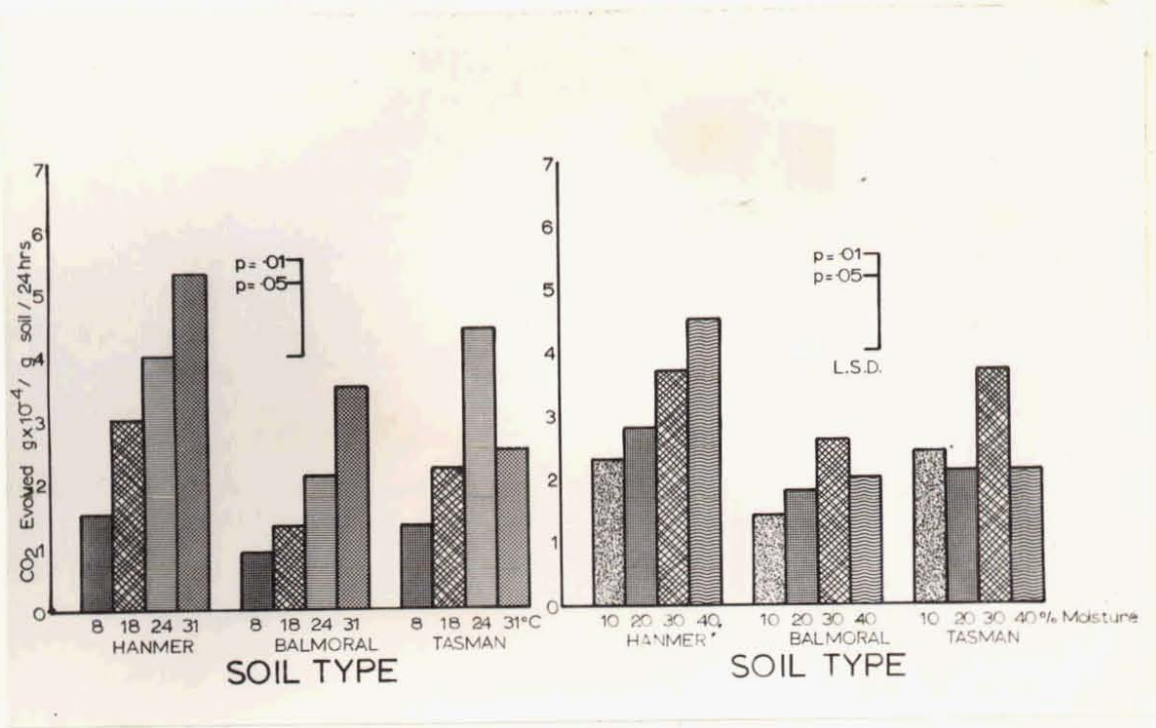


Fig.6.1.3 Fig.6.1.4

CO_2 evolution at moistures of 10% and 20%, as a group, were significantly different from that at 30% and 40%.

Soil x Temperature (Fig. 6.1.3)

Both Hanmer and Balmoral Forest soils showed an increase in CO_2 production with increasing temperature over the range 8° C to 31° C, while Tasman Forest soil showed a significant decrease from 24° C to 31° C. Since the Nelson area has a higher mean temperature (12.5° C, recorded at Nelson 12 miles east of Tasman Forest) than Hanmer (10.1° C) and Balmoral (10.7° C) (N.Z. Meteorological Service, 1966) it might be expected that micro-organisms found in soil from the Nelson area would be better adapted to higher temperatures than the other two soils. The possibility that at the higher temperatures water may have been the limiting factor in the Tasman Forest soil is not supported by data from the Balmoral soil which had a water holding capacity almost as low as the Tasman Forest soil.

Soil x Moisture (Fig. 6.1.4)

In Hanmer soil CO_2 evolution increased with increasing moisture from 10% to 40% while in Balmoral and Tasman Forest soils CO_2 production at 40% moisture was lower than at 20%.

Time x Temperature (Appendix 6.1B)

The major interaction occurred at 8° C where sampling period one was nearly four times as low as sampling period

two. These results, however, do not negate the significance of the temperature main effect.

Time x Soil (Appendix 6.1C)

There is only a slight interaction shown in this table.

Soil (Fig. 6.1.5.)

Soil collected from Hanmer Forest evolved the greatest amount of CO_2. Tasman Forest was next and then Balmoral soil evolved the least. These differences were not so obvious when composite samples from Hanmer and Balmoral were used - Sections 6.14 and 6.25.

6.113 EFFECT OF ENVIRONMENTAL FACTORS ON CO_2 PRODUCTION IN SOILS FROM TASMAN FORECT

RESULTS AND DISCUSSION

The Analysis of Variance Table in Appendix 6.1D shows Time, Moisture and Temperature as having significant effects. These results are set out graphically in Fig. 6.1.6, which shows the levels of environmental factors which differ significantly from each other. The main factors - Time, Moisture and Temperature - remain significant after division by the first order interactions as shown in Appendix 6.1D.

Moisture

Moisture contents from 0% to 20% are not significantly different but moisture contents of 25%, 28.5%, 35% and 40% do differ significantly from each other. A peak in CO_2 evolution rate was reached at 28.5% (equivalent to 60% W.H.C. in Tasman Forest soils). Above this value waterlogging reduced CO_2 production and at 40% moisture CO_2 production was equivalent to that at 20%.

Carbon dioxide evolution from soil with 0% moisture (air dry soil) which is equivalent to 3% moisture on an oven dry basis is higher than would normally be expected. The 3% moisture present together with the saturated atmosphere caused by the BaO_2 suspension contained above the soil may have allowed growth of micro-organisms.

Measurement error at low levels of evolution may be another possible cause of the high rates obtained. Although values obtained for 0% were twice as high as controls, the amount represented by this percentage difference was very small. Subsequent experiments were carried out using greater volumes of soil in an attempt to eliminate this uncertainty.

Temperature

An increase in temperature caused a highly significant increase in the rate of CO_2 evolution. The decline of CO_2 evolution between the temperatures 24° C and 31° C is slightly unusual as Alexander (1961) recorded that optimum respiration occurred between 30 - 40° C. The possibility that the

Fig. 6.1.6a Effect of soil moisture on CO_2 evolution from bulked soil sample from Tasman Forest.

Fig. 6.1.6b Effect of temperature on CO_2 evolution from a bulked soil sample from Tasman Forest.

Fig. 6.1.7 Effect of soil moisture on CO_2 evolution from soil samples collected at Tasman Forest and incubated at different temperatures.

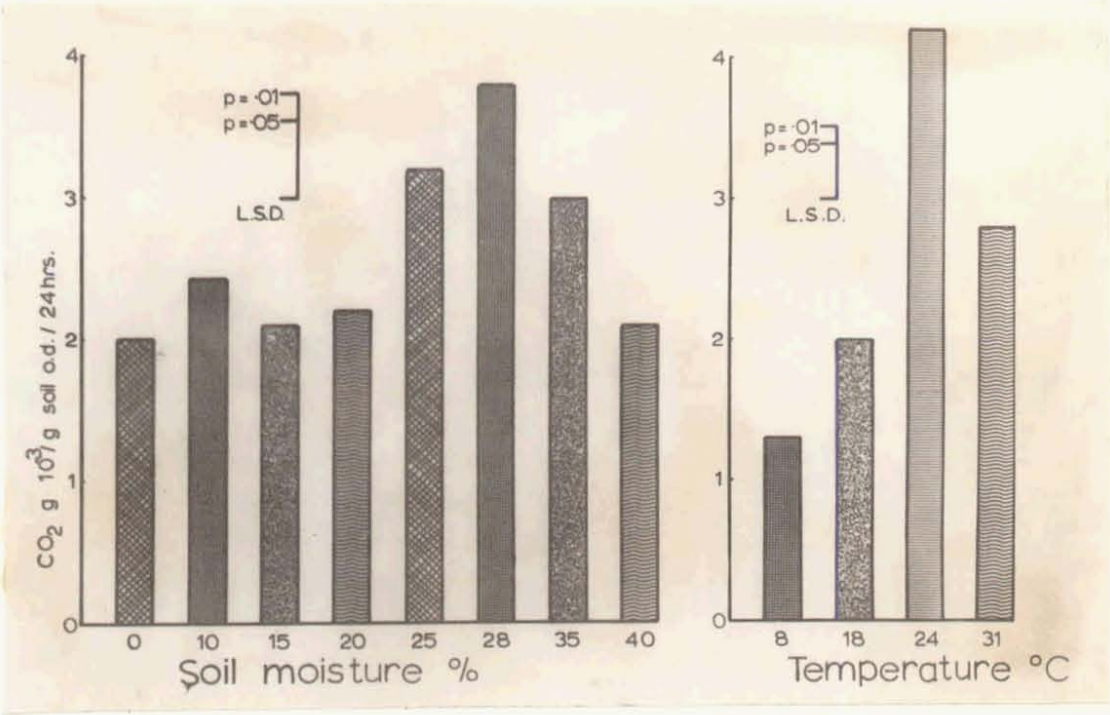


Fig.6.1.6a

Fig.6.1.6b

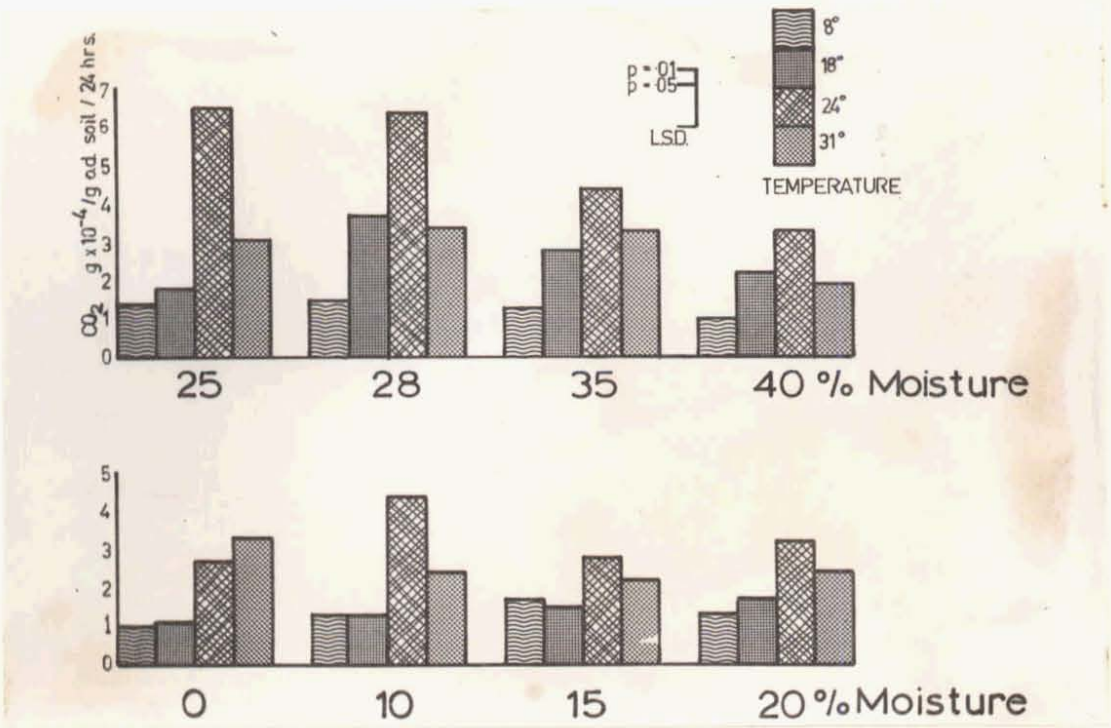


Fig.6.1.7

high temperature could have caused drying out was shown not to have occurred by results from a Balmoral soil with a similar W.H.C. which did not show this pattern. The overall increase in CO_2 evolution when the temperature was raised from 8° C to 24° C was almost threefold.

Moisture x Temperature

This interaction is presented in Fig. 6.1.7. At 0% moisture 21° C there was a greater evolution of CO_2 than 24° C in contrast to all other moisture levels. At this temperature the water vapour in the air above the soil would be greater than at 24° C. At other moisture levels the effect of temperature and water vapour was probably not so marked and temperature may have become the dominant factor. At 8° C CO_2 evolution was almost constant for all water levels while at 18° C CO_2 evolution increased at the 28.5% level. The differences between the 24° and 31° C rates became most marked at the 25% and 28.5% levels, possibly because at these temperatures with moisture being optimum the effect of high temperature could be the most important limiting factor.

Time x Temperature (Appendix 6.1D)

This interaction showed a greater difference between sampling time one and sampling time two at the 8° C temperature than at other temperatures. The difference between the two sampling times may have been due to a build up in the microbial population during the second period. Usually the reverse phenomenon occurs (Birch, 1958) with a flush of CO_2

evolution soon after wetting air dried soil. These interactions, however, did not affect the overall significance of the other environmental factors tested.

6.12 EFFECT OF TEMPERATURE, MOISTURE AND AGE ON CO_2 PRODUCTION IN LITTER AND DUFF

METHOD

Duff and litter samples were collected from the L, F and H layers of ridge site (P31) under mature P. radiata trees in Tasman Forest.

An arbitrary distinction was made between duff and litter. Needles in the litter sample were separate and fairly recognisable while duff was composed of smaller, less recognisable pieces.

After air drying litter was found to contain 15% and duff 27% moisture on an oven dry basis. The material which had been collected was thoroughly mixed and 20 g air dry samples of litter or 30 g duff were weighed into screw-capped bottles 6 cm in diameter and 15 cm high.

The moisture levels were adjusted to 20%, 60% and 100% W.H.C. by the addition of distilled water. An 8-dram vial containing 1.0 $\pm$ 0.2 g BaO_2 and five ml of water was placed in each jar. Jars were closed with plastic lids containing rubber inserts. Temperatures of incubation were 8° C $\pm$ 2° C, 18° $\pm$ 1° C and 24° $\pm$ 1° C. This gave an experiment with a 3 (moisture) x 3 (temperature) x 2 (replications) x 2 (substrates) design.

RESULTS AND DISCUSSION

Analysis of variance of results in this experiment are set out in full in Appendix 6.1E

Temperature

As shown in Fig. 6.1.9, the rate of CO_2 production at 8° C was significantly higher than at 18° C. This was due mainly to an anomalous value obtained in the third sampling period. Even disregarding this one set of readings the CO_2 evolution at 8° C was not significantly less than that at 18° C.

Moisture (Fig. 6.1.10)

The rate of CO_2 evolution at 20% W.H.C. was almost half that at 60% and 100% W.H.C. while 100% W.H.C. showed a slight, but not significant, decrease when compared with 60% W.H.C.

Effect of Substrate (Fig. 6.1.11)

Litter produced almost twice as much CO_2 as duff per unit weight of substrate. Litter and duff samples from under mature *P. radiata* trees showed oven dry weights of 440 g/m^2 and 1,540 g/m^2 respectively (see Section 5.3). Thus, it would appear that per unit surface area duff produces twice as much CO_2 as the litter.

Moisture x Temperature (Fig. 6.1.12)

The moisture x temperature interaction is difficult to explain. It would appear that at 20% W.H.C. temperature has

Fig.6.1.9 Effect of temperature on mean CO_2 evolution from duff and litter samples collected under mature (P31) trees in Tasman Forest. CO_2 evolution measured using method of Cornfield (1961).

Fig.6.1.10 Effect of moisture content on mean CO_2 evolution from duff and litter samples collected under mature (P31) trees in Tasman Forest.

Fig.6.1.11 Effect of substrate on CO_2 evolution rate measured by the method of Cornfield (1961).

Fig.6.1.12 Effect of temperature and moisture content on respiration of duff and litter samples using the method of Cornfield (1961).

Fig.6.1.13 The effect of moisture on CO_2 evolution with time from duff and litter samples collected from Tasman Forest.

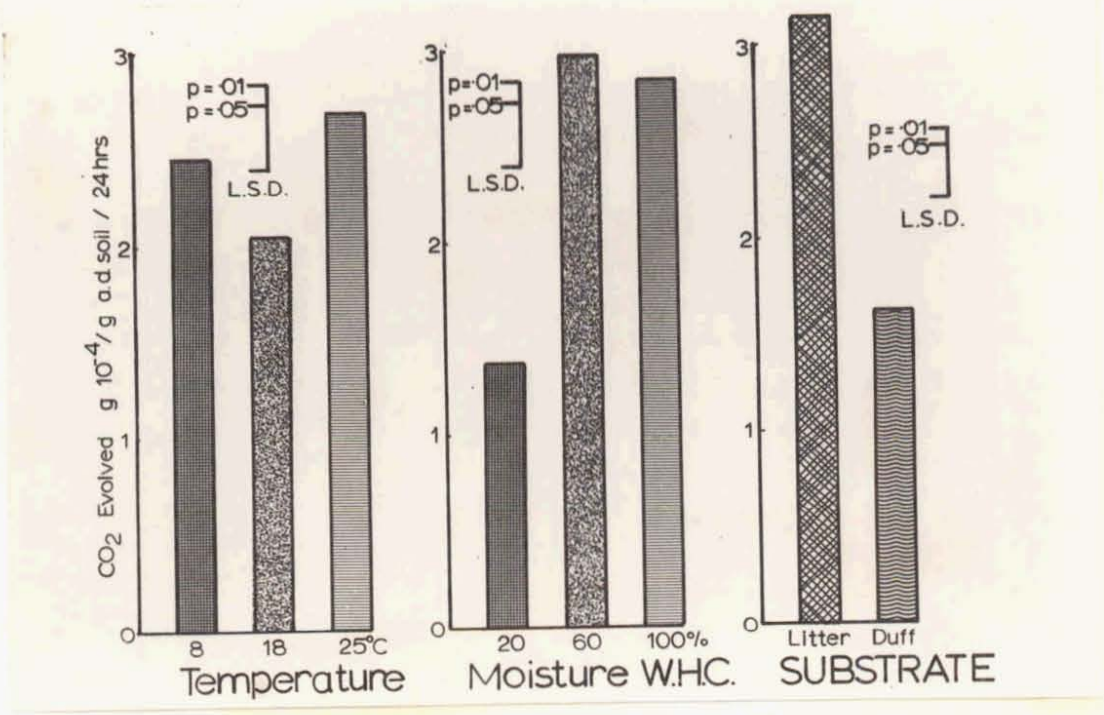


Fig.6.1.9 Fig.6.1.10 Fig.6.1.11

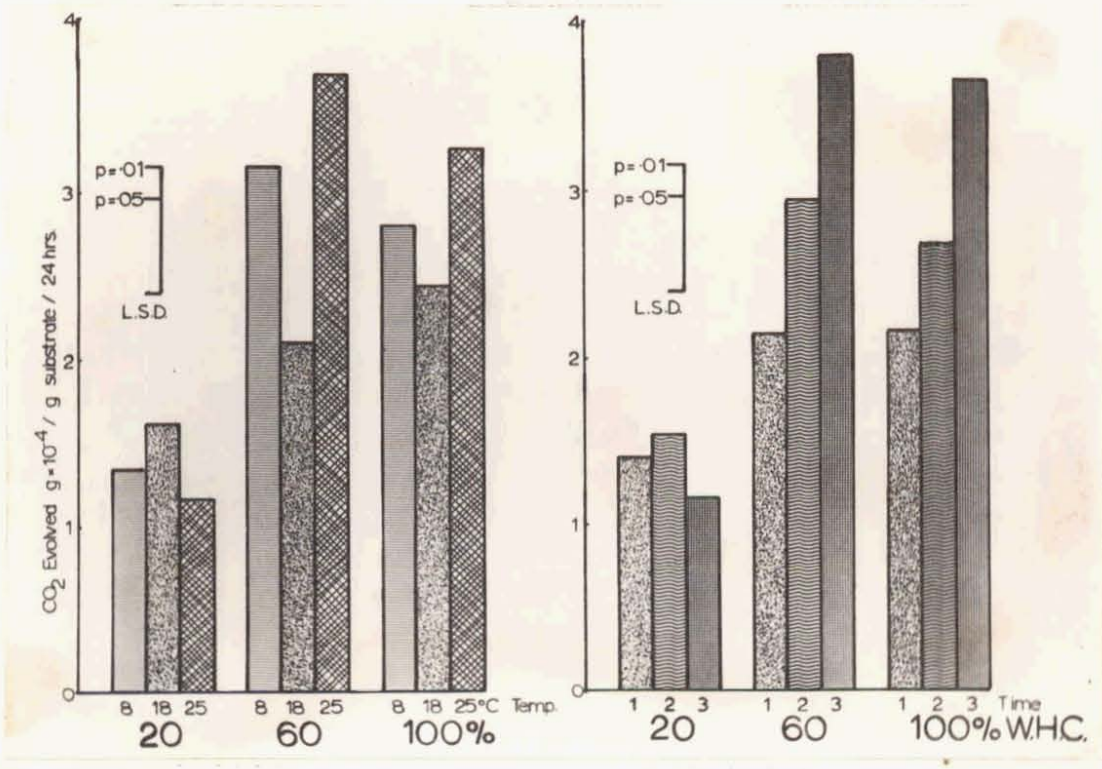


Fig.6.1.12 Fig.6.1.13

no significant effect on CO_2 production but at 60% and 100% W.H.C. samples held at 18° C showed a slight but significantly smaller CO_2 production than at 8° C and 25° C. Usually (Batholomew and Norman, 1946; and Drobnik, 1962) CO_2 production at a lower temperature is less than at the higher temperature although 8° C is closer to the mean temperature (12.5° C) than 18° C. It is possible that both 8° C and 25° C are closer to the optimum temperatures for particular species of fungi responsible for the major part of the decomposition.

Moisture x Time (Fig. 6.1.13)

At 20% W.H.C. the rate of CO_2 production did not significantly change over the three sampling periods whereas at the other moisture contents CO_2 production was significantly higher at each subsequent sampling period. This increase in CO_2 production was in accordance with the build up of fungal mycelium observed during this period.

Time x Temperature (Appendix 6.1F)

This interaction showed a high CO_2 production during period three at 8° C when compared with periods one and two. The build up at 8° C was probably slow but after it had occurred the rate of production was as high as that found at other temperatures. There was a reduction during the second period at 25° C, CO_2 production being higher during periods one and three.

These results may be explained by exhaustion of readily decomposable materials by the end of the second period in contrast to a more gradual build up of CO_2 production at 18° C.

Moisture x Replications (Appendix 6.1F)

There was no reason apparent why the replications should differ as they were selected on a random basis, also the main effect replications were shown to be not significant.

At 20% W.H.C. replications tended to differ but no explanation can be offered for these results. They do not, however, mask the effect of moisture.

6.13 THE EFFECTS OF ADDITION OF GLUCOSE, AMMONIUM AND NITRATE NITROGEN ON RESPIRATION OF SOIL AND LITTER SAMPLES COLLECTED FROM TASMAN FOREST

INTRODUCTION

In this experiment mineral nitrogen levels and carbon dioxide evolution were measured, carbon dioxide evolution rate was assumed to provide a measure of mineral nitrogen turnover while an estimation of the initial and final mineral nitrogen levels provided information comparable to that obtained when tagged nitrogen is used to estimate the turnover of nitrogen in soil. The experiment was also designed to determine the maximum rate of organic matter mineralisation under existing levels of mineral nutrients and also to determine whether the presence of excess mineral nitrogen would further stimulate CO_2 production. It was also desired to investigate the relative efficiencies of NH_4^+-N and NO_3^--N as sources of nitrogen for CO_2 production. In the same experiment the hypothesis that if the clay soil from 25 cm depth possessed sufficient oxidizable carbon and mineral nutrients its rates of CO_2 evolution would be similar to rates of CO_2 evolution in soil from the 0 - 2.5 cm layer, was also tested.

METHOD

Carbon mineralisation was studied using soil and litter samples collected in Tasman Forest on 25 September, 1968. Litter (F layer) and duff (H layer) were collected

from four sites on a ridge and adjoining gully at site P31 under a mature P.radiata stand. Soil samples were collected from the surface (0 - 2.5 cm) layer and 25 cm layer from sites R66-67. R65-66. R63 and R60, previously described.

All samples were air dried after collection. Soils were finely ground to pass through a sieve of 0.0116 in apperture and then bulked while litter and duff samples were broken down so that no piece was larger than 0.5 cm. Thirty g soil, 7 g duff and 5 g air dry litter were weighed out and placed in 5 cm diameter x 5 cm tall jars. Lids with rubber inserts were used to close the containers.

Amendments

a) Ammonium nitrogen : 75 ppm N as $(NH_4)_2SO_4$ solution.

b) Nitrate nitrogen : 75 ppm as KNO_3 solution.

c) Glucose : 10,000 ppm added in solution.

The three treatments were applied as a replicated factorial design giving an experiment using 2^3 x 2 x 4 jars. Jars were incubated at 24 $\pm$ 1° C for a total of two months. Carbon dioxide was determined using the method of Cornfield (1961). The intervals between changes of BaO_2 depended on the activity of the substrate and the time after initial wetting. The intervals of incubation between changes of BaO_2 were designated sampling periods one to five.

Results were analysed statistically on an IBM computer, using a programme written by the author.

RESULTS AND DISCUSSION

Litter

Insufficient glucose was added to litter and duff samples to cause serious immobilization of nutrients as occurred in the soil samples. In the third period of sampling after the initial flush of CO_2 evolution the effects of glucose became significant. The interaction (NH_4 + G) was also significant in this period probably due to the immobilization in the first two periods which meant that glucose could only be significant in the presence of NH_4-N. In sampling periods one and five different interactions became significant. However, no overall effect was apparent. The differences may have been caused by the differences in variation in the analysis of variance for periods one to five and therefore no conclusive result is apparent in this experiment.

Duff (Appendix 6.1H)

The rate of application of glucose in this part of the experiment was insufficient to cause any immobilization which would express itself in differences in CO_2 evolution rate. The wide variation found in the different analysis was probably responsible for the erratic appearance of significant treatments in the sampling periods.

Soil from the 0 - 2.5 cm depth (Appendix 6.1I)

In all four sampling periods the factor glucose was significant. This is a real effect, although the F value of 85.25 found in the fourth period was a result of the low error mean square found in that particular analysis. The significance of the other interactions was due to the same effect.

The absence of a significant interaction between glucose and mineral nitrogen meant that the soil nitrogen supply was sufficient to support the decomposition of glucose at the rate observed in this experiment.

Soil from 25 cm depth (Appendix 6.1J)

As with soil taken from the 0 - 2.5 cm depth the addition of glucose raised the respiration rate significantly at all four periods. The high F values found at sampling period three were due to the low error mean square at this period in contrast to other periods.

As observed in the soil from the 0 - 2.5 cm depth glucose application stimulated CO_2 evolution in the soil from 25 cm and the supply of mineral nutrients was sufficient for this rate of respiration.

General conclusions

Carbon dioxide evolution rates for the four substrates tested are presented in Fig. 6.1.14.

One % glucose had little effect on the duff and litter samples but had an effect on the 0 - 2.5 cm and 25 cm soil samples.

Sampling period	Duff	Litter	Soil 0-2.5 cm	Soil 25 cm
	No Glucose	No Glucose	No Glucose	No Glucose
1	8.16×10^{-4}	1.56×10^{-3}	1.39×10^{-4}	2.88×10^{-5}
2	1.65×10^{-4}	3.67×10^{-4}	1.64×10^{-5}	2.00×10^{-5}
3	1.33×10^{-4}	2.30×10^{-4}	1.75×10^{-5}	6.14×10^{-6}
4	1.16×10^{-4}	4.39×10^{-4}	-	-
5	2.15×10^{-4}	5.15×10^{-4}	1.41×10^{-4}	3.58×10^{-6}
	1% Glucose	1% Glucose	1% Glucose	1% Glucose
1	9.15×10^{-4}	1.86×10^{-3}	2.22×10^{-4}	2.30×10^{-4}
2	2.17×10^{-4}	8.87×10^{-4}	4.20×10^{-5}	4.10×10^{-5}
3	1.30×10^{-4}	1.48×10^{-4}	3.68×10^{-5}	3.55×10^{-3}
4	1.96×10^{-4}	3.68×10^{-4}	-	-
5	1.71×10^{-4}	8.87×10^{-4}	4.98×10^{-5}	2.45×10^{-5}

Fig. 6.1.14

Results of measurements of respiration of soils and soil components from Tasman Forest using method of Cornfield (1961), expressed as g of CO_2 per g of oven dry sample per 24 hours. Incubation was at 24 ± 1° C.

CO_2 evolution rates in unamended duff and litter where litter produced twice as much CO_2 as duff is similar to that found in Section 6.12. The CO_2 evolution rates found in this experiment were comparable to those found in Section 6.14 but were much lower than those found when 10 g samples of a different soil were used in Section 6.11.

The experiment showed that although 0 - 2.5 cm soil had a natural rate of CO_2 evolution 3.2 times higher than soil from 25 cm depth; with applied glucose the rates in the two soils were approximately equal. This suggests that a lack of available carbon rather than a physical factor or lack of mineral nutrients controls the rate of CO_2 evolution in the deeper soil layers. This phenomenon was also found by Robinson (1962) who worked on New Zealand mountain soils of low fertility.

6.14 CARBON DIOXIDE EVOLUTION FROM SOIL SAMPLES TAKEN FROM TASMAN FOREST, HANMER FOREST AND LINCOLN COLLEGE FARM AMENDED WITH CELLULOSE AND GLUCOSE.

INTRODUCTION

The rate at which CO_2 was evolved from soil samples treated with glucose was obtained in Section 6.13 where NO_3-N, NH_4-N and glucose was added to soil. To amplify these results it was decided to study the rate of CO_2 evolution from soil amended with cellulose. Cellulose was applied in amounts equivalent to those which were left under field conditions when mature trees were clear felled. It was desired to determine if the application of this amount of cellulose caused sufficient nitrogen immobilization so that when glucose was applied both to soils incubated with and without added cellulose the rate of evolution of CO_2 from the glucose would reflect the amount of mineral nitrogen left in the soil.

METHODS

Soil gathered from Lincoln College Dairy Farm, Hanmer Forest and Tasman Forest was air dried after collection. The samples were collected from under L.scoparium, mature P. radiata and regenerating P. radiata in Tasman Forest. Soil samples from the R66-67 and R65-66 sites were bulked and labelled R65-67 while soil from R60 and R63 sites were bulked and called R60-63.

This gave nine soil types as follows:

1. Lincoln
2. Hanmer
3. Manuka Ridge
4. P31 Ridge
5. P31 Gully
6. R65-67 Ridge
7. R65-67 Gully
8. R60-63 Ridge
9. R60-63 Gully.

Soils were treated as described in Section 6.13. Twenty g of air dry soil was placed in jars capped with lids containing rubber inserts (see Section 6.13). Carbon dioxide was measured using the method of Cornfield (1961) where CO_2 evolved was absorbed by BaO_2 which liberated O_2 in equivalent amounts.

Ball-milled cellulose (Macherey, Nagel & Co., Germany) was added to the dry soil at the rate of 0%, 3% and 6%. After incubation for one month, during which time the rate of CO_2 evolution was measured on three occasions (periods one to three), glucose was added to all soil samples at the rate of 1% and sampling for CO_2 was continued on one more occasion.

The results were analysed in two parts. Firstly, the results from ridge samples of each Tasman Forest soil type under P.radiata together with results from Lincoln, Hanmer and Tasman Forest soil under L.scoparium were analysed.

Secondly, soil types four to nine from Tasman Forest were analysed to test if the position from where the sample was taken resulted in a difference in CO_2 evolution. The effects of cellulose and glucose were analysed separately. The results and discussion have been divided into four sections (Sections 6.141 to 6.144).

RESULTS AND DISCUSSION

6.141 CARBON DIOXIDE EVOLUTION FROM SOIL SAMPLES FROM TASMAN FOREST, HANMER FOREST AND LINCOLN COLLEGE FARM

Means of significant factors found in this experiment are set out in Fig. 6.1.15 and the analysis of variance table is contained in Appendix 6.1K.

The mean CO_2 evolution rates (Fig. 6.1.16) for all soils during the second period showed a highly significant difference from the means of the first and third periods. Greatest CO_2 evolution occurred in the second period while the third period was not significantly different from the first period. The decline in the third suggests either an accumulation of products toxic to the micro-organisms, a reduction in the amount of available nutrients or a decline in the amount of available substrate. It is conceivable that during the preparation of ball-milled cellulose some of the cellulose was converted into more readily available substances which were used during the second period.

Fig.6.1.15 Mean CO_2 evolution rates from added cellulose in soils from Tasman, Hanmer and Balmoral Forests and Lincoln College. Carbon dioxide evolution was measured using the method of Cornfield (1961).

Fig.6.1.16 Mean CO_2 evolution rates for all soils used in the experiment with increasing time after application of the three rates of cellulose.

Fig.6.1.17 Mean rates of CO_2 evolution for all soils used in the experiment with three rates of added cellulose.

Fig.6.1.18 Rates of CO_2 evolution with increasing time after application of three rates of cellulose in different soils.

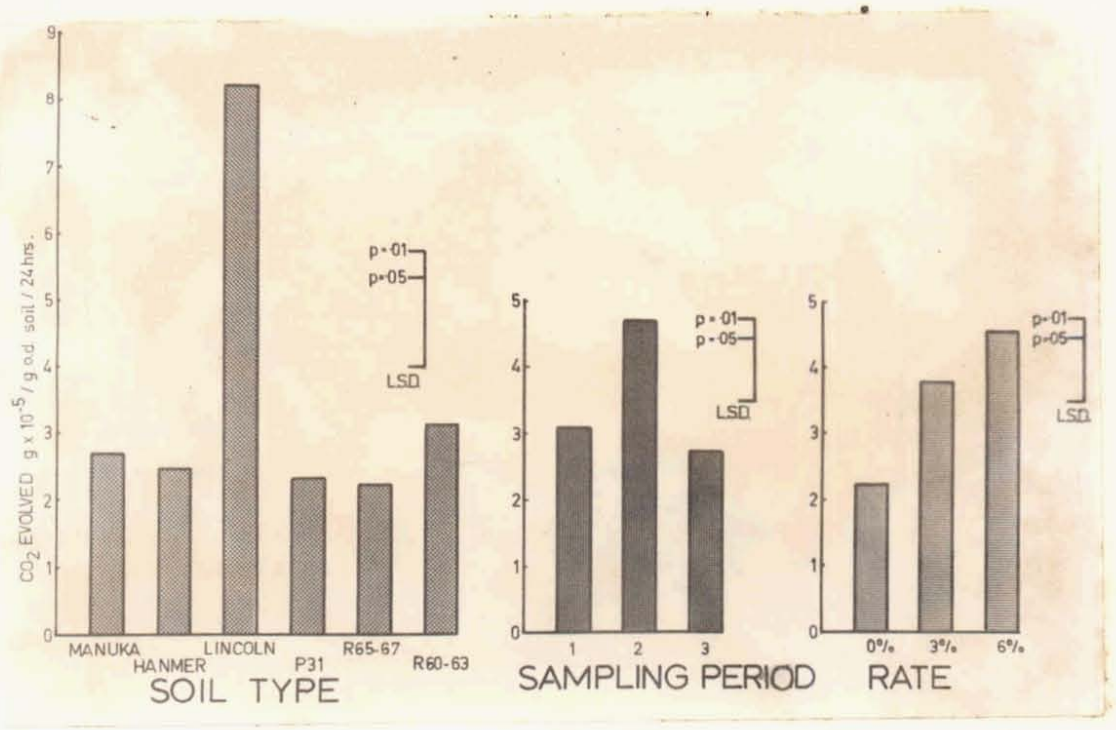


Fig.6.1.15 Fig.6.1.16 Fig.6.1.17

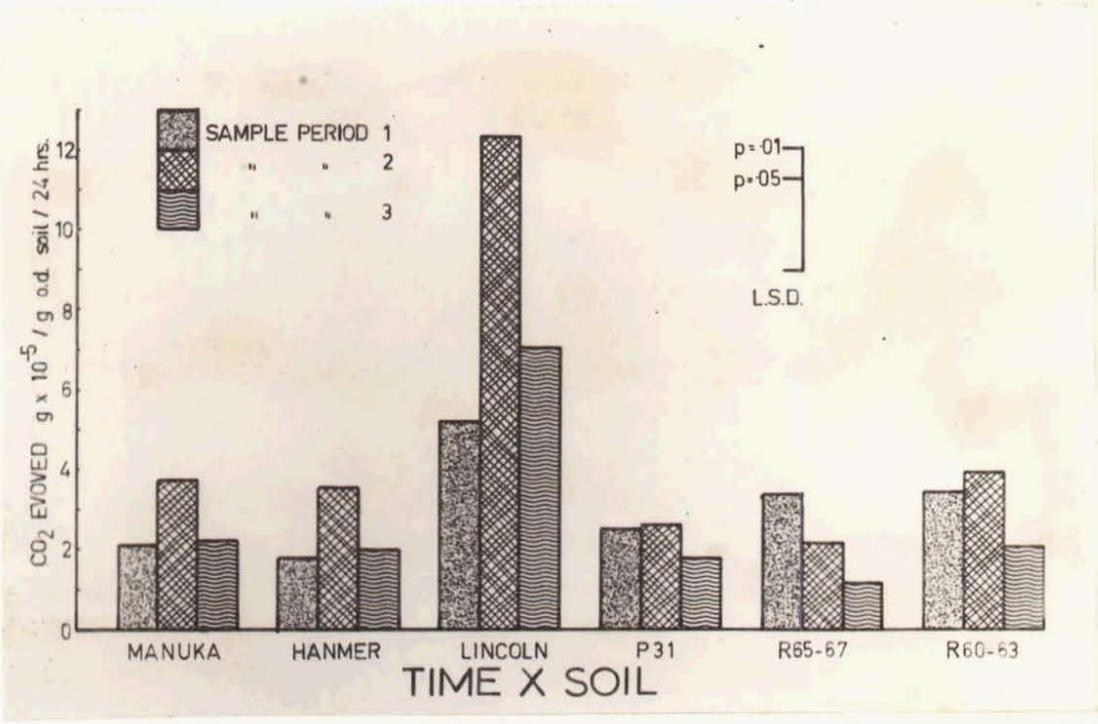


Fig.6.1.18

As shown in Fig. 6.1.17 there was a significant difference in the rate of CO_2 evolution between soils with added cellulose and those without but at the levels used the rates of application did not cause a significant difference.

Soil type affected the rate of CO_2 evolution. All Tasman Forest soils and Hanmer Forest soil were similar but Lincoln soil differed significantly from these as shown in Fig. 6.1.15., The time x soil interaction (Fig. 6.1.18) showed that the CO_2 evolution during the third period in Tasman Forest soil under L.scoparium, Hanmer Forest and Lincoln soils was greater than CO_2 production during the first period whereas the Tasman Forest soils under P. radiata showed the opposite trend. It is possible that in the Hanmer, Lincoln and Manuka soils the build up of microorganism numbers was less rapid than in the Tasman Forest soils under P. radiata.

Tasman Forest soil under L. scoparium and Hanmer soil showed a higher rate of CO_2 evolution when cellulose was added at 3% than 6% (rate x soil interaction - Fig.6.1.19). This suggests the existence of some inhibitory effect. On the other hand the other soil types showed a greater rate of CO_2 evolution with 6% than with 3% cellulose.

Fig.6.1.19 Rates of CO_2 evolution in soils from Tasman, Hanmer and Balmoral Forests and Lincoln College, with three levels of applied cellulose.

Fig.6.1.20 Mean CO_2 evolution for soil samples collected from under P.radiata stands in Tasman Forest with increasing time after application of three rates of cellulose.

Fig.6.1.21 Rate of CO_2 evolution from soils collected under P.radiata vegetation in Tasman Forest with three rates of cellulose application.

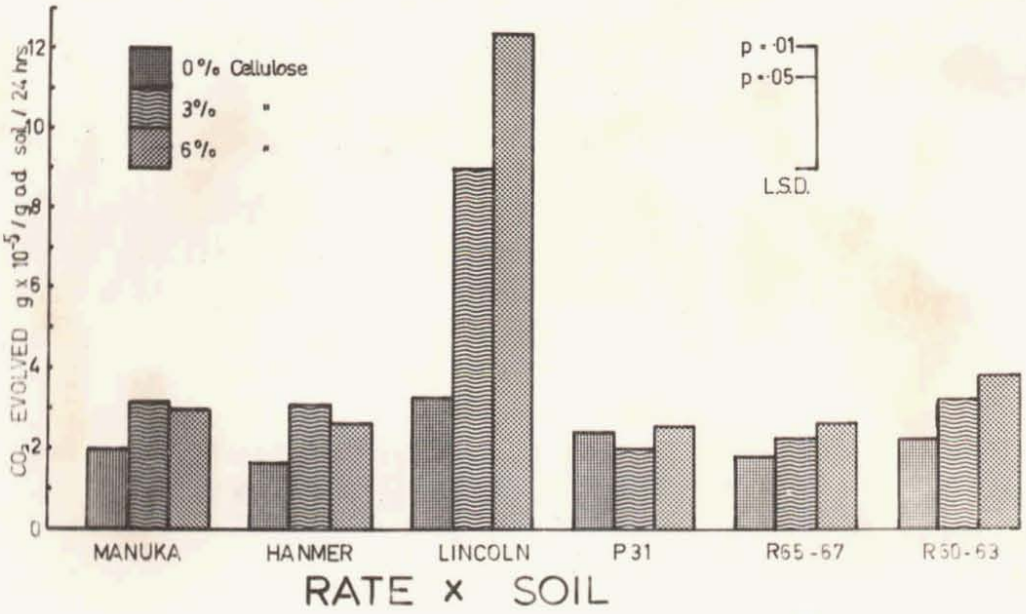


Fig.6.1.19

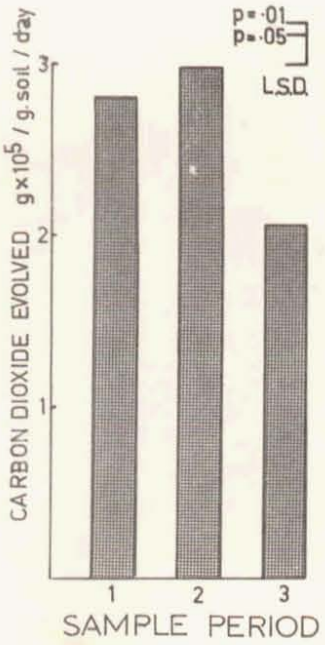


Fig.6.1.20

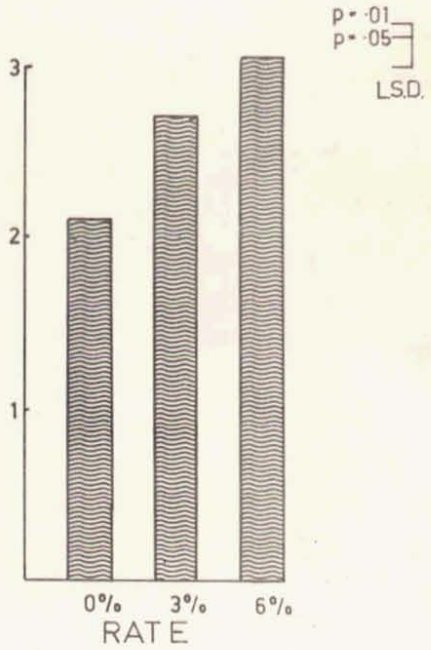


Fig.6.1.21

6.142 CARBON DIOXIDE EVOLUTION FROM SOIL SAMPLES FROM TASMAN FOREST UNDER P.RADIATA

Soil samples from ridge sites at Tasman Forest under P.radiata only were included in the analysis using soil from Tasman, Hanmer, and Lincoln College (Section 6.141) because L.scoparium was only found growing on a ridge site. In this analysis both ridge and gully soil samples from under P.radiata were included to test the effect of topographical position of the sample. The analysis of variance table for CO_2 evolution from Tasman Forest soil samples is set out in Appendix 6.1L.

In this experiment only the time interval during which CO_2 was evolved (Fig. 6.1.20) and the rate of cellulose application (Fig. 6.1.21) were significant. The first period of CO_2 evolution did not differ significantly from the second period but the third was significantly reduced in comparison with the first and second.

Results from both ridge and gully sites in Tasman Forest differed from the ridge samples from Tasman Forest alone, Hanmer and Lincoln soil samples as a group, in that the Tasman Forest ridge and gully soils showed a greater decline in CO_2 production in the third period.

All rates of cellulose application (Fig. 6.1.21) differed significantly in this experiment. This demonstrated that the soil was capable of increased CO_2 evolution when cellulose equivalent to the total organic matter which would remain after clear felling (see Section 6.31) were added.

Since clear felling residues contain some nitrogen and are partially composed of substances which are more resistant to decomposition than cellulose and are not all intimately mixed with the soil the 3% cellulose level would probably compare closely with the actual amount of material available for decomposition left after clear felling. The significant difference between the 3% and 6% rates indicates that Tasman Forest soil probably has the capacity to decompose more material than is added by clear felling provided it was composed entirely of a material of similar resistance to decomposition and nitrogen content as cellulose.

6.143 CARBON DIOXIDE PRODUCTION FROM GLUCOSE AMENDED SOIL SAMPLES FROM TASMAN FOREST RIDGE SITES, HANMER FOREST AND LINCOLN COLLEGE WITH PREVIOUS APPLICATION OF VARIOUS AMOUNTS OF CELLULOSE.

A glucose solution was added to the soil previously amended with 0%, 3% and 6% cellulose to determine whether the lack of some nutrient was limiting the decomposition rate and was responsible for the decline in CO_2 evolution in the third period. It was also designed to test whether the added cellulose immobilized significant quantities of nutrients which could be reflected by reduced decomposition of glucose in those soils containing the cellulose. The rate of added cellulose in the previous experiment had no significant effect on CO_2 from the glucose. The only significant effect was one of soil type where Lincoln soil was significantly different from all other soils except P31 Tasman

Fig.6.1.22 Rates of evolution of CO_2 from glucose applied to soils collected from Tasman Forest ridge sites, Hanmer and Balmoral Forests and Lincoln College previously amended with three rates of cellulose.

Fig.6.1.23 Rates of CO_2 evolution from glucose applied to soils supporting *P.radiata* in Tasman Forest previously amended with three rates of cellulose.

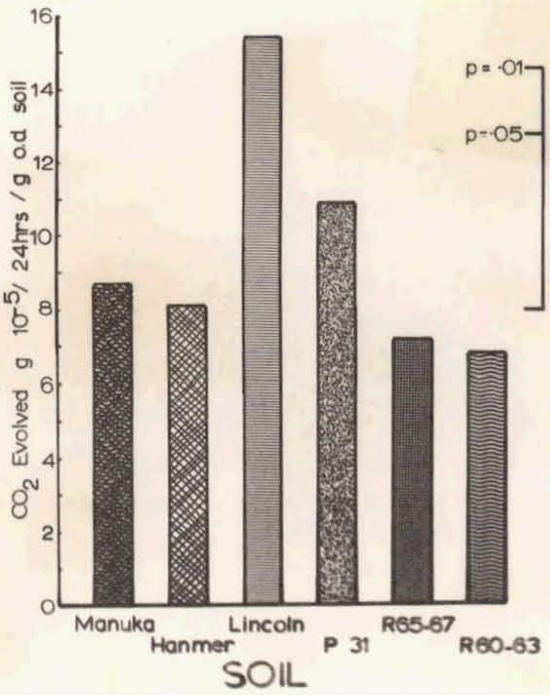


Fig.6.1.22

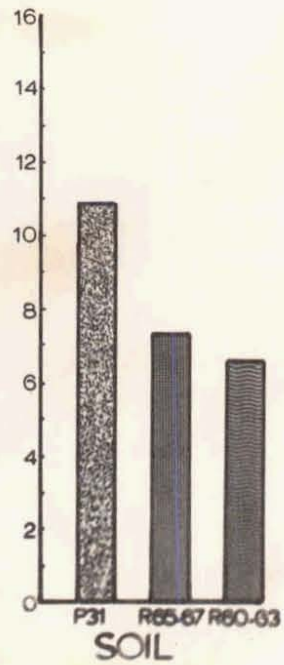


Fig.6.1.23

Forest soil (Fig.6.1.22, and Appendix 6.1M)

On the one hand the failure to find any difference from using various rates of cellulose may mean that nutrients were not limiting. On the other hand the higher decomposition rate in a more fertile Lincoln soil suggests the existence of limiting environmental or nutritional factor or factors in the other soils tested. A possible explanation is that Lincoln soils possessed a microflora capable of breaking down a larger fraction of the cellulose and possessed enough soil nitrogen to also break down large amounts of glucose.

6.144 CARBON DIOXIDE PRODUCTION FROM GLUCOSE AMENDED SOIL SAMPLES COLLECTED FROM RIDGE AND GULLY SITES IN TASMAN FOREST PREVIOUSLY AMENDED WITH DIFFERENT RATES OF CELLULOSE

The only factor possessing an F value which was nearly significant at the 5% level in the analysis of variance table (Appendix 6.1N) was the time elapsed since clear felling (Fig.6.1.23).

The rates of decomposition of glucose decreased as the age of regeneration after clear felling in the stands P31, R65-66 and R60-63. Nutrient availability may follow the same sequence.

The absence of any position effect when either the cellulose or when cellulose + glucose was added suggests that nutrient availability for decomposition is comparable in both ridge and gully sites.

6.15 CARBON DIOXIDE PRODUCTION IN SOIL FROM TASMAN FOREST

INTRODUCTION

The rate of carbon mineralization is dependent on the number of micro-organisms present and the efficiency of each individual organism. The number of micro-organisms present is controlled by many variables including limiting environmental factors such as temperature, moisture, the amount of nutrient available, etc. Under the conditions found in the Tasman Forest lack of mineral nutrients and moisture are likely to be the controlling factors. The rate of evolution of CO_2 from the substrate may give a measure of the gross amount of nitrogen mineralization at any one time if it is assumed that a certain amount of CO_2 production is associated with an amount of nitrogen turnover.

METHODS

Carbon mineralization was studied using cores of soil obtained from six Tasman Forest sites on two occasions (July, and August, 1967). Three cores, 3 cm in diameter and 25 cm long, were extracted with a stainless steel sampler from each site. The cores were placed in new plastic bags for transport to the laboratory.

The units for measuring CO_2 evolved from the soil were similar to those described by Stotzky and Mortensen (1957). Air was drawn through the apparatus with a water operated

vacuum pump. The CO_2 in the air entering the system was removed by passing it through a soda lime tower before being led along a copper manifold to which the units were connected. The respiration chambers were connected to a gas washing bottle of the Freidreich type where CO_2 from the soil micro-organisms was absorbed by 0.1 N NaOH. The change in conductivity of the solution due to the reaction of CO_2 with NaOH indicated the amount of CO_2 evolved from the sample.

Each washing bottle was fitted with platinum electrodes connected to a Radiometer CDM 2d MHO meter through a switching box. The electrodes were approximately ¼" long and were pressed parallel on to a perspex mounting block. The rate of air flow through each unit was adjusted by means of a screw clamp on the rubber tubing leading to the outgoing manifold. The units were maintained in a temperature controlled room at 26° C ± 1.5° C and the effect on the solutions was measured by reading a control unit and compensating for temperature changes. Each pair of electrodes was standardized using NaOH solutions with known amount of Na_2CO_3 added and a graph was drawn for each electrode unit.

RESULTS

The results of this experiment are presented in Table 6.1.23.

Table 6.1.23 The amount of CO_2 in g x 10^3 $CO_2/yr/m^2$ at a constant temperature $26^o \pm 1^o$ C evolved from soil on 25 cm depth collected on 4 July 1967.

	SITE					
	RIDGE			GULLY		
	4 July	28 August	Av.	4 July	28 August	Av.
R66-67	4.4	4.2	4.3	6.3	4.3	5.3
R65-66	3.0	4.2	3.6	5.4	4.2	4.8
R63	-	7.6	7.6	-	10.2	10.2
R60	7.3	14.6	11.0	3.5	5.8	5.4
Average			6.6			6.4

The ground surface area of soil removed when the three cores were extracted was estimated and the results were converted to a m^2 basis. Water content at the time of collection was maintained throughout the incubation period. Imperfect functioning of new electrodes, especially low readings caused by air bubbles on the electrodes may have caused some differences.

For this reason a standardization experiment was set up to obtain some idea of the variation likely to be found. Finely ground well-mixed soil from an R60 site was used in all units. Using this information the variation of the average value in Table 6.1.23 was found to be 6.5 ± 0.5 g x 10^3 $CO_2/yr/m^2$.

DISCUSSION

The results showed an increase in CO_2 production in the older regeneration sites (R60 and R63) and slightly greater CO_2 production in site R66-67 than on R65-66. A comparison of averages showed little difference.

The average rate at Tasman Forest 6.5×10^3 g $CO_2/m^2/yr$ at a constant temperature of 26° C and a depth of 25 cm is high compared with field values given by Schulze (1967). The extrapolation of his data for daily averages to cover full 24 hours/day at day temperature, gave soil respiration values of 3.1×10^3 g $CO_2/m^2/yr$ for tropical savanna and deciduous forest, 13×10^3 for tropical gallery and wet forest, and 19×10^3 for secondary growth.

Robinson (1962) found values of approximately 17×10^3 g $CO_2/m^2/yr$ under the same conditions as the results presented in this report estimated assuming a similar weight for Nelson and Craigieburn soils. He used the 0-15 cm fraction therefore his soil would have been collected from 1.6 times more surface area than the Nelson soils. Allowing for this gave a value of 10×10^3 g $CO_2/m^2/yr$ which is similar to the Tasman Forest soils.

Other workers (Witkamp and van der Drift, 1961; and Wallis and Wilde, 1957) report values of approximately $10-70 \times 10^3$ g $CO_2/m^2/yr$ (measured over 24 hours) using continuous air sampling whereas Feher (1933) and Lundegardh (1927) found values of $8-20 \times 10^3$ using periodic sampling. The lowest of these values are similar to those found at Nelson.

CHAPTER 6 (continued)

ENERGY DISSIPATION UNDER CONTROLLED CONDITIONS

6.2 OXYGEN ABSORPTION

6.21 INTRODUCTION

Numerous workers (Rovira, 1953; Chase and Gray, 1953; Chase, 1958; Gilmore, Damsky and Bollen, 1958; Katznelson and Rouatt, 1957; Katznelson and Stevenson, 1956; Gaarder, 1957; and Stout and Dutch, 1958) have used a manometric or similar technique to study the metabolic activity of the soil ecosystem. This technique suffers from certain disadvantages, for example, samples have to be thoroughly homogenized before testing and unnaturally low CO_2 concentrations may be present in the reaction vessel caused by the presence of alkali; nevertheless, manometric techniques provide a very accurate method for determining metabolic activity under controlled environmental conditions.

The Warburg apparatus was used in this work to increase the precision of the results obtained using the method of Cornfield (1961) reported in Section 6.1. Although

Cornfield's method was sufficiently accurate to obtain significantly different results it was felt that a more accurate method would allow soils and treatments to be more readily distinguished and a check made between the two methods.

6.22 GENERAL METHOD

Warburg apparatus

The methods used in the three experiments using the Warburg apparatus (Braun Model V166) were similar except that experience led to minor modifications which improved later experiments.

In general, the method of Umbreit et al. (1949) was followed, but some modifications were required since a solid and not a liquid was used in the respiration chamber.

Soil samples were air dried, finely ground to pass through a sieve with 0.5 mm aperature and weighed into 15 ml Warburg flasks (Braun 3045). Care was taken to prevent soil from entering the centre well but any deposited there was later removed by tilting the flasks after the soil in the main chamber had been wetted and had become cohesive.

Amendments were added, either in solution to the surface of the soil in the vessel, or incorporated when the soil was dry, before the flasks were filled.

A solution of alkali was added to the centre well after it had been rinsed several times with distilled water

to remove the last traces of soil. Gaarder (1957) pointed out that the centre well of the flask must not contain soil because, under strongly alkaline conditions, oxygen is absorbed by chemical oxidation of phenolic and other organic compounds.

A pipette was used in the first experiment to add the KOH solution but later the use of a 10-ml hypodermic syringe was found to reduce the chance of drops of alkali being spilled. In the first two experiments 16% (W/V) KOH was used in the centre well but in the third experiment, because of its longer duration, 10% (W/V) KOH was used to reduce the extraction of soil water and to prevent the KOH creeping over the rim of the centre well, which has been reported to occur even when grease was used (Chase and Gray, 1957). Figure 6.2.1 shows how the filter paper wick was shaped so that contact with the rim of the centre well was avoided.

Manometers were read at intervals during the day and, at night, stopcocks were held open by fine wire inserted through the hole.

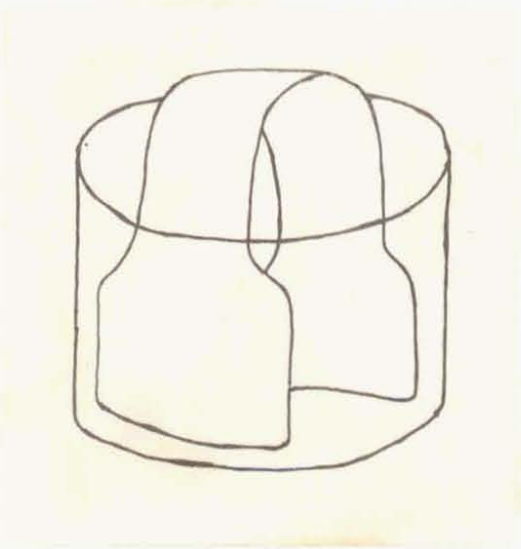


Fig. 6.2.1 Shape of filter paper wick used to increase absorbing surface of KOH in Warburg flask.

6.23 EFFECT OF ADDED GLUCOSE ON SOIL RESPIRATION

METHOD

Soil, collected from eight sites at four depths, was bulked and ground, as described in Section 6.22, before use.

Glucose was added to five g aliquots of soil as a solution in amounts equivalent to 0%, 3%, 6%, 12% and 18% glucose.

Oxygen absorption was measured on the first, second, third, fourth, seventh and eighth days after addition of the glucose for periods of 3 - 5 hours per day.

RESULTS AND DISCUSSION

Analysis of variance for this experiment is presented in Table 6.2.3.

Treatment

Results are shown in Fig. 6.2.2. The soil sample with the addition of 3% glucose displayed a marked increase in oxygen absorption over the control soil. The 6% rate was significantly lower than the 3%. On the other hand the 12% and 18% levels are not significantly different from control levels. If the lack of nutrients was controlling O_2 absorption there would probably be a constant amount of O_2 absorption from the 3% to the 18% levels instead of a decline as shown in Fig. 6.2.2. Rather it possible that some effect such as osmotic pressure may have been responsible as suggested by Stotzky and Norman (1961).

From this experiment it may be concluded that the addition of glucose in amounts equivalent to half the amount or residues deposited in or on the soil at the time of clear felling causes the soil to increase its O_2 absorption rate 6.4 fold without the addition of mineral nutrients.

Time

Fig.6.2.4 shows the overall effects of time. There was a build up from the first day to the third and then a levelling off until the eighth day. The differences between the first, second and third days are almost significant.

TABLE 6.2.3

Source of variation	S.S.	df	M.S.	F	
Reps	2.02	1	2.02	1.59	
Treatments	159.20	4	39.80	31.45	**
Day	34.40	5	6.88	5.44	**
Reps x Treatment	31.25	4	7.81	6.17	**
Reps x Day	7.39	5	1.48	1.17	
Treatments x Day	47.40	20	2.37	1.87	
Error	25.30	20	1.27		
Total	306.90	59	5.20		

Oxygen uptake by Tasman Forest soil samples amended with 0%, 3%, 6%, 12%, 18% glucose, measured with a Warburg apparatus.

The control soil reached a peak by the second day but 3% and 6% treatments took three to four days until a peak in glucose mineralization was reached.

Replication x Treatment

Due to small but consistent difference in manometers some treatments showed one replicate to be consistently higher than others and vice versa. This, however, had little effect on the overall significance of the Treatment effect.

Fig.6.2.2 The effect of added glucose on O_2 uptake in a bulked soil sample collected from ridge and gully sites under four ages of P.radiata regeneration in Tasman Forest.

Fig.6.2.3 The change of O_2 uptake rate with time in a bulked soil sample amended with glucose. The soil was collected from Tasman Forest.

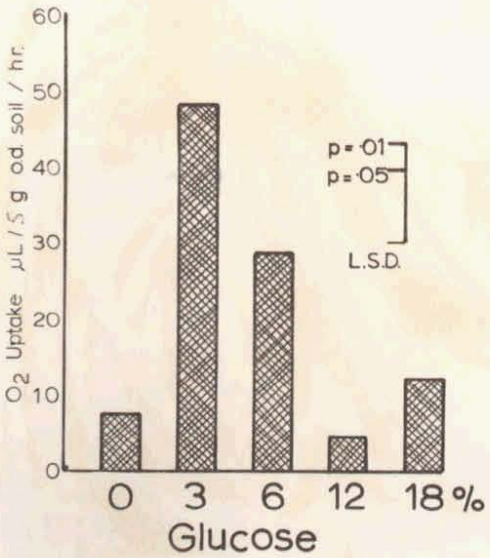


Fig.6.2.2

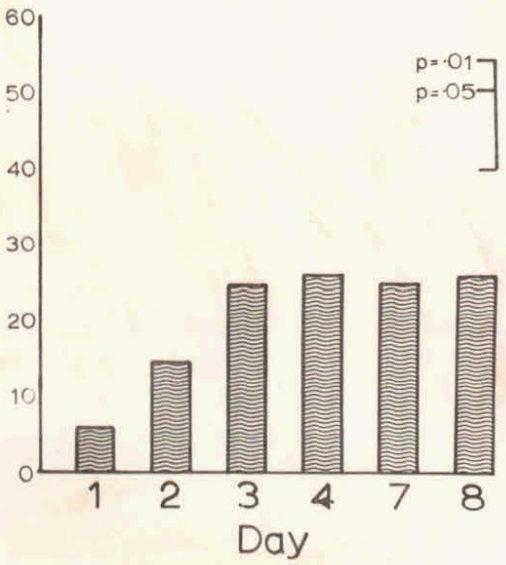


Fig.6.2.3

GENERAL DISCUSSION

Stotzky and Norman (1961) found that the maximum rate of evolution of CO_2 occurred 9 - 15 days after glucose was added to the soil. In this study maximum uptake occurred by the second day which was more akin to the results obtained by Chase and Gray (1957), Drobnik (1958), Katznelson and Stevenson (1956), Koeph (1954), Lees (1949), Newman and Norman (1941), Stotzky et al. (1956) and Stotzky and Mortensen (1957, 1958). Stotzky and Norman (1961) suggest that their results could have been due to a low endogenous microbial respiration of the soil together with limiting nutrient availability. The rapid rate of increase found in Tasman Forest soil samples therefore suggests that there was no available nutrient shortage. With the addition of nutrients to their soil samples Stotzky and Norman (1961) found that the metabolism on the addition of glucose declined quickly after a peak had been reached. They explained a slow rate of decline as being due to slow rate of remobilization of the limiting nutrients. Since Tasman Forest soil samples show a slow rate of decline it is possible that there was a shortage of some element which was slowly mobilized to allow decomposition of the glucose.

6.24 EFFECT OF NITROGEN ON SOIL RESPIRATION

INTRODUCTION

Since the addition of nitrogen did not produce any significant effect on CO_2 evolution, as described in Section 6.13, even when glucose and nitrogen were added, it was decided to try the same experiment using the more precise Warburg apparatus. The Warburg apparatus is more accurate than the BaO_2 method (Cornfield, 1961) used in Section 6.13 and would demonstrate any smaller effects if such existed.

METHOD

The soil sample used was a composite sample of soil collected from eight sites at four depths under *P.radiata* regeneration in Tasman Forest. Nitrogen at a rate of 100 ppm was added as $(NH_4)_2SO_4$ and glucose was added in solution in an amount equivalent to 10,000 ppm of soil. A nitrogen-free solution was added to each 5 g soil sample. The composition of the 0.9 ml of solution added is set out below :

K_2HPO_4	0.800	g
KH_2PO_4	0.200	g
$MgSO_4 \cdot 7H_2O$	0.500	g
$FeCl_3$	0.050	g
$MnSO_4 \cdot 4H_2O$	0.005	g
$ZnSO_4$	0.005	g
$CuSO_4$	0.005	g
Na_2MoO_4	0.005	g
H_2O	1000	g

Distilled water was added to bring the soil to 60% W.H.C. All treatments were applied in triplicate.

RESULTS AND DISCUSSION

The analysis of variance of the results is shown in Appendix 6.2L.

Even though the treatment effect is significant in the analysis (Fig. 6.2.9a) when it is divided by the interactions containing this factor, the significance disappears. Only the factor day remains significant.

The interaction treatment x day is set out in Fig. 6.2.9b. In general there is a decline of O_2 uptake with time and the control soil absorbed more O_2 on the fifth day than other soils, but little else of interest is apparent.

The application of nitrogen did not stimulate O_2 uptake in the soil suggesting that nitrogen availability was sufficient for maximum decomposition rate. The application of glucose also did not affect the rate of O_2 uptake. This is contrary to the results found in Section 6.13 where the addition of glucose stimulated CO_2 evolution. In the experiment described in Section 6.13 no mineral nutrients other than nitrogen were applied. In this experiment the application of an N-free salt solution may have meant that the rate of O_2 uptake in the control soil was maximum under the environmental conditions in the experiment, and even the

Fig.6.2.9a Oxygen uptake in a bulked soil sample obtained from under P.radiata in Tasman Forest. The soil sample was amended with NH_4 -N, glucose and NH_4 -N + glucose. The results are an average of measurement over five days.

Fig.6.2.9b Oxygen uptake in a bulked soil sample from Tasman Forest over a period of five days. Soil was amended with glucose, NH_4 -N and glucose + NH_4 -N.

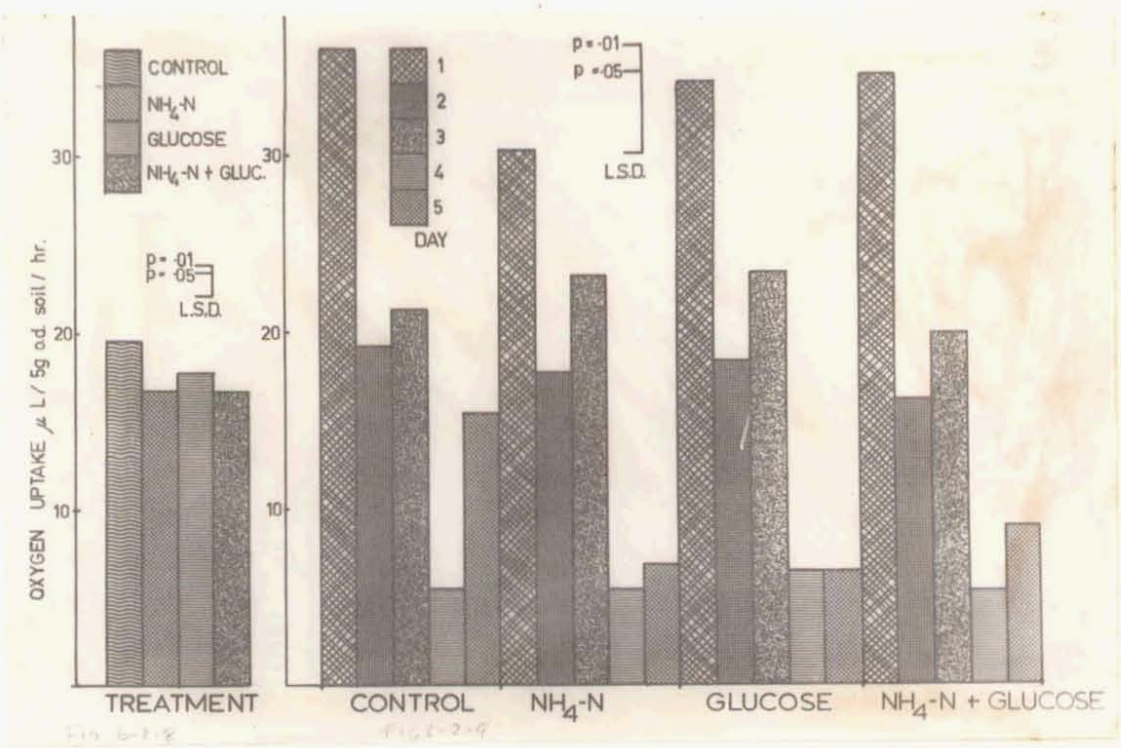


Fig.6.2.9a Fig.6.2.9b

addition of a readily available substrate would not stimulate O_2 uptake. The lack of response of O_2 uptake rate with the addition of glucose and nitrogen showed that nitrogen was not limiting the O_2 uptake due to glucose alone.

The results of this experiment confirm the results obtained in Section 6.13 where it was found that the addition of nitrogen did not stimulate respiration in unamended soil.

6.25 THE EFFECT OF TEMPERATURE AND SOIL TYPE ON OXYGEN ABSORPTION IN UNAMENDED SOILS

INTRODUCTION

Katznelson and Stevenson (1956), using two types of soil, found that at 30° C there was little difference in O_2 uptake between 40% and 70% W.H.C. Maximum O_2 consumption occurred at 40% W.H.C. in a range of soils containing from 31% to 62% O.M. while O_2 absorption in a soil containing 4.3% O.M. steadily increased up to 100% W.H.C. (Gaarder, 1957).

Chase and Gray (1957) studied the effect of moisture over the range 30 - 90% saturation in intervals of 15%. Using a muck soil they found that only the 30% moisture level was significantly different from the other levels while in a loam soil none of the moisture levels in this range gave significantly different results. From Gaarder's (1957) results it appears that in soils of low O.M. content the concept of water holding capacity is of limited value in describing the availability of soil water to micro-organisms.

Because the rate of O_2 absorption has been found to vary little in the range 40 - 70% W.H.C. in most soils it was decided to study the effects of temperature. Also, when using the Warburg apparatus to measure respiration, temperature is more easily controlled than moisture. Moisture levels are best controlled using an apparatus similar to that described by Bartholomew and Norman (1946). However, the possibility remains that the 60% W.H.C. used in the experi-

ment described below may not have been the optimum for respiratory activity in the soils with low O.M.

Although effects of a change in vegetation was not one of the primary fields for study, soils from a succession of vegetative types were examined to determine whether a vegetational change could be correlated with changes of organisms and dynamic processes occurring within the soil.

Gaarder (1957) found a relationship between O_2 consumption and some types of vegetation from Western Norway, using a Warburg apparatus. Soil supporting fir and blueberry had a greater oxygen consumption per unit weight than soil supporting beech and poor hill grass. However, on an organic matter basis fir and beech had a greater uptake than heather and blueberry. High correlation between CO_2 evolved and O.M. content of the soil ($r = +0.95$) found suggested that differences in soil respiration per unit of O.M. under different vegetations are insignificant and that the amount and not the availability of carbon present was the important factor. This conclusion was also reached by Bunt and Rovira (1955). The actual relationships found by Gaarder (1957) were :

(1) O_2 (ul O_2 /g dry soil/hr) = 0.446 + 0.316 O.M. (% of dry soil)

(2) CO_2 (ul CO_2/g dry soil/hr = 0.464 + 0.272 O.M. (% of dry soil).

Stout and Dutch (1968), however, found higher values for CO_2 evolution (2.75 times higher) than those obtained

using Gaarder's (1957) regression even though respiration was carried out at approximately the same temperature in both cases (Fig. 6.2.5). Gaarder, however, studied soils with a wider range of O.M. content (0 - 80%). A Western Norwegian soil containing 23.5% O.M. would therefore evolve as much CO_2 as a New Zealand forest soil containing 7.2% C. These results emphasise a difference in availability of carbon in the soil of the two countries.

Fig. 6.2.5

Rate of carbon dioxide production from soils of different productivities

Figures taken from Stout and Dutch (1968) compared with Gaarder's (1957) regression equation.

Vegetation	Rate CO_2 ul/g dry soil	Rates estimated using Gaarder's regression
Low producing grassland	2.05	0.79
High " "	3.50	1.00
Cultivated soil	3.40	1.71
Established pasture	4.14	2.11
Forest soil	6.84	2.42

Stout and Dutch (1968) found that rates of CO_2 evolution per unit of O.M. in soils were similar even from under grass of different productivities. (170 ul CO_2/g O.M./hr). On the addition of glucose rates of CO_2 evolution in the soils supporting the more productive grass community were greater than soil supporting less productive grass (Stout and Dutch, 1968). They did, however, find that the same soil supporting different vegetations had different basal rates of

CO_2 evolution per unit O.M. Basal rates of cultivated soil were greater than forest soil which were, in turn, greater than pasture soil. The same relationship applied with glucose response but the effect was not marked in any soil. The data of Stout and Dutch (1968) suggest a difference in availability of carbon in a particular soil supporting different vegetations and a similarity in soils with a similar vegetation type.

Experiments were therefore designed to investigate differences in the rate of O_2 uptake on both a unit soil and unit O.M. basis, in different soils supporting the same vegetation and the same soil with different vegetation types. It was also desired to discover whether temperature had an effect on the respiration rates, especially when comparing one soil with another.

6.251 OXYGEN ABSORPTION AT DIFFERENT TEMPERATURES

Method

Five g samples of soil from Hanmer, Balmoral and Tasman Forests and Lincoln College were treated as described in Section 6.22. Distilled water was added to bring the soil moisture to 60% W.H.C. Temperature was changed throughout the incubation period as follows :

Days	Temperature
1- 8	23.4° C
9-16	13.6°
17	23.4°
18-20	25.4°
21	23.4°
22-23	27.4°
24	23.4°

KOH was changed at seven-day intervals during the experiment.

This experiment was analysed in separate parts so that readily apparent causes of variation were removed to allow minor sources of variation to be studied.

DISCUSSION

6.2511 METHODS

Changes in O_2 absorption rates during the day

The figures for the change in O_2 absorption throughout the day (= repsday) are presented in Fig. 6.2.6. All components of the histograms are taken from those analyses of variance tables which showed the repsday factor to be significant. (Appendix 6.2A). All three analyses show different trends. In the analysis comparing 27° C with 23° C (Appendix 6.2B) and analysis of the equilibrium phase at 23.4° C (Appendix 6.2C) low values are found early in the day while in the analysis of overall O_2 rate at 23.4° C

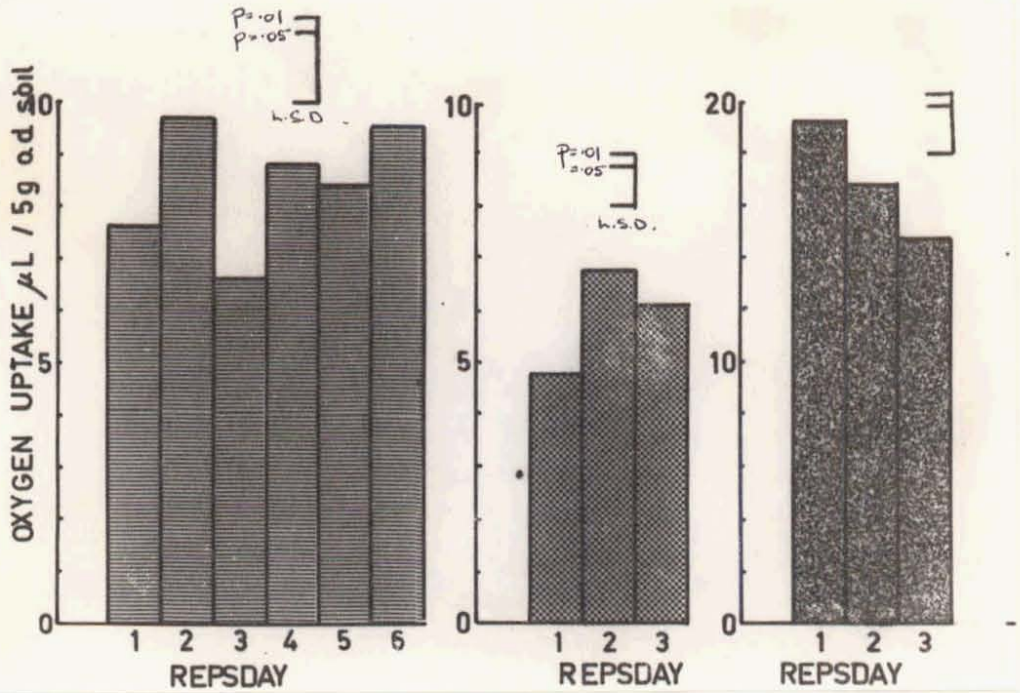


Fig.6.2.6

Change in oxygen absorption throughout the day in different experiments using the Warburg apparatus. Soil samples were exposed to the atmosphere during the night and readings were taken at intervals during the day.

(Appendix 6.2D) values declined throughout the day.

It was originally postulated that declining oxygen concentrations throughout the day would cause some pattern. Since no pattern was evident, although this factor in particular experiments was significant, it is likely that some more complex controls were in operation.

6.2512 OXYGEN ABSORPTION AT 13.6° C.

Analysis of the variation is presented in Appendix 6.2E, but the main features are reproduced in Fig. 6.2.7.

Effects of time after commencement of incubation at 13.6° C.

Data from days nine, 10, 14 and 15 were used in this analysis. Day nine was the first day that the temperature was lowered to 13.6° C, as explained in section on methods (6.251). All days were either significantly or nearly significantly different from each other. The histogram in Fig. 6.2.7 is bimodal. Since soils had been previously incubated for eight days at 23.4° C the micro-organisms may have become adapted to the reduced temperature and been responsible for the increased rate between the first and second day.

The low value on the 14th day is harder to explain. Perhaps the micro-organisms responsible for O_2 absorption at 23.4° C kept the O_2 absorption rates high until they were

Fig.6.2.7 Oxygen uptake at 13.6° C from soil samples from Lincoln College, Hanmer, Balmoral, under L.scoparium in Tasman Forest and under mature and young P.radiata in Tasman Forest. Replication was measured using a Warburg apparatus after soils had been previously incubated for eight days.

Fig.6.2.8 Oxygen uptake at 23.4° C in soil samples from Lincoln College, Hanmer, Balmoral, under L.scoparium, mature and young P.radiata in Tasman Forest. Mean of four days' measurement.

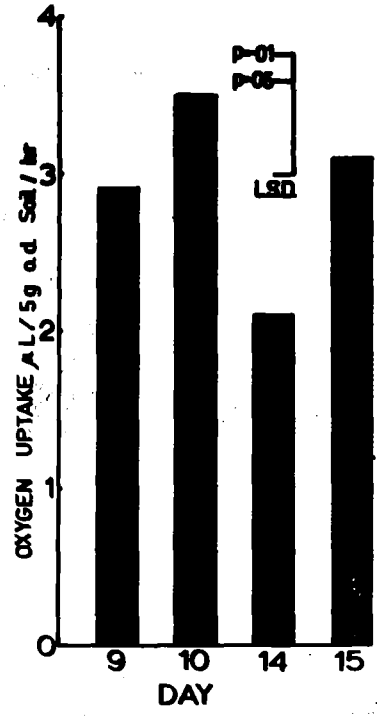


Fig.6.2.7

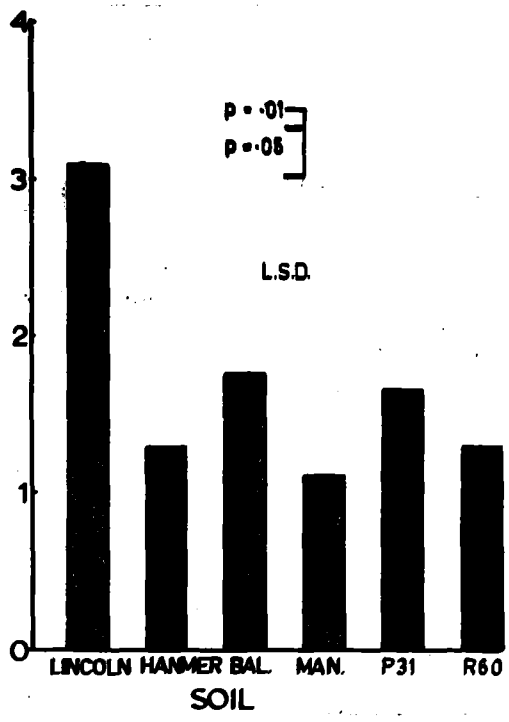


Fig.6.2.8

affected by the change in temperature to an extent which caused the decline in O_2 absorption between the 10th and 14th day. Between the 14th and 15th day micro-organisms may have changed sufficiently to allow the same rate of O_2 evolution as occurred at 23.4° C, but were better able to survive at 13.6° C.

6.2513 OXYGEN ABSORPTION IN SOIL INCUBATED AT 23.4° C.

The general results of this experiment are presented in Fig. 6.2.8. Data used in the analysis were taken from the period from day one to day 24 on days when incubation was carried out at 23.4° C. (Appendix 6.2D).

Effect of Soil Type

All soils differed significantly. (Fig. 6.2.8). Averaged over 24 days Lincoln College soil absorbed approximately twice as much O_2 as the other soils tested. The difference between Hanmer and Lincoln soils is in contrast to the more rapid rate of breakdown of root-wood blocks in Hanmer soils. Wood decomposition rate, therefore, seems to be controlled by factors different from those controlling general O_2 absorption. Hanmer soil absorbed less O_2 than Balmoral soil but it must be remembered that the stones, which comprised approximately half of Balmoral soil, were removed before this soil was weighed into Warburg flasks. Because of the high % of stones the amount of O_2 absorbed per unit surface area of ground in the original forest would

have been approximately half the value reported here. It seems that soil from Tasman Forest supporting P. radiata has a higher metabolic rate than soil from under L. scoparium in Tasman Forest. The soil sample from under L. scoparium was collected from a ridge site whereas the other Tasman Forest soils were a composite of ridge and gully soils. This would help to explain some of the differences. Soil from under mature P. radiata (P31) had a higher O_2 absorption rate than soil from (R60) regeneration. This could probably be accounted for by the presence of more litter on the soil surface under mature trees in comparison with that found under nine year old regeneration.

If the nitrogen content of the three previously mentioned Tasman Forest soils is approximately equal then the soils with the highest O_2 absorption rate may have the greatest nutrient immobilization. Since soil under L. scoparium has the lowest rate of O_2 absorption it may possess more available nitrogen for the pine trees established on recently cleared manuka soil in contrast to that on clear felled areas with a previous P. radiata crop. Again if O_2 absorption rates are a general indication of the overall fertility of the soil then the soil from Hanmer and Balmoral are similar to soils from Tasman Forest but are far less fertile than soil from Lincoln College.

Effect of Time

Fig.6.2.11 shows the classic build up in rate of O_2 absorption on the second day after rewetting and then a decline continuing until the 21st day (Birch, 1959). All days differed significantly. Chase and Gray (1957) applied the ideas of Miller et al. (1936), Corbet (1931 and 1934) and Lemmermann and Weissman (1924). They regressed log rate of O_2 uptake with log time to measure the constants of the equation

$$\log r = \log F' - m' \log t$$

where log F' and m' are constants.

Corbet (1934) proposed that m (gradient) should be considered a laboratory constant since it depends more on laboratory conditions than soil characteristics. F is a fertility constant which is dependent on the carbon content of the soil at the beginning of the experiment and other related factors.

The data obtained in this study was analysed on an IBM 1130 computer and the resulting equations are presented in Fig. 6.2.10 and Appendix 6.2A. Results from this study tend to support the work of Chase and Gray (1957) in that the equations for different soils obtained in this study have a similar gradient, especially when the first day is omitted from the analysis. The poor fit of Hanmer soil when day one was included in the analysis was due to a low figure obtained on that day. When this was removed the equation became similar to other soils.

Corbet's (1931 and 1934) proposal, supported by Chase

Fig.6.2.10a Regression of log rate of O_2 uptake from soil samples versus log time of incubation after rewetting of the air dry sample.

Soil was collected from :

L = Lincoln College
P31 = Mature P.radiata in Tasman Forest
R60 = Regeneration in P.radiata in Tasman forest
M = L.scoparium in Tasman Forest
B = Balmore State Forest
H = Hanmer State Forest
Total = Average of above soils.

Fig.6.2.10b Same as Fig.6.2.10a except that results obtained on day one were omitted from this analysis.

Fig.6.2.11 Oxygen uptake in soil samples over a period of 24 days measured with a Warburg apparatus. The values in Fig.6.2.11 were obtained when the soil sample was held at 23.4° C but at intervals between these readings the incubation temperature was changed to 13.6° C, 25.4° C and 27.4° C.

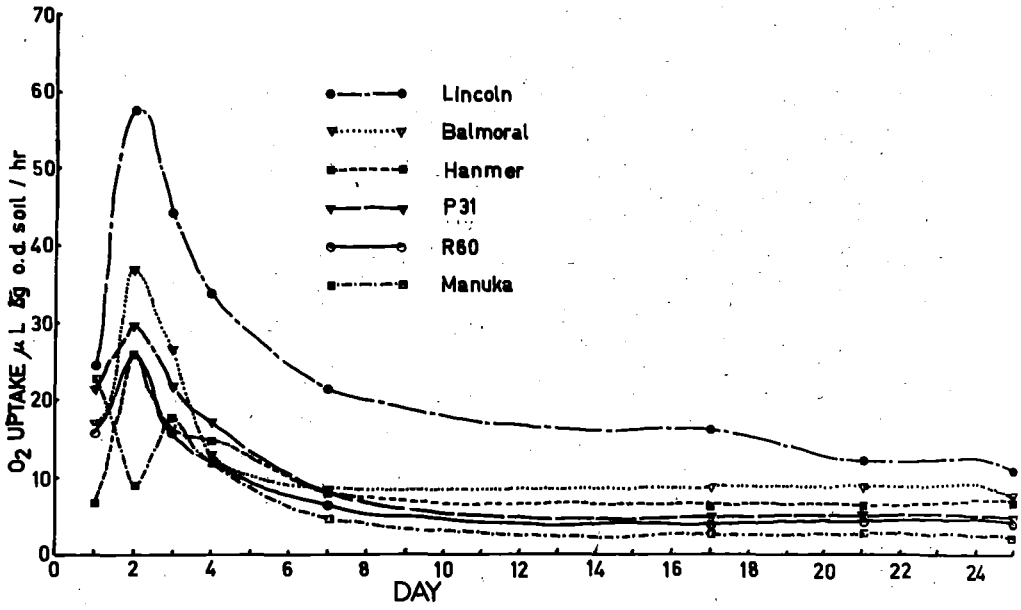


Fig.6.2.11

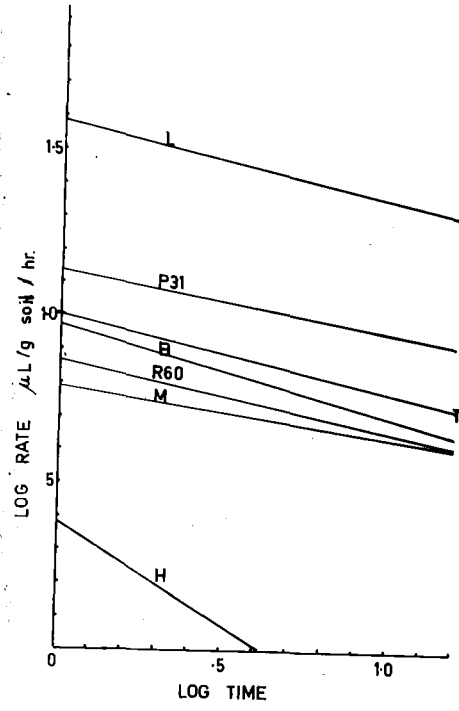


Fig.6.2.10a

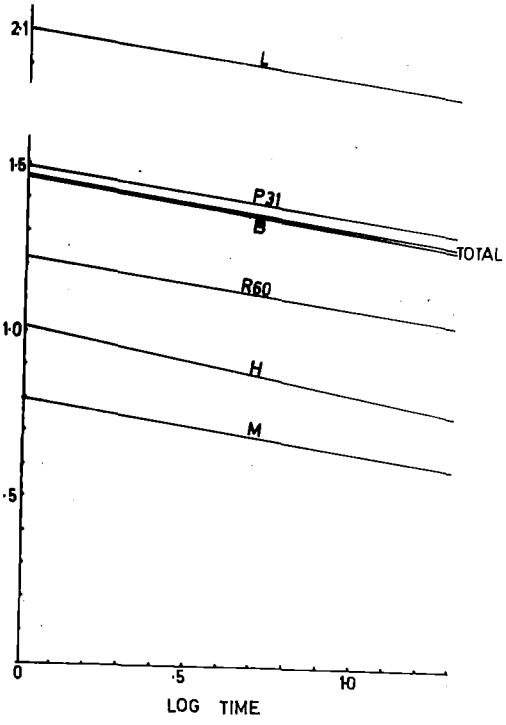


Fig.6.2.10b

and Gray (1957) that the gradients should be considered a laboratory constant since the gradient depended more on the laboratory (i.e. immediate environmental conditions) rather than soil characteristics is supported by Fig. 6.2.10. Since, in this study, the gradients were approximately equal to those obtained by Chase and Gray (1957) this particular slope may be a universal feature of all unamended soils rather than a characteristic of the laboratory conditions of incubation.

Effect of Soil x Day Interaction

Fig.6.2.13 shows differences between rates of O_2 evolution between the first and second days after rewetting to be the major cause of the soil x day interaction. Manuka soil shows an unusually high rate on the first day in comparison with other soils. Since both replications showed that, it is probably a real effect. If this particular soil had possessed a greater number of micro-organisms relative to the equilibrium number of organisms it would then have been able to absorb O_2 rapidly after rewetting. The decline in O_2 uptake on the second day, however, does not add support to this theory. The presence of a readily available substrate, such as glucose, which was exhausted rapidly may explain the results. Even glucose requires an incubation time of one to two days before maximum utilization is achieved, and the substance would have to be more readily available than glucose.

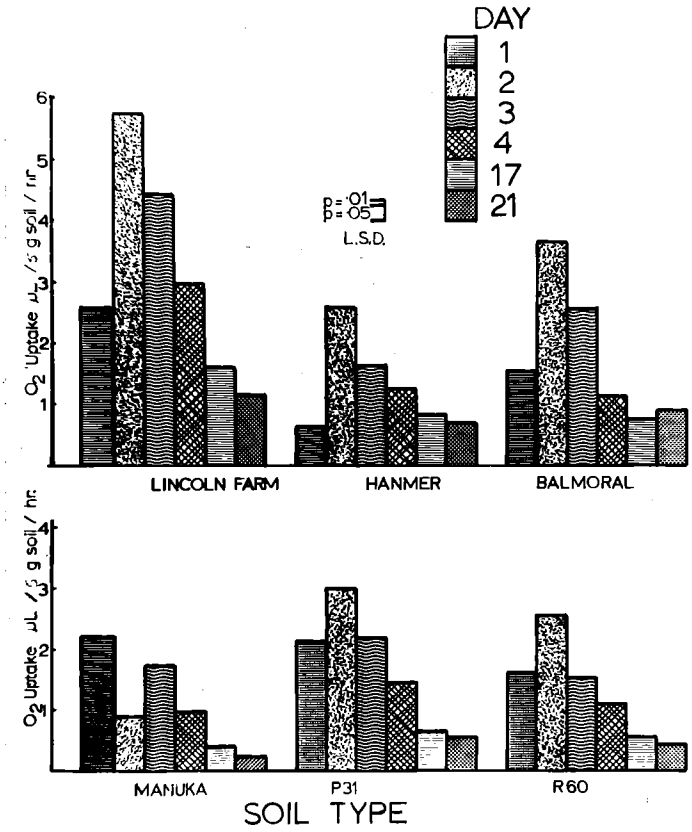


Fig.6.2.13

Oxygen uptake, measured in a Warburg apparatus of soil samples incubated at 23.4° C at intervals during a period of 24 hours.

The possibility that the uptake was non-biological is probably the best explanation considering the rapid nature of the response. However, it is difficult to further explain this except to point out that phenolic compounds sometimes absorb oxygen under alkaline conditions (Gaarder, 1957) or cell free enzymes may have caused a rapid O_2 absorption until the supply was exhausted (Drobnik, 1960).

In all soil samples except Lincoln soils there is no significant difference between the 17th and 24th day. The other soils had probably come to equilibrium whereas Lincoln soil had not. On the other hand, the method may not have been sensitive enough to show small declines in non-Lincoln soils, as from Fig. 6.2.11 it would appear that an equilibrium had been established.

In general, Tasman Forest soil samples have a smaller first to second day O_2 uptake rate than other soils. This suggests that in the dry state Tasman Forest soils retain a greater percentage of their optimum number of micro-organisms than other soils. The annual rainfall distribution for the three forest areas is presented in Table 4.2.1, Section 4.2. This table shows that the distribution of rainfall in Tasman Forest is less evenly distributed than in Balmoral and Hanmer Forests, although the overall rate is higher in Tasman than in Balmoral. This fluctuation in moistures may help to explain the greater stability in air dry soils of micro-organism numbers in Tasman Forest soil because the micro-organisms would be better adapted to fluctuations in water supply.

6.2514 RATE OF OXYGEN ABSORPTION IN HANMER, BALMORAL, AND TASMAN FOREST SOIL SAMPLES AFTER EQUILIBRIUM HAD BEEN ESTABLISHED.

Introduction

The analysis of this part of the experiment was designed to test whether the soils from different places and under different types of vegetation were significantly different from each other once the initial burst of activity had ceased and near equilibrium conditions had been established (day seven to day 25) (Fig. 6.2.11). The details of the analysis of variance of this section of the experiment are presented in Appendix 6.2F while significant factors have been graphed in Fig. 6.2.12.

Soil

All soils were significantly (p 0.05) or nearly significantly different from each other. Oxygen uptake in soil samples taken under L. scoparium in Tasman Forest was half as rapid as the rate displayed by soil from under mature P. radiata (P31) trees.

Soil under seven year old regeneration (R60) showed less O_2 uptake than soil from under mature P. radiata (P31). The soil surface under mature P. radiata has greater amounts of litter on the surface which were incorporated into the sample. Litter was incorporated so that the amount of O.M. in the final sample would approximate field conditions and the results could be expressed per unit ground surface. Soil under seven year regeneration on the other hand does not

possess this more readily available material in such great amounts. The absence of this litter may be responsible for the difference rather than any difference in the soil itself.

Balmoral soil showed an unexpectedly high value when compared with Hanmer soil but it must be remembered that Balmoral soil contains approximately 50% of its volume in stones and the actual rate per unit surface area would be more equivalent to that found in L.ssoparium soils.

Day

Fig. 6.2.13 shows that equilibrium was not attained by the seventh day. Since there was no significant Soil x Day interaction this did not affect the analysis and the effect of the soil factor.

Soil x Replication (Appendix 6.2G)

Although this interaction is significant it does not affect the significance of the soil factor.

Repsday x Day (Appendix 6.2H)

The first reading for days seven, 17 and 21 was lower than the two subsequent readings taken on that particular day. On the 25th day the first reading was higher than the second. There were also inversions on the 17th and 27th days as compared with the seventh and 25th day, with respect to the second and third readings for the day. The variation shows no regular pattern and probably has little, if any, biological significance.

6.2515 OXYGEN ABSORPTION AT DIFFERENT TEMPERATURES AFTER SOILS HAD COME TO EQUILIBRIUM

RESULTS AND DISCUSSION

Oxygen uptake rates recorded from different soils at various temperatures were taken from the analysis of variance tables in Appendices 6.2E, 6.2B, 6.2I, and recorded in Fig. 6.2.14.

In Fig. 6.2.14 the results of rates of O_2 uptake in soil samples from Tasman (R60, P31, manuka), Hanmer, and Balmoral Forests and Lincoln College farm at 13.6° C, 23.4° C, 25.4° C and 27.4° C are set out. Only values of O_2 uptake recorded after the ninth day were used in Fig. 6.2.14.

A large difference in the ratio of O_2 uptake between 13.6° C and the other temperatures exists in soil samples from Tasman Forest in comparison with the soils from Hanmer, Balmoral and Lincoln. In Tasman Forest soil samples the greatest difference occurs between 25.4° C and 27.4° C. Both sets of soils, therefore, show a marked increase in O_2 absorption at a particular temperature, but the Hanmer, Balmoral and Lincoln soils differ in showing this response at a lower temperature than Tasman Forest soils. This may be related to the mean annual temperature of the region where the soil samples were collected, because the Tasman Forest area has a mean temperature of 12.5° C, whereas Hanmer-Balmoral-Lincoln region has a mean temperature of 10.6° C. The reason for this marked response at a temperature not

Fig.6.2.12a Oxygen uptake at 23.4° C in soil samples from Hanmer, Balmoral and Tasman Forests after six days' pre-incubation at 23.4° C.

Fig.6.2.12b Change in oxygen uptake with time in soil samples obtained from Hanmer, Balmoral and Tasman Forests. Samples were incubated for six days at 23.4° C before readings were taken.

Fig.6.2.14 Rate of oxygen uptake from Tasman, Balmoral and Hanmer Forests and Lincoln College Dairy Farm soil samples held at different temperatures in the Warburg apparatus.

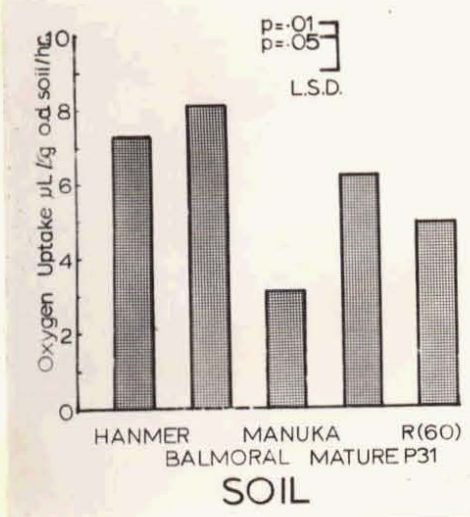


Fig.6.2.12a

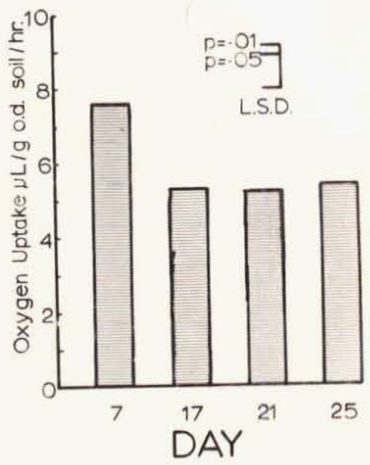


Fig.6.2.12b

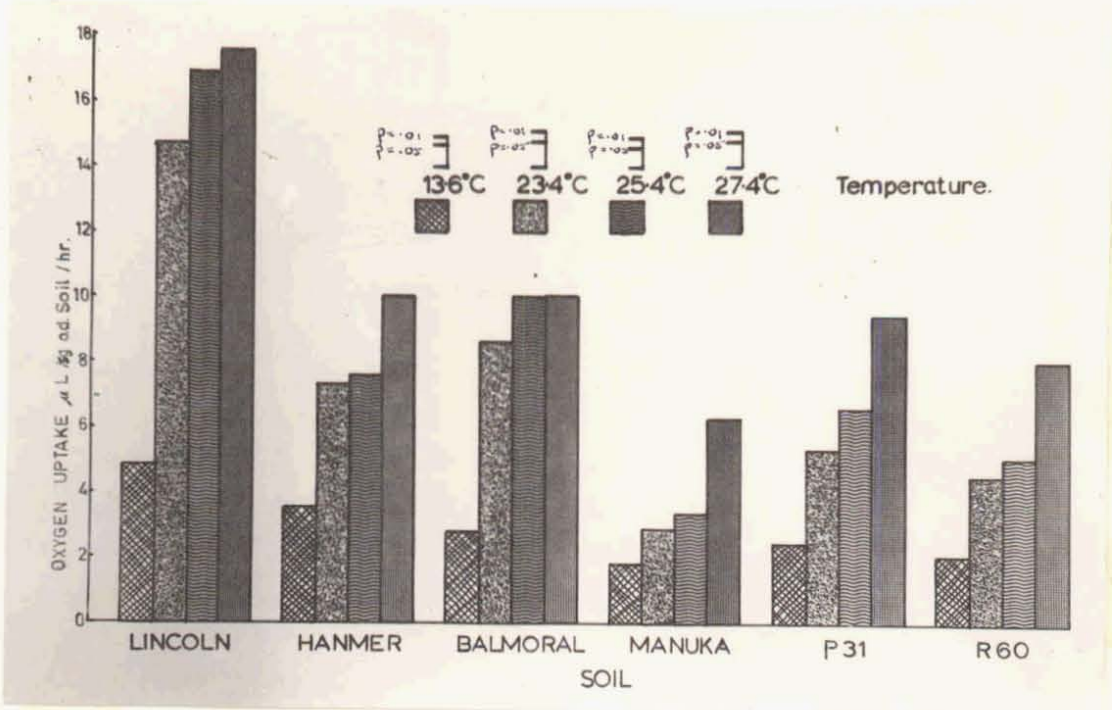


Fig.6.2.14

often experienced in the field may be non-biological or it may be associated with a change in the micro-organisms where a more thermophilic microflora utilize O_2 to a greater extent.

In Tasman Forest soil there was also a greater difference between O_2 absorption at 13.6° C compared with 23.4° C in soil planted with P. radiata than with soil under L. scoparium, which showed very little difference between the two temperatures. This is more likely to be due to a difference in microfloras than a climatic factor as all sites were within a half-mile of each other.

6.31 ROOT WOOD DECAY WITH ADDED MINERAL NUTRIENTS

The effect of various nutrients on the rate of decay of 1-inch cubes of root wood buried in soil, collected from Tasman Forest, was studied under laboratory conditions. This experiment was designed to see if any of the nutrients which were tested were limiting for the growth of micro-organisms involved in the decomposition of root wood. Nitrogen, phosphorus and boron were considered to be the elements most likely limiting and were therefore added individually; other elements were added as a group.

METHOD

The root wood blocks were obtained from a recently clear felled area in Tasman Forest by digging and chopping out large sections of root wood which were milled into small planks and further cut into cubes. This method resulted in some differences in composition of individual blocks because they were obtained from different regions of the root.

Soil from an R60 area in Tasman Forest was finely ground and 489 g oven dry weight of soil were placed into jars 17-cm tall by 9-cm diameter. Soil samples were treated with all combinations of additives (H. Horn, pers. comm.) as listed in Table 6.3.1.

All treatments except sawdust were added in solution to the soil. One, previously weighed, root wood block was

added to each jar and the soils were brought to 60% W.H.C. In order to achieve maximum nitrogen mineralisation by the "wetting-drying" effect (Birch, 1958) and achieve more natural conditions soils were periodically allowed to become dry. Duplicate jars containing soils from Hanmer Forest and Lincoln College Dairy Farm were added as controls. These soils received no amendments.

Root wood blocks were harvested and dried for two days at 70° C under vacuum. Drying before the root wood blocks were placed in the soil was carried out in the same manner. Control blocks showed that the difference between the results from the two drying treatments differed by 2%.

Table 6.3.1 Treatments added factorially to 1-inch root wood cubes in 489 g soil.

1.	$(NH_4)_2SO_4$	0.28460 g/jar
2.	Na_2BO_3	0.02500 "
3.	KH_2PO_4	0.08040 "
4.	*P.radiata* sawdust	25.25000 "
5.	Minor elements	
	KCl	0.14230 "
	$CaCl_2$	0.14230 "
	$MgSO_4$	0.01250 "
	$FeSO_4$	0.01250 "
	$MnCl_2$	0.01250 "
	$CuSO_4$	0.00130 "
	$ZnSO_4$	0.00130 "
	$Na\ MoO_3$	0.00005 "
	$Na\ C\ O_3$	0.00005 "
6.	Control	0.00000 "

RESULTS AND DISCUSSION

The analysis of variance of results is presented in Table 6.3.2. Only the addition of sawdust and minor elements significantly decreased the amount of decomposition of root wood cubes. Three of the interactions were significant.

The nitrogen x sawdust interaction (Table 6.3.3) shows that nitrogen by itself suppressed the rate of breakdown of root wood. This was also shown by the negative effect of the nitrogen treatment. The addition of sawdust had an even greater effect in suppressing the rate of decomposition. When both nitrogen and sawdust were present the decomposition rate was more rapid than with sawdust alone. This means that the sawdust caused a nitrogen deficiency which was partly reduced by the added nitrogen. A similar phenomenon was noted by Lu and Bollen (1957). Carbon dioxide evolution from a soil containing 2000 ppm carbon in the form of ground up residues, including Pinus sp. wood, was less with added NH_4NO_3 than without. These authors could provide no adequate explanation and felt that the small pH changes of less than one unit were insufficient to explain the depression.

When the residues were incubated in bulk they lost weight more rapidly if nitrogen was added. This suggests that the supply of nitrogen from the soil was adequate and any excess caused a reduced rate of decay. On the other hand, in the absence of soil the supply of nitrogen was limiting for decomposition.

Table 6.3.2 Analysis of variance of results of root wood decay. Second order and high-order interactions used as error in the 2^5 factorial design.

Interactions analysed in Table 6.3.3

	Main Effects	S.S.
N	-55.299	
P	68.699	
C	-155.699 **	
B	52.300	
T	-199.499 **	
NP	-40.300	
NC	132.500 **	
NB	-7.500	
NT	51.099	
PC	-97.899 *	
PB	-47.099	
PT	-81.299	
CB	-10.300	
CT	154.700 **	
BT	14.100	
Error		
Total		9260.0

N = Nitrogen
P = Phosphorus
C = Sawdust
B = Boron
T = Minor elements

Table 6.3.3 Analysis of first order interactions from analysis of variance of root wood decay.

	No Sawdust	Sawdust
No Nitrogen	690.8	114.4
Nitrogen	315.2	268.8

	No Minor Elements	Minor Elements
No Sawdust	857.2	148.8
Sawdust	236.4	146.8

	No Sawdust	Sawdust
No Phosphorus	336.4	220.8
Phosphorus	669.6	162.4

The interaction sawdust x minor elements (Table 6.3.3) showed that sawdust markedly reduced the rate of decomposition of root wood blocks. The presence of minor elements alone even further reduced the rate so that when both treatments were added the effect produced was no greater than that caused by the minor elements alone. There are two possible explanations which may help to explain the results. Firstly, some element or elements in the minor element group were toxic to the micro-organisms which were responsible for the decomposition of the root cubes. Since some of the elements present in the minor element treatment were used in other treatments several possibilities can be elminated. Those likely to be responsible include :

Ca, Cl, Mg, Fe, Mn, Cu, Zn, Mo and V.

The second possibility is that the addition of these elements had caused an imbalance of nutrients and this, in turn, impaired the uptake of nitrogen, phosphorus or some other element by the micro-organisms.

The sawdust x phosphorus interaction is shown in Table 6.3.3. Phosphorus by itself markedly increased the decomposition rate of the root wood blocks. Sawdust, on the other hand, decreased the rate. When both sawdust and phosphorus were added together the rate declined even further than with sawdust alone. It is possible that the addition of phosphorus accentuated the deficiency of some other element. Adams (1969, pers. comm.) found that phosphorus levels in needles possessed a high correlation with tree

growth. This suggests that phosphorus may be limiting for both tree growth and the rate of decomposition of root wood.

The non-significant phosphorus x minor element interaction showed the same trend as the sawdust x minor element interaction except that phosphorus by itself stimulated decomposition rather than depressed it, as was the case with the sawdust treatment. This suggests that the minor elements produced some toxic effect and the effect was not due to an imbalance of nutrients. From a practical point of view several suggestions can be made from the results of this experiment, but more small trials would be needed before large scale trials would be warranted. If the decomposition of residues causes an immobilization of nutrients at any stage during the growth of the second regeneration trees then a reduction in the rate of decomposition would cause less immobilization of nutrients. The application of NH_4-N should reduce the rate of decay of woody residues and, at the same time, provide nitrogen for tree growth unless the rate of decomposition of the residues is initially rapid enough to create a shortage of nitrogen which would, in turn, cause nitrogen to be immobilized. On the other hand, the application of the minor elements may retard decomposition. Experiments would need to be conducted to determine which element or elements were responsible for the reduction in the decomposition rate. Rates of application and the time the element persisted in the field after application would need to be determined.

The application of phosphorus should stimulate decomposition provided the initial rate of decomposition was sufficiently low, otherwise the addition of phosphorus would cause a decline in the decomposition rate.

The possible toxic effects of one of the elements listed previously suggests caution with the application of large amounts of copper when spraying for Dothiostroma pini (Gilmour, 1967). If this element is responsible for the reduced rate of decomposition then forests sprayed with copper may experience a large build up of residues.

Wood blocks in soil collected from Hanmer State Forest lost 73% of their original weight while those in soil from Lincoln College Dairy Farm lost 30%. Lincoln soil possesses more organic matter and therefore probably more nitrogen than Hanmer soil. The results can therefore be explained if it is postulated that Hanmer soil possesses a fungal flora better adapted to wood decomposition.

6.32 STUDIES ON NEEDLE DECOMPOSITION WITH FUNGI ISOLATED FROM NEEDLES COLLECTED IN TASMAN FOREST

INTRODUCTION

In order to study the rate at which those fungi which had been most frequently isolated from P.radiata needles collected from Tasman Forest caused decomposition of needles, a factorial experiment was set up in which eight species of fungi were inoculated on to sterilized pine needles. The factorial design of the experiment also made it possible to determine whether or not there were any antagonisms between the isolates and also to determine whether the presence of more than one species affected the ability of individual fungi to decompose the pine needles under laboratory conditions.

Patterns of colonization of fungi (see Section 10.1) on recently dead tissue have been more intensively studied than the factors likely to be responsible for these patterns. The ability of a species to reduce the growth rate of another fungus by the production of some substance or detrimental environmental condition will determine the pattern of colonization at least in part. Other workers have studied factors which also determine the patterns of colonization. For example, spore survival has been studied by Hogg (1966). Yadav and Madelin (1968), Macauley and Thrower (1966) and Hogg (1966) have studied in pure culture the ability of fungi to use substances extracted from living material. Knowledge that a particular species can utilize a certain compound in

pure culture is suggestive of its role in decomposing biological material under natural conditions. A better way of determining what compounds a particular species is able to attack is to inoculate the fungus into sterile biological material and analyse the material after it has been decomposed (Hering, 1967; and Yung Chang, 1967).

Only Saito (1958 and 1960) has studied antagonisms between different groups of fungi. In this study an attempt was made to see if the same antagonisms occurred between related species.

METHOD

Green needles were collected from P.radiata trees growing on Temuka silt loam one mile north of Lincoln College as material from Tasman Forest was not available at this time. The needles were removed from the branches and thoroughly mixed.

Five g of fresh whole needles were weighed to the nearest 0.01 g and placed in 15 x 2.5 cm boiling tubes together with 10 ml of distilled water. The tubes were plugged with cottonwool. Sterilization was effected by placing the tubes in an anaerobic jar and applying a partial vacuum. Ethylene oxide liquid was poured into a funnel connected to the apparatus and sucked into the jar, where it vaporised immediately, by momentarily opening the valve.

The tubes were left in the jars for two days before removal for airing. The contents of four tubes were oven

dried at 102 $\pm$ 2° C for 24 hours, cooled in a desiccator and weighed.

Fungi were obtained from needles collected in Tasman Forest and were the most common species isolated in Section 10.1.

To prepare inocula for the tubes needles were cut into 1-cm lengths placed in 4-Oz jars plugged with cottonwool to which 10 ml of water had been added and sterilized by autoclaving at 121° C for 20 minutes. Each of the eight jars were inoculated with one of eight fungi used in the experiment and jars were incubated at 25° C for 10 days to allow the fungus to infect all pieces of needle.

Needles in the boiling tube were inoculated by transferring single one cm piece of previously inoculated needle. The experiment was designed as a quarter replicate of a 2^8 factorial design (Cochran and Cox, 1950). Defining contrasts used were ABCEG, ABDFH and CDEFGH. This allowed all two factor interactions to be estimated. In cases where the boiling tubes were not inoculated with a total of eight fungi 1-cm pieces of sterile autoclaved needle tissue were added to make the amount of needle tissue in each tube equal.

Each boiling tube, together with an 8-dram vial containing 1 $\pm$ 0.2 g BaO_2 and 5-ml water, was placed in screw capped glass jars 6 cm diameter x 15 cm tall. The jars were incubated at 24 $\pm$ 1° C.

To test whether or not a tightly compact cotton wool bung would restrict the rate of gaseous exchange between the

contents of the boiling tubes and the atmosphere more than a loosely compacted bung, a test using H_2S was set up. Hydrogen sulphide was generated in a closed system containing boiling tubes complete with loose and compacted bungs. The time taken for the H_2S to diffuse into the boiling tube was estimated by a change in colour of lead acetate paper inside the boiling tube. Differences between the rate of di ffusion of the H_2S through the two types of cotton wool bungs were not significant, so a tightly compacted bung was used in the experiment.

Names of the fungi identified are set out in Table 6.3.5 and abbreviations are used in the text.

RESULTS AND DISCUSSION

Analysis of variance was carried out using the method of Yates (Cochram and Cox, 1950). All first order interactions were determined. Second and higher order interactions were used as error. Only one fungus caused a significantly different loss of weight (Appendix 6.3A) while three first order interactions were significant; two at the 1% level. The interaction tables are presented in Table 6.3.4.

The interaction BPF x Fus shows that when fungus BPF and Fus are added alone there was a stimulation of breakdown of needles. Where fungi BPF and Fus were grown together inhibition occurred. This could possibly be explained by

G	=	Sterile mycelium
P	=	Pestalotia congena
BP	=	Sterile mycelium
BPF	=	Sterile mycelium from bark.
Tr	=	Trichoderma viride
Fus	=	Fusarium sp.
R	=	Piricauda sp.

Fig.6.3.5 Fungi isolated from needles collected in Tasman Forest.

Table 6.3.4 Analysis of interaction from analysis of variance presented in Appendix 6.3A.

	No Fus	Fus
No BPF	25.12	28.16
BPF	28.60	24.92

Analysis of interaction of fungus BPF and fungus Fus.

	No Tr	Tr
No R	24.56	29.00
R	28.48	24.76

Analysis of interaction of fungus R and fungus Tr.

	No Fus	Fus
No P	24.24	26.44
P	29.48	26.64

postulating the production of mutually antagonistic substances by both species.

A similar situation existed in the case of the interaction R x Tr. Tr is a well known antagonist but in this case both R and Tr seem to be antagonistic.

The third interaction was a little different. Fungus P by itself caused more decay than Fus by itself, but the two fungi together caused a slightly greater rate than fungus Fus by itself. It would appear from this that fungus Fus has had an antagonistic effect on the ability of fungus P to break down needles. Thus the fungus P has a significant effect only in the absence of fungus Fus.

CHAPTER 7

ENERGY DISSIPATION UNDER FIELD CONDITIONS

INTRODUCTION

The rate of carbon mineralisation in the field is governed by the ease with which individual carbon compounds can be mineralised and the availability of other essential nutrients, for example, nitrogen for the mineralising flora. The chemical composition of the compounds being decomposed will influence the rate at which these minerals are made available to the flora. Any changes increasing the rate of decomposition, such as the addition of readily available energy sources, will allow increase in population and as a consequence a depletion of available mineral nutrients. The length of time of this depletion will depend on the chemical composition of the materials undergoing decomposition.

In order to gain an understanding of the reasons for a mineral nutrient shortage it is important to know the rate and magnitude of change of energy dissipation or carbon mineralisation after clear felling, and the chemical

composition of the most available energy sources. To elucidate these points the decomposition of a major component of slash leaf litter has been studied on several sites.

7.1 LEAF LITTER

REVIEW OF LITERATURE

Methods

Methods devised for measuring energy dissipation from decaying biological material have usually involved finding the weight loss of a certain amount of the material over a period of time. Weight loss is composed of two elements. Firstly, weight loss due to mineralisation of various elements and, secondly, weight loss due to movement of compounds or materials not fully mineralised away from the material being studied. One way to measure the mineralisation without loss due to transport of unmineralised substances is to measure the mineralisation products. For example, Witkamp (1966c) found that during the first year of litter decay about 40% of the weight loss appeared to be independent of microbial activity and only 16 - 30% of the substrate loss was recovered as CO_2. These data suggested a considerable transport to deeper layers of soluble leaf material and physical and chemical breakdown.

Before the rate of breakdown can be calculated two variables need to be known, i.e. the amount of energy dissipated and the time taken for this dissipation. Either

an approximation to the instantaneous rate can be calculated using a method for studying CO_2 evolution, or a long term weight loss approach can be used.

If it is assumed that all deciduous leaves fall at the same time in one particular species of tree and the year of fall of each leaf can be determined, the rate of energy dissipation can be calculated by sampling at litter fall, and re-sampling after an interval of time (Lunt, 1933; and Remezov, 1961). Leaves identified at a particular time and later re-sampled can be also used to study weight loss. Identification can be accomplished either by placing the leaves in a container (Mikola, 1960; Bocock et al. 1961; and Shanks and Olson, 1961) or tagging individual leaves (Hayes, 1965). If the weights of the litter layers, provided litter layers are present, and the annual litter fall is known, the amount of decomposition can be calculated (Jenny, Gessel and Bingham, 1949; Olson, 1963, and Kendrick, 1959). Each method is an approximation and the most accurate method represents a compromise between the conditions prevailing and the nature of the information required.

Container Method. The rigid containers used by Falconer et al. (1933), Gustopon (1943) and Lunt (1935) do not allow litter in them to become an integral part of the general decomposing material although they protect the contents from interference by falling branches. They share disadvantages with the more flexible type of containers (nylon net, glass wool, etc.), in that, the microclimate

inside may not be comparable to that outside, especially water relations. The size of the holes presents a problem. On the one hand, the larger the holes the more the natural conditions inside the bag will be but, on the other hand, the larger the holes the more likely that observed loss in weight will be due to the loss of small undecomposed fragments. This difficulty is also found when individual leaves are marked for study, but here the environment near the decomposing leaf is completely natural. Aperture size also may restrict the entrance of some larger anthropods and annelids and a compromise must be reached. However, the restrictions can be used to advantage in some cases when the influence of a section of the decomposer population is to be studied.

Age Class Method

The method outlined by Jenny et al. (1949) is useful in situations where increasing age of litter is related to increasing depth within the litter layer. This method has the disadvantage of requiring an accurate measurement of the amount of litter fall per unit time. Even though Bray and Gorham (1964) have reported a constant litter fall in a closed canopy over a period of years, there is some evidence for annual variation (Alway and Zon, 1930).

Rate of Breakdown

The original concept of Justus Liebig (1840) that "the essential material available in amounts most closely approaching the critical minimum will tend to be the limiting one", with the addition of other ideas, expands into the

general hypothesis of limiting factors. This concept can be readily applied to factors affecting the rate of decay of plant material and the decay limiting factors reported by various workers are probably an expression of this principle. At any one time there is at least one biotic environmental or other factor acting to restrict the greater activity of some or all members of microbial population. The factor responsible may change as others are varied.

Some of the more common factors likely to have an effect on the decomposition of organic material include :

1 a) Climate (temperature, moisture, etc.)

1 b) Forest cover (which itself may influence other factors)

1 c) Stage of decay of leaves

1 d) Species of plant which produced the leaves

1 e) Variations within the leaves themselves

2 a) Differences due to the many methods used by various workers.

Handley (1954) considers that climate is the major influence in litter breakdown. In nature it is difficult to compare the effects of one climatic factor with another because it is usually not possible to find sites where all other variables are constant. Mikola (1960) studied pine and spruce stands in southern and northern Finland and found that mean temperature was the most important factor affecting the rate of decomposition. The rate of litter decomposition increased proportionately to the mean summer temperature.

At 1 year from	27.3 to	34.6%)	rise in summer from
2 years	41.3	52.6%)	8.5° to 13.5° C.
3 years	43.3	48.0%)	

Temperature was found to be dominant over moisture in the climate of East Tennessee where inside litter bags moisture rarely became the limiting factor. Witkamp (1963c) found, by factor analysis, that temperature was 64% responsible for limiting the rate of decomposition moisture 5%, bacterial numbers 16% and was litter age 5% responsible.

The decomposition of Nothofagus sp. leaves in New Zealand was studied by Dutch (1965) who found that after three years loss of weight was greater in wetter sites. He found, with fresh leaves, that the greatest activity occurred in the wetter months of February to August. He concluded that moisture had more effect than temperature. A laboratory study of rates of decomposition of leaves of many species was reported by Daubenmire and Frusso (1963). These authors found no significant correlation of decay in various leaves. They found, however, that the rate of decomposition of all leaves except Pseudotsuga sp. and Abies sp. leaves must have had some other limiting factor controlling their rate of decomposition.

Temperature was shown to be significant in the study of leaf litter breakdown in the Great Snowy Mountains and Oak Ridge by Shanks and Olson (1961). They found a linear decrease in the rate of breakdown of 1.33% per 1° C drop in temperature. This agreed with Mikola's (1960) rate of

change of 1.75%/° C in the first year breakdown (Y) and was related to altitude X (in thousands of feet) by the equation

$$Y = K - (\simeq 2.40\ X)$$

The factor K depended on the type of forest under which the litter was decomposing. Latter and Cragg (1967) also found that the dry weight loss of 20 - 30% per year observed in Juncus sp. material on a low level site (Allen in Latter and Cragg, 1967). Clymo (1965) recorded a 17% dry weight loss of Sphagnum sp. at Moor House, England, in one year compared with 20% from a site at a lower altitude. This example shows that a change of the factors important in decomposition is not always associated with climatic factors associated with an altitudinal change, and other factors may be the limiting ones.

Bocock (1960) found that ash leaves disappeared faster than oak leaves, and, in general, leaves decomposed faster on mull humus than mor, and Mikola (1960) reported that birch leaves decomposed faster than pine needles. Shanks and Olson (1961) found differences due to different leaf species as well as variations due to cover. Witkamp (1966c) considered that the dominant factor controlling microbial densities on litter was the species of leaf, especially when the leaves were fresh and in bulk. If the climate is constant then the type of leaf species decomposing may influence the rate of decomposition.

Weetman (1965) studied the decomposition of black spruce needles north of Baie Comeau, Quebec, and found that

decomposition was related to the degree of artificial thinning. A lower weight loss was observed in the 100% thinned stands, 4% and 17% weight loss in first and second growing seasons respectively compared with the unthinned 12% and 25% weight loss. This was apparently not due to temperature which was higher in the 100% thinned but, in all probability, to a difference in moisture. Since thinning results in many changes these differences could be attributed to many causes which only a rigorous investigation would reveal.

Differences due to variation within the leaves themselves were noted by Heath and Arnold (1966) who found that leaves grown in the sun were less decomposed both in the presence and absence of earthworms per unit time than shade grown leaves. Heath and Arnold (1966) contended that palatability of leaves to earthworms and other animals depended on the polyphenol and sugar content. The results reported by Heath and King (1964) supported this contention, in that, they found that the palatability of oak leaves increased as their polyphenol content decreased.

METHODS

The decomposition of leaf and ground litter was studied, using bags made from nylon material of mesh size 1.3 mm. In March, 1967, eight bags containing 25 g (o.d.) of needles from recently felled trees were placed on a

recently felled site containing only ground litter from the original stand. Samples were weighed in the field using a spring balance and one of these samples was brought back to the laboratory, dried at 102 ± 2° C, and weighed. Each bag was secured, using four aluminium pegs which were pushed into the soil with the top half bent over to secure each edge of the bag. Another set of eight bags was placed on one recently felled site among a dense accumulation of fresh needle litter. This latter site was approximately 50 yards further down the slope than the former.

In July, 1967, another set of 16 bags was placed on a recently felled site close to the other two sites. Two bags from this site were taken to the laboratory for analysis at approximately two-monthly intervals.

A further set of eight bags was placed at the U (R63) site in July, 1967. Each bag contained 16.75 g (0.0W) of leaf material from four-year old trees and was set out in the same manner as other bags on younger regeneration sites. This site was slightly less exposed because of tree cover than the other sites where litter bags had been set out.

The use of these bags enabled the rate of decomposition to be studied under approximately natural conditions.

RESULTS AND DISCUSSION

An outline of the results obtained are presented in Fig. 7.1.1.

Results show that there has been a similar rate of

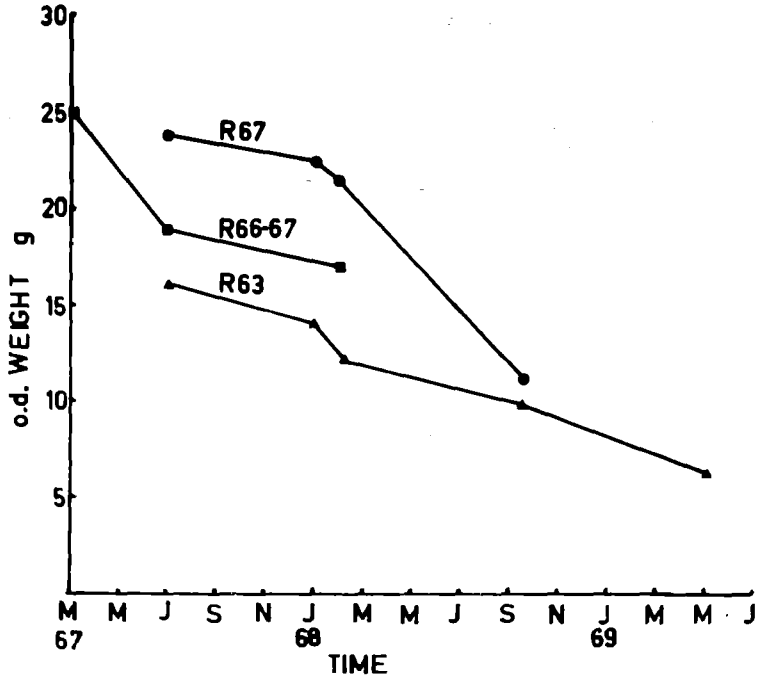


Fig.7.1.1

Loss of weight of P.radiata needles contained in nylon bags laid out on three sites. Needles used were obtained from mature P.radiata trees and R63 regeneration.

decomposition of the litter at all three sites. Thus, it may be concluded that climate and not age of the tree producing the leaves has had the greatest influence on the decomposition rate. The results in this study may give an exaggerated picture of the true rate in the field because the compaction of leaves and the presence of the nylon bag would have an influence on the moisture relations of the leaves. In summer, the soil surface dried out and the moisture retained in the closely packed needles could have produced a greater rate of decomposition than in more exposed needles. Earthworms are fairly common in Tasman Forest and the small size of the nylon net apertures may have restricted some larger animals from gaining entrance, which would cause the values obtained in the nylon bags to be less than under natural conditions. The high decomposition rate found in January-February, 1968, is surprising since, although temperatures were high, the surface of the ground was usually dry at this time. The decomposition rate of 43% year in bags on sites is comparable to the results obtained by Will (1966) working with the same species. Since the results presented by overseas workers obtained under vastly different conditions, it is difficult to make comparison but, in general, except for tropical conditions reported by Hopkins (1966) who found total leaf decomposition to be complete in about four months, rates are similar for different types.

Bocock	(1960)	100% - 50%	in 1 year in Hardwood
Bocock and Gilbert	(1957)	83% - 17%	in 6 months "
Shanks and Olson	(1961)	75% - 25%	
Weetman	(1965)	25% - 4%	in 1 growing season on conifers
Heath and Arnold		100%	oak and beech) in one year.
Mikola	(1960)	27% - 35%	in pine needle) in one year.
Mikola		32% - 54%	in beech leaf) in one year.

Conifer leaves showed approximately 25% - 45% decomposition whereas values of 100% in one year have been reported for some hardwood leaves.

7.2 DECAY OF ROOT WOOD BLOCKS UNDER FIELD CONDITIONS

INTRODUCTION

It was decided to study the rate of decomposition of root wood under field conditions together with a study on the rate of decomposition of needles (see Section 7.1). The relative rate of breakdown at various soil depths was studied to assess the activity of soil micro-organisms at these depths.

Root wood blocks were also buried at three age classes of regeneration both on ridges and in gullies. Since root wood was the major component of slash likely to cause the immobilization of mineral nutrients it was decided to see if the ridges possessed soil which would cause root wood to decay faster there than in the gullies. Visual observation of the soil suggested that the root wood would decay more rapidly in gully sites.

METHOD

One-inch cubes of wood extracted and cut in the manner prescribed in Section 6.3 were tied in a line with nylon thread. A hole was dug and the blocks were placed in the hole at 25, 10, 5 and 2.5 cm depths. Soil was replaced as close to its original position as possible. One set of root wood blocks remained in the field for 8½ months between

March, 1967, and January, 1968. A second set remained for 22 months, including two winters and two summers, from July, 1967 to May, 1969. Root wood blocks were extracted from the soil and dried at 70° C for two days in a vacuum oven. Blocks not put out in the field were used as controls in the drying process. Blocks were weighed after drying and dry matter loss was expressed as a % of the original weight.

RESULTS AND DISCUSSION

Analysis of variance of the results is presented in Appendix 7.2A.

Position (Fig. 7.2.1) was found to be highly significant even when divided by the first order interactions containing the factor position. The rate of decay on ridge sites was almost 2½ times the rate in gully sites. This difference could explain the poor growth of pine trees on ridge sites because immobilization caused by the rapid decomposition rates may cause the nutrient deficiencies. This, however, does not explain why decomposition on the ridges was faster than in gullies. The difference in rates of decomposition was probably not caused by water excesses or deficiencies because analysis of variance of water content collected on four occasions showed no difference in water content of the soil between ridge and gully sites. Adams (1969, pers. comm.) could not find any significant difference between ridge and gully sites in levels of mineral nutrients. However, available nitrogen results presented in Section 9.1

showed differences between ridge and gully sites, but the relative difference between the two positions changed from positive to negative with the age of regeneration. Probably conditions of some kind on the ridge sites favour the growth of wood rotting micro-organisms.

The effects due to factors which vary with depth (Fig. 7.2.2) were greatest at the 5 cm depth. Although it was found that moisture content was highest in the top layers of the soil the availability of nutrients may be higher at this depth than at any other. Decomposition rate at 25 cm depth was three-quarters that at five cm depth which does not appear to be very marked considering the clayey appearance of the soil at 25 cm depth.

Rates of decomposition increase with age (Fig.7.2.3) of regeneration. Conditions at R60 favoured faster decomposition rates than those at R66-67. The more even microclimate after canopy closure at R60 or the greater availability of mineral nutrients may be responsible for the differences. Soils from these various places brought together under identical environmental conditions would help elucidate this problem.

The depth x position interaction (Fig. 7.2.4) shows that the difference between ridge and gully sites increases with increasing depth. This suggests that some factor such as drainage or aeration was operative in this instance because nutrient availability probably would not change in this manner.

Fig. 7.2.1 Weight loss in root wood blocks buried on ridge and gully sites in Tasman Forest for 22 months. Blocks were buried under three ages of P.radiata at four depths.

Fig. 7.2.2 Weight loss in root wood blocks buried at four depths in soil in Tasman Forest. Blocks were buried on ridge and gully sites in stands of regeneration of three ages.

Fig. 7.2.3 Weight loss in root wood blocks buried under three ages of P.radiata regeneration in Tasman Forest.

Fig. 7.2.4 Weight loss in root wood blocks buried at four depths in the soil on both ridge and gully sites in three stands of P.radiata regeneration of different ages for 22 months.

Fig. 7.2.5 Weight loss in root wood blocks buried in ridge and gully sites under three ages of P.radiata regeneration.

Fig. 7.2.6 Weight loss in root wood blocks buried at four depths in the soil under three ages of P.radiata regeneration on both ridge and gully sites.

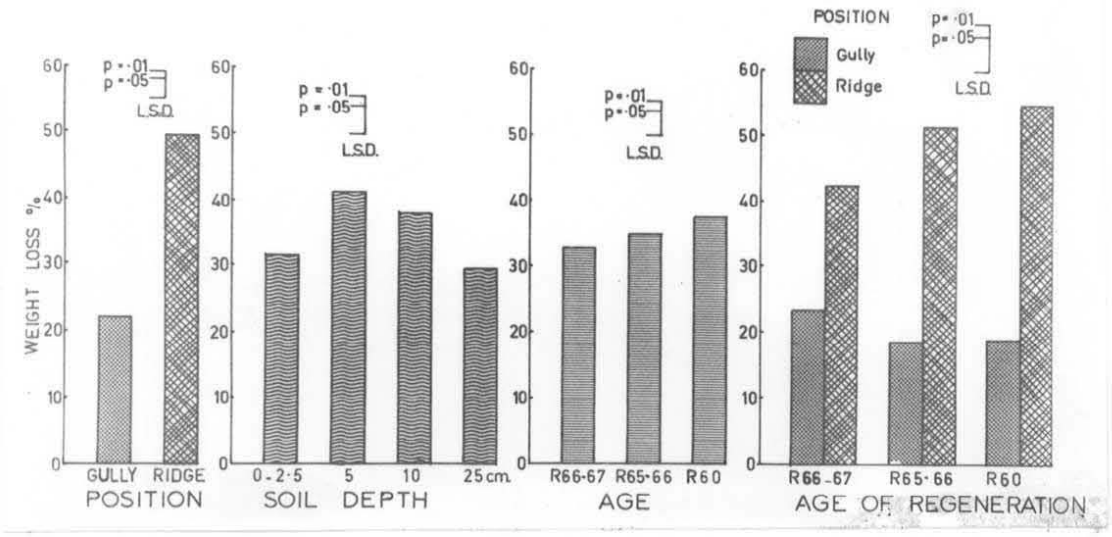


Fig.7.2.1 Fig.7.2.2 Fig.7.2.3 Fig.7.2.5

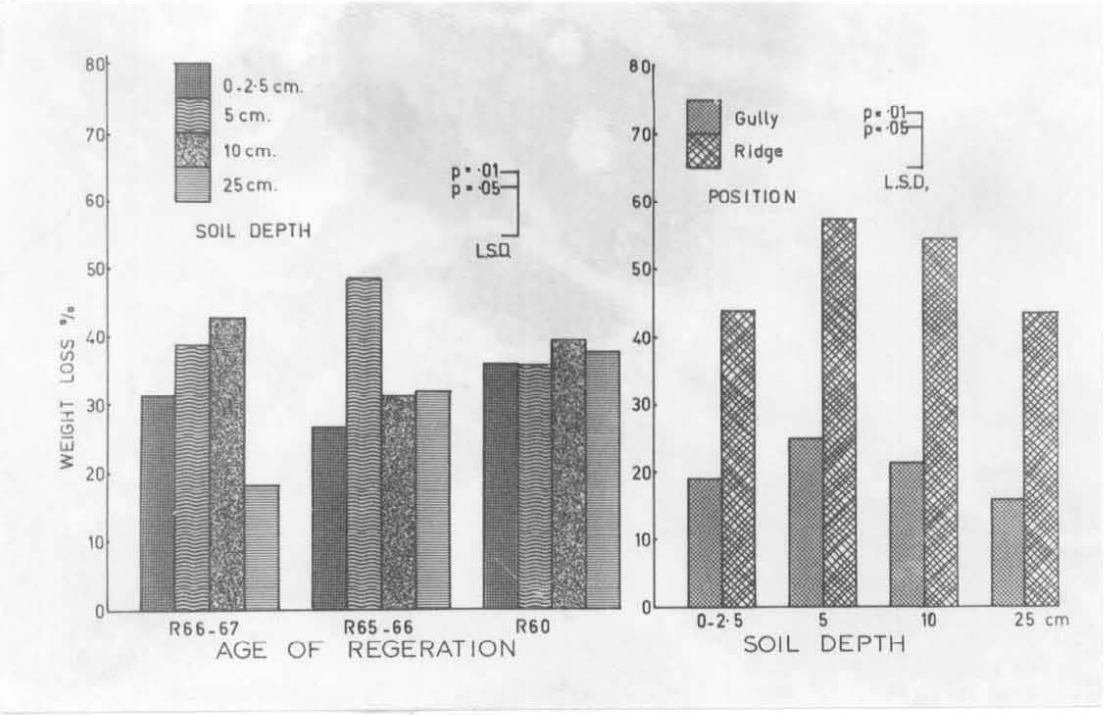


Fig.7.2.6 Fig.7.2.4

The age x position interaction (Fig. 7.2.5) also showed that the difference between ridge and gully sites increased with age of regeneration. This appears contrary to Whyte's (1966) postulation that regeneration growth rate on the ridges increases after five to seven years if it is postulated that increased decomposition rate observed in this study is correlated with increased nutrient immobilization and decreased tree growth rate.

The depth x age interaction (Fig. 7.2.6) is rather complicated. At the R65-66 sites the rate of decomposition at 5 cm depth was different to other depths while at R60 the rate of decomposition was constant at the four depths. The rate of decomposition at the R66-67 site rose at the first three depths from 31% to 42% then declined rapidly at 25 cm depth. There appears to be no overall pattern in these results.

The overall rate of breakdown was 6.3% in the first 8½ months from March, 1967, to January, 1968, and 32.2% from July, 1967, to May, 1969. The decay of needles on the soil surface was not much more rapid (approximately 50% in 22 months). The decomposition of 33% of the root wood in 22 months is equivalent to the loss of 25,000 lb/acre (28,000 kg/ha) under field conditions. Assuming a nitrogen content of 0.05% for the root wood (Orman and Will, 1960) would mean that roots in Tasman Forest would release 12.5 lb N/acre/22 months (14 kg/ha). On the other hand, if the micro-organisms responsible for the decomposition of root

wood extracted nitrogen from the soil until a C:N ratio of 20:1 was obtained then they would require approximately 625 lb/acre/year. However, Cowling and Merrill (1966) have found that wood decomposing fungi do not require such large amounts of nitrogen.

Even though it is uncertain what C:N ratio the micro-organisms responsible for decomposing the root wood left after clear felling in Tasman Forest needed, it is possible that some immobilization of nitrogen occurred especially on the ridge sites.