AN EXPERIMENTAL TEST OF THE IMPORTANCE OF LITTER AND SOIL TYPE IN THE DECOMPOSITION OF FIVE FYNBOS BIOME LITTER TYPES

Donovan Kirkwood

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Supervisor: Dr. W.D. Stock

Abstract

The relative effects of litter and soil type on the decomposition of leaf litter characteristic of five fynbos biome ecosystems were studied by means of a laboratory based microcosm experiment. After incubation it was found that:

(1) Decomposition is influenced by litter type and quality. Poor quality litter, such as that produced by *Leucadendron laureolum* and *Leucospermum parile*, characteristic of nutrient poor acidic fynbos ecosystems is resistant to decomposition. Higher quality litters, such as those produced by *Diospyros whyteana, Sideroxylon inerme* and *Euclea racemosa*, from more nutrient rich forest, thicket and dune fynbos soils, exhibit higher rates of decomposition. It is likely that the degradablity of a particular litter would reinforce patterns of nutrient cycling in its own ecosystem.

(2) The effect of the soil type upon which the litter rested was variable, although unexpectedly, rates were highest on nutrient poor acidic soils and lowest on organic rich forest soils. This is probably a result of short experiment duration and microclimate favouring fungal decomposers on these soils.

(3) Decomposition of litter derived from the alien tree, *Acacia cyclops*, may be more variable between soil types than has previously reported. The higher rates of decomposition by this litter compared to those of sclerophyllous fynbos species indicates the important effect this invasive species may have on nutrient cycling in invaded ecosystems.

The usefulness of laboratory based, controlled microclimate litter decomposition experiments is discussed.

Introduction

Nutrient cycling patterns in the fynbos biome are widely divergent, both as a result both of the variety of soil types, and the characteristic vegetation types which each sustains (Stock and Allsopp 1992). Fynbos biome soil types vary greatly in nutrient status, as well as occurring under a wide range of climatic conditions. This results in great variation in the nutrient status of litter produced (Cowling and Holmes 1992) and influences litter decomposition and nutrient cycling. Despite the expected wide range of nutrient cycling patterns, most studies have only considered N and P cycling at the coastal lowland fynbos site at Pella (Stock and Allsopp 1992). Thus little is known of rates of nutrient return from litterfall in fynbos systems.

There are indications that in fynbos systems, poor quality litter results in extremely slow decomposition rates. It is thus likely that fire, not decomposition, is the most important process whereby nutrients are released from organic matter in these systems (Stock and Allsopp 1992). However other vegetation types within the fynbos biome, such as thicket, have more alkaline, nutrient rich soils and produce higher quality litter. Decomposition processes would presumably be important in mineralisation and nutrient cycling in these systems (eg. Cowling 1984).

Apart from the influence of climate (Alexander 1977, Bunnel et al. 1977), decomposition of litter by microbes is dependant both on the quality of the litter (Bunnel et al. 1977), and the soil with which the litter is in contact (French 1988). Many workers have reported that the rates of decomposition of plant materials depend on the nitrogen content or C:N ratio of the tissues, with protein-rich substrates readily metabolised by microbes (Alexander 1977). Other litter characteristics can also be important. These include phosphorus content (Alexander 1977, Read and Mitchell 1983), levels of easily metabolised soluble carbohydrates (Beare et al. 1992) and levels

of resistant carbohydrates such as lignin and cellulose (Alexander 1977, Read and Mitchell 1983). Studies in various ecosystems have demonstrated that decomposition rates in natural litter and artificial substrates are also related to various soil characteristics (Alexander 1977, French 1988). These include chemical factors such as pH (Alexander 1977), general soil nutrient status, soil nitrogen, phosphorus and calcium content and the presence of soluble carbohydrates (French 1988). In addition, decomposition of poor quality litter shows greater response to increases in soil nutrients than higher quality litter (French 1988). Both an adequate temperature and the presence of sufficient moisture are necessary for litter decomposition to occur (Bunnel et al. 1977).

It seems likely that in natural systems, nutrient cycling results in positive feedback loops. Nutrient poor ecosystems, other than tropical rain forests (Stock and Allsopp 1992), have slow growing plants that use nutrients efficiently. Plants in these systems produce poor quality litter that decomposes slowly. By contrast, plant species from nutrient rich ecosystems grow rapidly and produce easily degradable litter, resulting in rapid nutrient cycling. New research is demonstrating that these species effects can be as or more important than abiotic factors in controlling ecosystem fertility (Hobbie 1992).

Fynbos biome soils tend to have a very low nutrient status associated with their great age and a long history of leaching. Because of this, the major reservoirs of phosphorus and nitrogen in this mediterranean ecosystem are living plants and soil organic matter. Since this organic matter is the major source of some important plant nutrients, especially nitrogen and phosphorus, measurements of litter quality and decomposition rates are amongst the data needed to assess decomposition and mineralisation processes in fynbos ecosystems (Read and Mitchell 1983). Simple experiments involving the use of litter bags to assess weight loss of litter in the field and laboratory provide a good

estimate of the importance and rates of microbial decomposition in ecosystem nutrient cycling (Bocock et al. 1960).

This laboratory based study aims to test the effects of both litter type and soil characteristics on decomposition of the litter of species characteristic of each of five fynbos biome ecosystems. These include a range from low nutrient status sclerophyllous litter from fynbos to higher nutrient status mesophyllous litter from forest. This should provide some insight into the importance of decomposition in the nutrient cycling of these systems, as well as testing ideas concerning decomposition of different quality litters on soils of varying nutrient status. It would be expected that highest decomposition (ie. weight loss) would occur in the higher nutrient status, non-sclerophyllous leaves, resting on organically rich, fertile soil. Conversely, the lowest decomposition should occur in a sclerophyllous species on an infertile, probably acidic soil.

Methods

Experimental design

The litter of six species was incubated in the laboratory on soils from five different sites in the Cape. Every combination of soil and litter was composed of five replications, each of which was enclosed in a separate sealed micro-environment.

Soil and litter origins and sampling

Soils and litter samples were collected from five ecosystems in the Cape. These were:

(1). Mountain fynbos, forming an open graminoid shrubland with emergent mid-high *Leucadendron laureolum* shrubs. This site was in the Silvermine Nature reserve, 18°24'E and 34°10'S, immediately north of the Ou Kaapse Weg road and to the east of the main reserve entrance. The soil is a grey sand derived from Table Mountain Sandstone.

(2) Sand plain lowland fynbos from the fynbos biome intensive study site at Pella, 18°31'E and 33°31'S, north of Cape Town. This is a distinct form of coastal fynbos (Moll et al. 1984, cited by Mitchell et al. 1986), consisting of low sclerophyllous vegetation growing in acidic sands aeolian in origin, with low phosphorus status. The vegetation of the site sampled consisted of *Thamnocortus punctatus-Leucospermum parile* shrubland growing on Constantia soil (Mitchell et al. 1986).

(3) Afromontane forest growing in the Orange Kloof Ravine, south of Tafelberg, 18°24'E and 33°50'S. This forest grows on an Oakleaf soil form (Macvicar et al. 1977). *Diospyros whyteana* was a common understorey species.

(4) *Sideroxylon inerme* coastal thicket growing close to the sea below Scarborough in the Cape Peninsula, at 18°22'E and 34°12'S. This grew on an organic rich Fernwood sand (Macvicar et al. 1977).

(5) Dune fynbos from an area inland of Long Beach in Kommetjie at 18°20'E and

34°09'. Care was taken to collect soil in an area remote from any *Acacia cyclops* stands, due to the influence these alien nitrogen fixers might have on the soil nutrient content. This vegetation grew on similar Fernwood sands to the thicket site described above, although with a lower organic matter content. Both these coastal calcareous dune sands would have generally higher soil nutrients relative to other fynbos communities (Cowing and Holmes 1992).

Soils were collected by placing excavated intact profiles in 13 cm plastic pots. These were brought back to the laboratory and air dried at 25°C until the start of incubation.

Litter was collected from a variety of individuals of one representative species at each site. These were, *Leucadendron laureolum* at Silvermine, *Leucospermum parile* at Pella, *Diospyros whyteana* from the forest site, *Sideroxylon inerme* from the coastal thicket site and *Euclea racemosa* and *Acacia cyclops* from the dune fynbos site. All these species, except *D. whyteana* are the dominant or co-dominant species at the relevant site. *D. whyteana* was selected as the leaves of this understorey species are easily accessible. Only senescent leaves ready to abscise naturally were collected. This was necessary because plants may withdraw considerable quantities of soluble nutrients from the leaves prior to abscission and leaf fall (Read and Mitchell 1983). For example Mitchell et al. (1986) showed that mature, attached leaves of *Leucospermum parile* contained higher quantities of soluble carbohydrates, but a lower proportion of lignin than leaf litter. Thus decomposition in harvested mature leaves is not comparable to that of naturally produced litter.

Experimental setup

The litter was oven dried at 80°C until constant weight was reached. Leaves were then placed in a single layer in litter bags (10 × 10 cm nylon mesh, mesh size 1.45 mm) and weighed on a four place Mettler balance. The average weight of oven dry leaves in each litter bag was 1.54±0.42 g. Each pot was moistened with 75 ml of water (10% by volume), before the litter bags were placed on the soil surface (Fig. 1). These were then incubated at 25°C for 110 days before harvesting and final determination of weight loss of the litter samples. Only one sample was spoiled (one replicate of *Euclea racemosa* litter on coastal thicket soil).

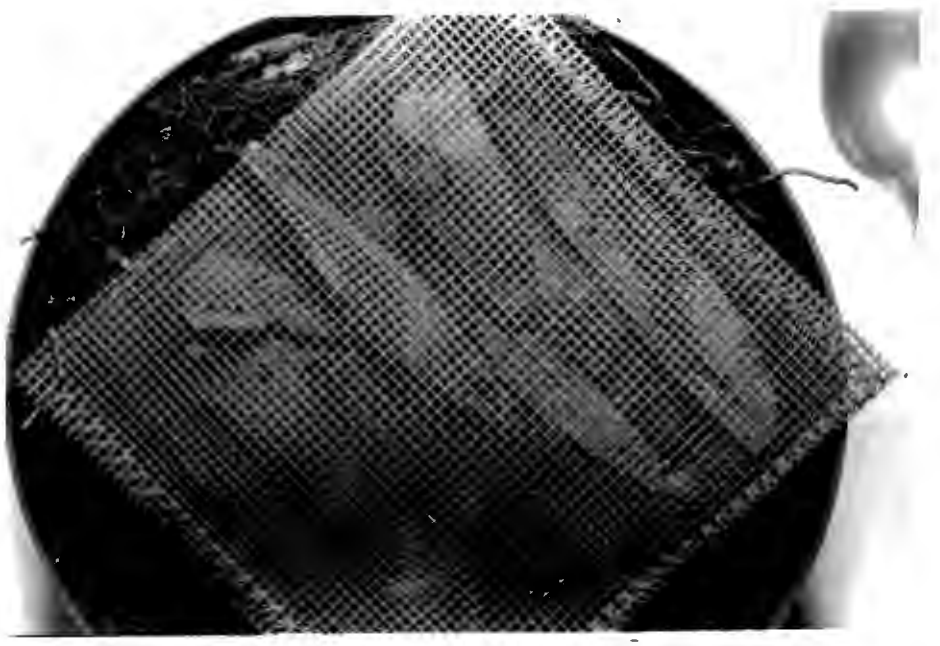

Figure 1. Illustrating how the 10 × 10 cm litter bags (mesh size 1.45 mm) containing a single layer of leaves were placed in full contact with the soil surface. (Litter of *Leucospermum laureolum* on forest soil)

The pots were then placed in a 52 × 75 cm polyethylene bag, which was filled with compressed air and tied closed (Fig. 2).

Figure 2. Experimental setup, showing soils in 13 cm diameter pots with litter bags enclosed in polyethylene bags. These were incubated at 25°C for 110 days.

Polyethylene bags were used to create a suitable microclimate for decomposition. The interior of inflated bags provides an aerobic environment, being permeable to O_2 and CO_2 (Pastor et al. 1984), but impermeable to water. The incubation temperature of approximately 25°C allowed for a high rate of decomposition as most of the fungi and bacteria involved in normal terrestrial decomposition processes have temperature optima for activity between 25 and 35°C (Read and Mitchell 1983).

Soil analyses

Soil moisture contents in every pot were determined gravimetrically, from soil samples weighed immediately after opening of the bag. The same samples were then ashed in a muffler furnace at 450°C for 4 hours to determine organic content. The pH of each soil type was determined from 3 replicates. Air dry soil (20g) was mixed into 50 ml of a 0.1 Molar $CaCl_2$ solution. After 50 minutes the samples were stirred again. After standing for a further 10 minutes, pH readings were taken using an electronic pH meter.

Data analyses

A two-way ANOVA was used to test the variation in percentage weight loss of litter between soil types as well as between litter types in all 149 samples. One way ANOVAs were used to test the variation in water content and organic content for the different soil types, as well as the variation in percentage weight loss for litter on each soil type. Tukey multiple range tests (Zar 1984) were used in all cases to test for significant variation between treatments at the 95% confidence level. All statistical tests were performed using STATGRAPHICS.

Turnover times for the litters were calculated using the model presented by Read and Mitchell (1983). This simple model estimates the decomposition constant (k) or fraction of mass lost by organic matter:

$$\frac{X_t}{X_0} = e^{-kt}$$

X_t is the mass of litter or litter constituent remaining at time t, X_0 is the original mass. An estimate of the mean resident or turnover time is obtained of the organic matter is obtained from 1/k. This simple model does seem to be realistic, as mass change in decomposing litter over time does appear to show constant fractional loss (k).

RESULTS

General

Weight loss was detectable in all samples, with average mass loss through decomposition (n = 149) being 6,79 ± 4.01 %. After incubation many of the litter samples were extensively colonized by saprophytic fungi (Fig's 3 and 4).

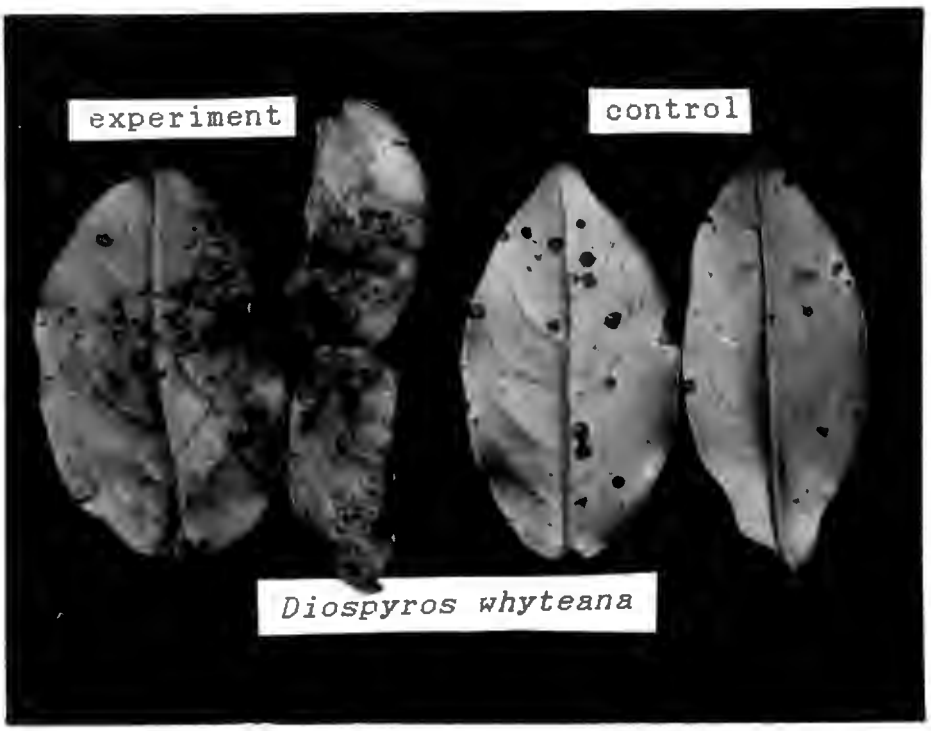

Figure 3. Examples of *Diospyros whyteana* leaves after a 110 day incubation period in a sealed microenvironment (experiment). Note the conspicuous fungal infection compared to leaves stored in air dry conditions for the same period (control).

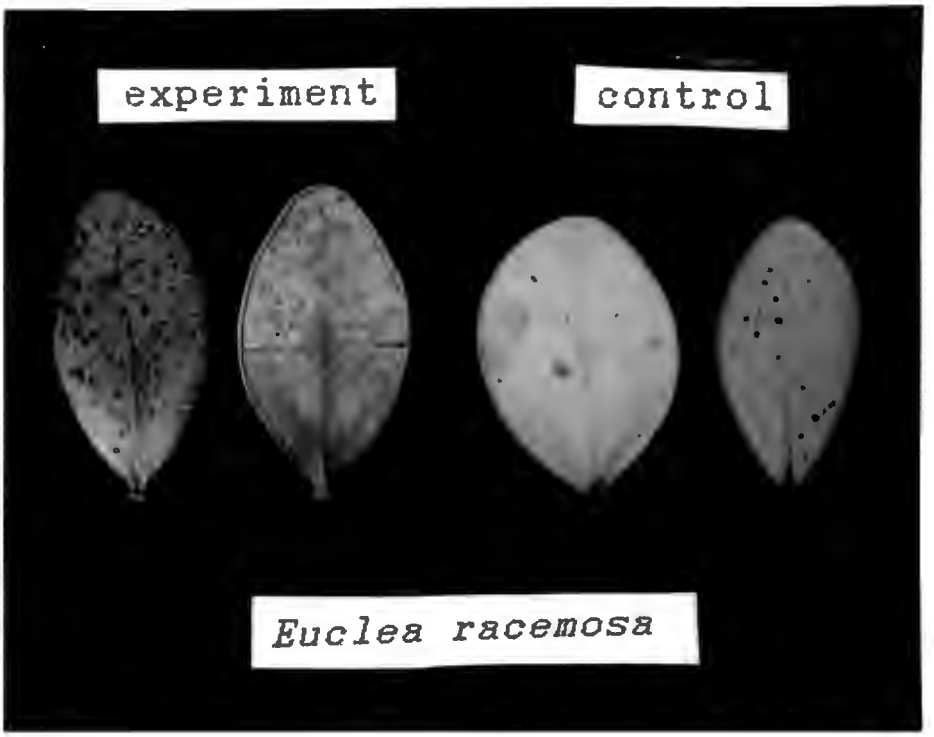

Figure 4. Examples of *Euclea racemosa* leaves incubated in a sealed microenvironment for 110 days (experiment) as well as air dry leaves stored for the same period (control). Note that colonisation by two species of fungi has in the experimental treatment.

There was significant variation in the degree of litter decomposition after incubation at both the level of the soil type ($p < 0.0001$), and the litter type ($p < 0.05$). There was no significant interaction between the effects of soil and litter types on decomposition ($p > 0.05$).

Effect of litter type on decomposition

The effect on decomposition of the litter type (species) averaged across all soils (Fig. 5) was less marked than the effect of soil type on the decomposition of all species' litter (Fig. 7).

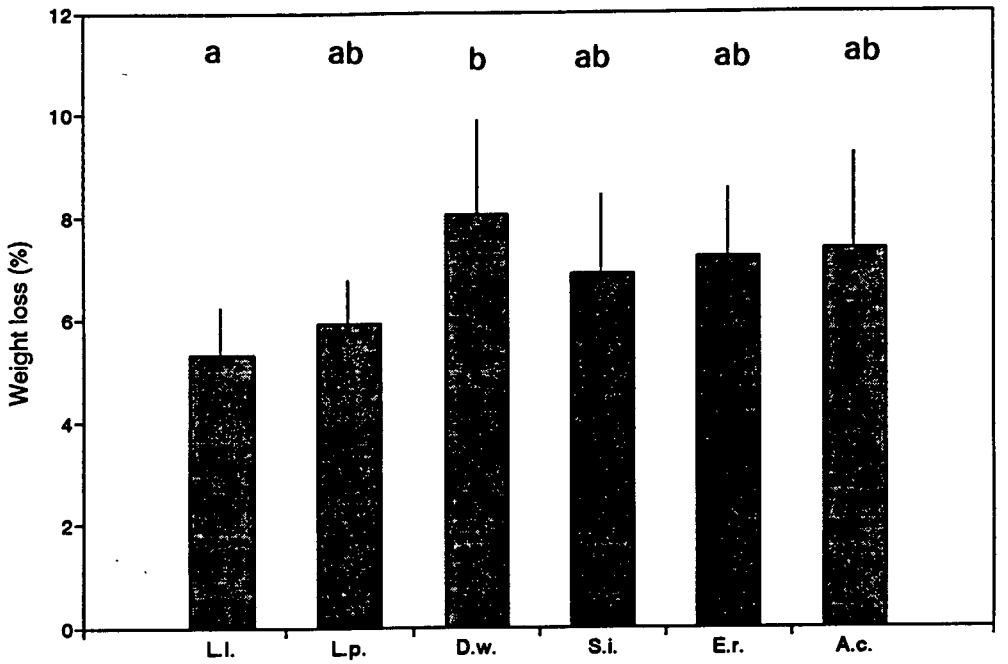

Figure 5. Percentage weight loss of the 6 study species averaged across all soils. ANOVA shows variation between treatments to be significant ($p < 0.03$). Error bars represent 2 S.E. The alphabetic characters are the results of a multiple range test, showing significant variation ($p < 0.05$) between individual treatments.
(L.l.= *Leucadendron laureolum*, L.p.=*Leucospermum parile*, D.w.=*Diospyros whyteana*, S.i.=*Sideroxylon inerme*, E.r.=*Euclea racemosa*, A.c.=*Acacia cyclops*)
Error bars represent 2 S.E.

A species (litter type) effect on decomposition is apparent however, indicating that substrate is important. In figure 5 it can be seen that the litter of the two sclerophyllous fynbos species, *Leucadendron laureolum* and *Leucospermum parile*, showed lower weight loss than the other four species. Only *L. laureolum* and *Diospyros whyteana* litter decomposition differ significantly from one another at the 95% confidence level however. *D. whyteana* litter showed almost 50% greater weight loss than *L. laureolum*. *L. parile, Sideroxylon inerme, Euclea racemosa* and *Acacia cyclops* litter decomposition do not differ significantly either from one another or from *L. laureolum* and *D. whyteana* decomposition at this level.

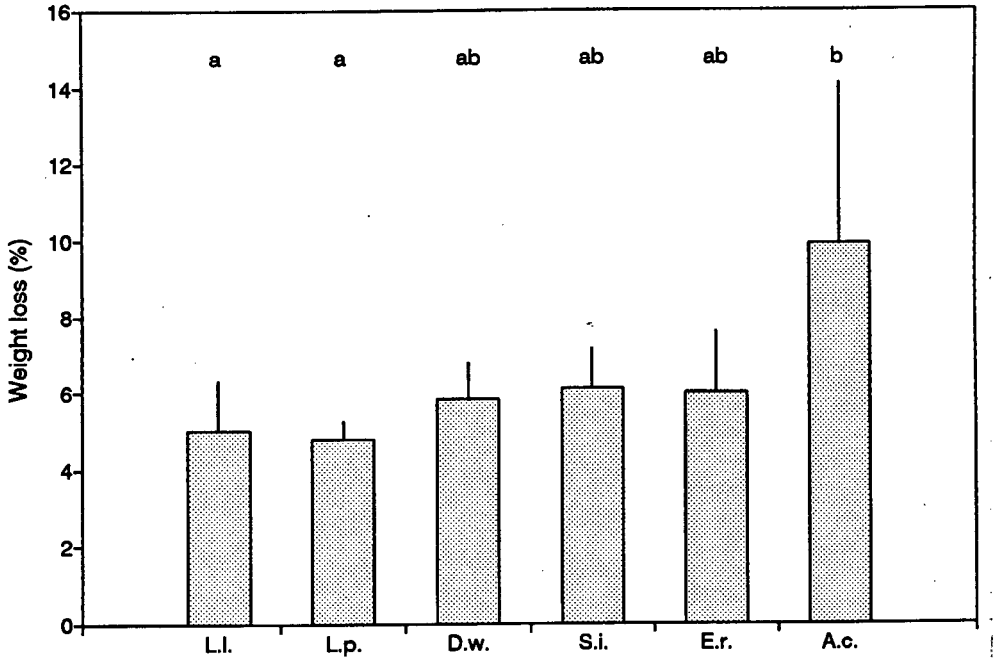

Figure 6. Weight loss (% of original dry mass) of six species' litter on dune fynbos soils. ANOVA indicates that variation between treatment is significant ($p < 0.05$). Alphabetic characters indicate the results of a multiple range test, showing significant variation between treatments ($p < 0.05$). Error bars represent 2 S.E.
(L.l.=*Leucadendron laureolum*, L.p.=*Leucospermum parile*, D.w.=*Diospyros whyteana*, S.i.=*Sideroxylon inerme*, E.r.=*Euclea racemosa*, A.c.=*Acacia cyclops*)
Error bars represent 2 S.E.

If the decomposition of all the species' litter on individual soil types is considered, only values from the dune fynbos soil show significant variation between species ($p < 0.03$). Litter from *A. cyclops* shows highest decomposition at this site (Fig. 6), although this value only differs significantly from the lowest value (*L. laureolum* decomposition) at the 95% confidence level.

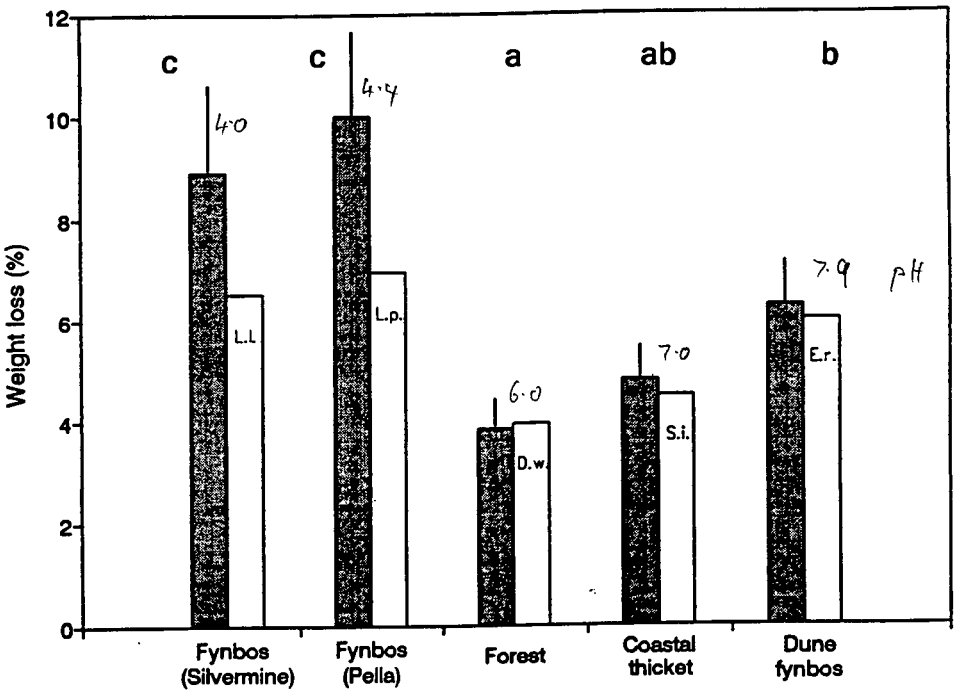

Figure 7. Weight loss (as % of original mass) of litter on five Cape soils.

▓ Average weight loss of 6 species' litter. Error bars represent 2 S.E. ANOVA indicates that variation between treatments is highly significant. Alphabetic characters are the result of a multiple range test showing significant variation between individual treatments ($p < 0.05$)

□ Weight loss of litter of the home species from each ecosystem.

Effect of soil type on litter decomposition

Decomposition of litter on the various ecosystems' soils (Fig. 7) showed clear patterns of variation. Litter on the acidic fynbos soils from Silvermine and Pella showed significantly greater weight losses than the forest, coastal thicket or dune fynbos soils. Although decomposition of litter on coastal thicket soils was not significantly different from that on forest and dune fynbos soils, the decomposition of litter on dune fynbos soils was significantly greater than that on forest soils at the 95% confidence level. Note that weight loss by litter of *L. laureolum* and *L. parile* on their home soils of Silvermine and Pella is lower than the average weight loss for all species' litter. The non-sclerophyllous litter of *D. whyteana, S. inerme* and *E. racemosa* on each home soil shows approximately equivalent weight losses to the average values for all species litter. Thus all species show higher rates of decomposition on the low nutrient, acidic fynbos soils than either of the fynbos species which naturally occur there.

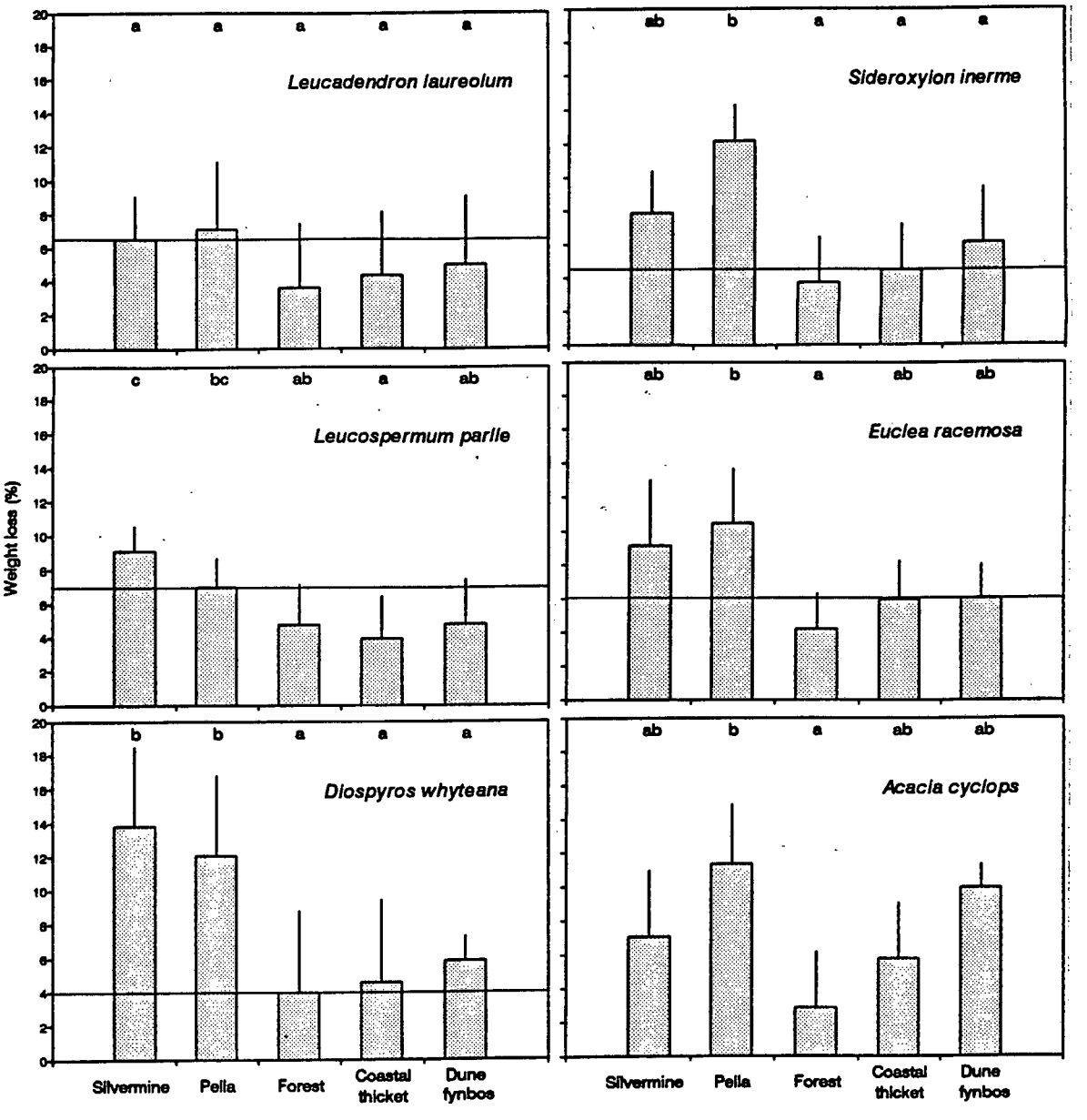

Figure 8. Weight loss (% of original dry mass) in the leaf litter of six species after incubation on soils from 5 ecosystems. Note the dotted horizontal line indicating the decomposition of litter on the soil from its own ecosystem. Error bars represent 2 S.E. Alphabetic characters indicate the results of multiple range tests, showing significant variation between individual treatments ($p < 0.05$). ANOVA results are presented in the text.

When the decomposition of each species' litter on these soils is considered (Fig. 8), all values, except those of *L. laureolum*, show significant variation between the different soil types (*L. laureolum*: $p > 0.05$, *L. parile*: $p < 0.0003$, *D. whyteana*: $p < 0.0002$, *S. inerme*: $p < 0.004$, *E. racemosa*: $p < 0.03$, *A. cyclops*: $p < 0.04$). The general pattern of decomposition of the 6 individual species' litter on the 5 ecosystem's soils

(Fig. 8) is similar to the values averaged for all species (Fig. 5). Decomposition is higher on the acidic fynbos soils of Silvermine and Pella than at other sites for all species except *Acacia cyclops*. The litter of *A. cyclops* showed higher decomposition on dune fynbos soil than on Silvermine soil. Decomposition of this litter is still the highest on Pella soil however. In most cases, except for *D. whyteana* and *S. inerme*, these differences between the acid fynbos soils and the other soils cannot be clearly seen in the results of the multiple range tests. However, where decomposition on both acidic fynbos soils does not differ significantly from that on other soils, at least one or two of the values on the non-fynbos soils are significantly lower than those from Silvermine or Pella soils.

Another trend that emerges from the data presented in figure 8 is that leaf litter decomposition of the two sclerophyllous fynbos species, *L. laureolum* and *L. parile*, shows less variation from site to site than that of the other species. Both *L. laureolum* and *L. parile* have ranges in average decomposition at each site of only 3.6 and 5.1% respectively, lower than those for decomposition of the other species' litter. Ranges in average decomposition between soils for the other species are: 9.86% for *D. whyteana* , 8.50% for *A. cyclops* , 8.46% for *S. inerme* and 6.28% for *E. racemosa*.

The fractional loss rate (k) for litter in each of the treatments described above can be calculated from a simple exponential decay model (see methods) described by Read and Mitchell (1983). The inverse of this calculated value (1/k) gives an estimate of mean resident or turnover times for the litter (Table 1).

Table 1. Turnover times (1/k) in years of litter from five species on the soils of five Cape ecosystems.

	Fynbos (Silvermine)	Fynbos (Pella)	Forest (Orange Kloof)	Coastal Thicket (Scarborough)	Dune Fynbos (Kommetjie)
L. laureolum	4.5	4.0	8.4	6.7	5.9
L. parile	3.2	4.1	6.1	7.5	6.1
D. whyteana	2.3	2.3	7.7	5.0	5.0
S. inerme	1.8	2.4	8.1	6.7	4.8
E. racemosa	3.1	3.1	7.0	4.9	4.9
A. cyclops	4.2	2.7	10.6	5.0	2.9

Since the values presented in table 1 are derived directly from data presented in figure 8, the trends will not be discussed here. These values will be used to relate decomposition rates to those demonstrated in other studies.

Soil characteristics

Organic contents of the soils collected from the five ecosystems (Fig. 9) show significant variation ($p < 0.0001$).

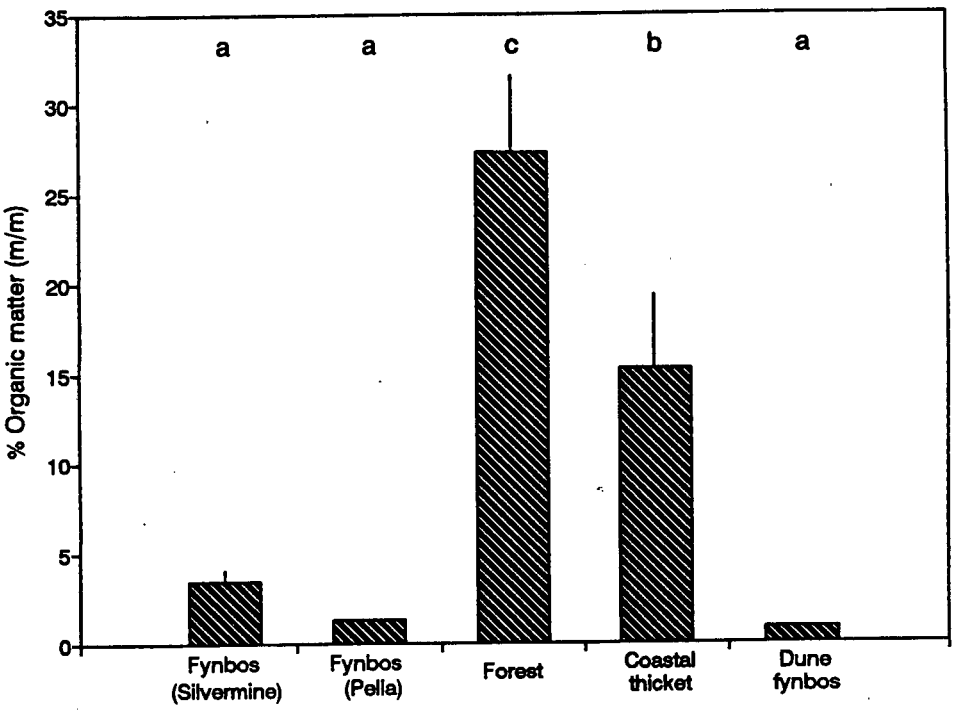

Figure 9. Percentage organic matter content (gravimetric) of 5 soils from Cape ecosystems. Error bars represent 2 S.E. ANOVA reveals highly significant difference between treatments ($p < 0.0001$). Alphabetic characters indicate the significant variation between individual treatments from a multiple range test ($p < 0.05$).

As can be seen in figure 9, the forest soil has the highest organic content, followed by the coastal (*Sideroxylon*) thicket soil. Both of these differ from one another and the three fynbos soils at the 95% confidence level. There is no difference between the organic contents of the three fynbos soils at this significance level however.

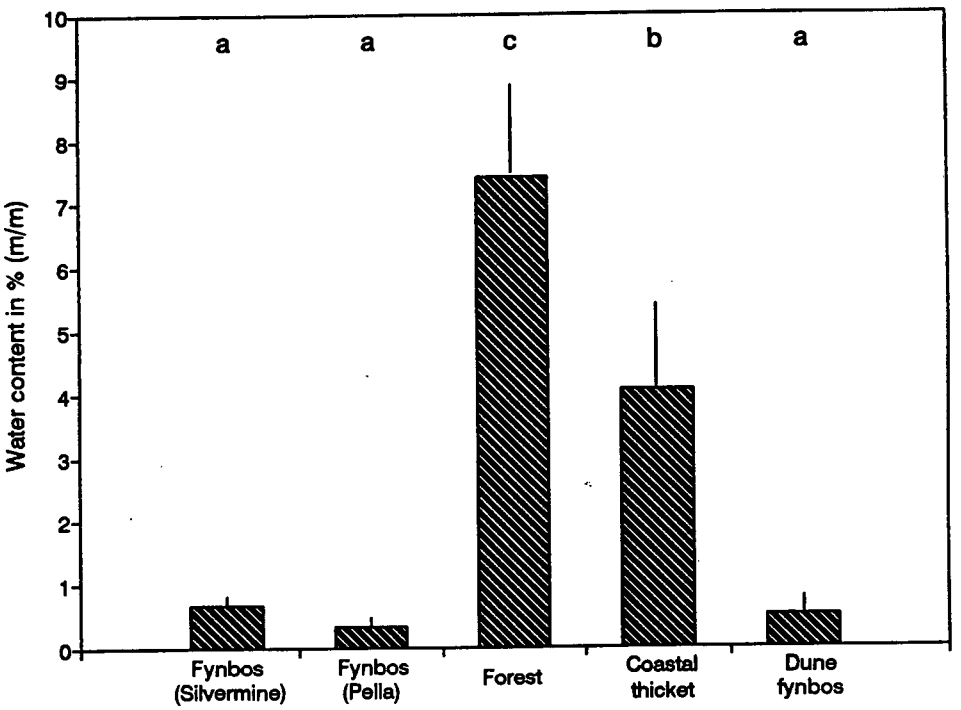

Figure 10. Water content (gravimetric) of soils from 5 Cape ecosystems. Error bars represent 2 S.E. ANOVA reveals a highly significant variation between treatments ($p < 0.0001$). Alphabetic characters represent significant variation between individual treatments ($p < 0.05$) from a multiple range test.

Although the same quantities of water were added to all soils, variation in their organic content resulted in a corresponding variation in the gravimetric water content. Soil water content (Fig. 10) shows exactly the same pattern of significant variation ($p < 0.0001$) between soil types as can be seen for soil organic content. A regression analysis reveals that soil organic content explains 82% of the variation (D.F. = 147) in soil water content. Although these results show high water contents in the soils containing large amounts of organic matter, it is likely that these in fact have lower water potentials than the sandy soils of Silvermine, Pella and the dune fynbos.

The pH values of the soils used in this study cover a wide range, from the highly acidic soil of the mountain fynbos at Silvermine to the mildly alkaline soils from beneath dune fynbos in Kommetjie (Table 2).

Table 2. The pH values of five Cape soils used in this litter decomposition study. Each cell represents the mean of 3 values and the standard deviation.

Soil origin	pH ± S.D.
Fynbos (Silvermine)	4.0 ± 0.1
Fynbos (Pella)	4.4 ± 0.1
Forest (Orange Kloof)	6.0 ± 0.2
Coastal Thicket (Scarborough)	7.0 ± 0.1
Dune Fynbos (Kommetjie)	7.9 ± 0.3

Soil characteristics and decomposition

Neither soil organic content, nor gravimetric water content explain the variation in the degree of decomposition of litter on the different soils (Fig's 6 and 8). Regressions of log organic content and log water content vs. percentage weight loss in each sample explained only 16 and 11% of the variation in litter weight loss respectively (D.F. = 149). Patterns of weight loss on the different soils (fig's 7 and 8) may be related to pH however. It is clear that average weight loss was always highest on the two highly acidic fynbos soils from Silvermine and Pella. Decomposition on the other three soils however increased with increasing pH.

DISCUSSION

This laboratory based microcosm experiment appears to be suitable for evaluating the effect of both soil and litter type on litter decomposition rates, even over a relatively short period. High weight loss by litter (average weight loss of all litter was 6.8% of original dry mass) allows clear distinctions to be made between the effects of different treatments.

Variation in decomposition due to litter type

Decomposition patterns in the litter of the species used in this study were as expected. As many previous studies have indicated (Alexander 1977; French 1988; Hobbie 1992), rates of weight loss due to microbial activity were lower in the poorer quality litter types than in non-sclerophyllous species. For example, *L. parile* litter from Pella has been shown to have nitrogen contents of only 5.7 $mg.g^{-1}$ of dry mass, associated with a high carbon content of 508 $mg.g^{-1}$ (Mitchell et al. 1986). This equates to a C:N ratio of 89. *L. parile* had a lower decomposition rate than all species except *L. .laureolum.* The only significant difference however, was between the sclerophyllous *L. laureolum* litter and the litter of *D. whyteana.* Since *D. whyteana* grows on nutrient rich forest soils (Cowling and Holmes 1992) it is likely to have the highest nutrient content of all the species considered. All non-sclerophyllous species lost similar amounts of weight, although the litter likely to be most nutrient rich, with the lowest C:N ratios (*D. whyteana,*) showed the highest degree of decomposition after the incubation period. Another indication of the comparatively low decomposition rates of the two sclerophyllous fynbos species' litter is that they lose a substantially lower proportion of their original mass compared to the average values of all species on the soils from their own ecosystems. This effect might be compounded by the low nutrient status of the soils. The non-sclerophyllous species' litter would probably be less affected by these poor soils as the litter provides a more suitable substrate for microbial

decomposition.

The two sclerophyllous fynbos species' litter decomposition also show a lower range of variation between soil types than the more mesophyllous species. This result is unexpected, as earlier workers have demonstrated that poor quality substrates usually show greater response to differences in soil characteristics, especially nutrient status (French 1988). This response may be a result of the ability of fungal hyphae to transport nutrients from the soil to make up deficiencies in the litter. The lack of response to soil type in *L. laureolum* and *L. parile* litter may be due the presence of secondary metabolites. Sclerophyllous fynbos leaves typically contain high levels of tannins and polyphenols (Read and Mitchell 1983). It is likely that these substances, which are not easily metabolised, actively inhibit decomposition (Stock and Allsopp 1992).

Implications of varying litter decomposition rates for ecosystems

This variation in degradability would have significant impact on nutrient cycling processes at the ecosystem level. It seems likely that in nutrient poor systems such as fynbos, the resultant production of resistant litter would reinforce patterns of low decomposition and mineralisation from litterfall (Stock and Allsopp 1992). However, when non-sclerophyllous species invade these systems, nutrient inputs to the system from litterfall may substantially increase its nutrient status. Manders and Richardson (1992) have demonstrated that forest species can establish on nutrient poor fynbos soils in the absence of fire. Similarly coastal thicket species may establish on a variety of soils (Cowling 1984; Cowling and Holmes 1992).

These species effects on ecosystem nutrient cycling due to litterfall and decomposition are particularly important when considering the impacts of invasive alien vegetation. Witowski (1991) demonstrated that *Acacia saligna* in sand-plain lowland fynbos and

Acacia cyclops in dune fynbos both substantially elevate the N status of these systems. In addition, the turnover times of the litter of the alien *Acacia* species were substantially lower than those of indigenous species (*L. parile* and *Pterocelastrus tricuspidatus*). The results presented here indicate that results such as these should be interpreted with caution. Although the turnover times (table 1) of *A. cyclops* litter on calcareous soils may be substantially lower than any other species, as has been demonstrated by Low (1988, cited by Stock and Allsopp 1992), this situation does not hold across soil types. In addition turnover times do not seem to be closely related to soil pH. On the acid sands of Pella, *A. cyclops* again showed lower turn over times than all other species. On forest soils however, turnover times of *A. cyclops* were higher than any other species. Thus although litter of the alien *A. cyclops* can show substantially higher decomposition rates than indigenous species, under certain conditions this situation may even be reversed. This calls into doubt the generality of results by workers such as Low (1988) who found distinctly different enrichment of calcareous soils and acid, sandy soils by *Acacia* species.

Comparison with field decomposition rates

It is also appropriate to compare the results of these laboratory based microcosm experiments to actual conditions in the field. Although litter turnover times calculated from the constant fractional loss rate (k) have been used as a convenient estimate of decomposition rates of litter, few examples are available from Cape ecosystems. Mitchell et al. (1986) however have calculated turnover times for leaf litter of *L. parile* at Pella to be 14.5 years. The turnover time for *L. parile* litter on Pella soil in the laboratory is approximately 1/3 of this value. Litter decomposition in the experiment described here is thus proceeding at a much faster rate than under natural conditions. It is unlikely that the absolute values of constant microclimate laboratory based experiments such as these could be extrapolated to predict field conditions, even with corrections for temperature and soil moisture content. It has been shown that litter

decomposition may be dependent on rainfall pattern (eg. Santos et al. 1984) rather than amount. Also the role of soil invertebrates other than microbes, none of which are included in microcosm experiments, may be important in many systems (Etherington 1982). Microcosm experiments can thus add to knowledge of the relative importance of various litter types as well as soil quality in determining observed decomposition patterns. Such experiments however, provide little insight into rates of decomposition occurring in the field.

The importance of soil type

Patterns of decomposition of all litter types on the different ecosystems' soils were diametrically opposed to those which would be predicted from knowledge of the soil characteristics. Microbial decomposition of litter is generally thought to be highest on nutrient and organic rich soils (Alexander 1977, French 1988, Hobbie 1992) with a relatively high pH (Alexander 1977) such as the forest and coastal thicket soils used in this study. Acidic soils with low levels of soil nutrients , especially N and P and a low organic content such as those from the fynbos ecosystems of Silvermine and Pella should inhibit microbial decomposition compared to that occurring on other soils. In addition the higher gravimetric water contents of the organic rich soils should reinforce the expected pattern. This pattern is not observed however (Fig. 7), and there is a large difference between expected and actual observed patterns of weight loss by litter on these soils.

The explanation for these differences is likely to hinge on the time scale of the study, as well as the unnatural microclimatic conditions resulting from the experimental setup. It is likely that most weight loss associated with decomposition was a result of fungal activity, rather than the action other microbes. The majority of litter samples were colonised by saprophytic fungi. Fungi are active in xeric conditions, whereas bacteria require a moist substrate for optimal activity (Alexander 1977). Beare et al. (1992)

demonstrated that fungi had a greater influence on the decomposition of surface litter, while bacteria were more important in the decomposition of buried litter. Further, fungi are favoured over bacteria on acidic soils, especially near a pH of 4 (Etherington 1982). These factors are likely to favour decomposition by fungi on the Pella and Silvermine soils.

In addition to the importance of fungal activity, these unexpected patterns are probably exacerbated by differences in the microclimates between treatments. Although the same quantity of water was added to every treatment, there was great variation in gravimetric water content after incubation (fig 10). This variation seems to be mainly dependant on the varying organic contents of the soils. What is likely is that with equivalent volumes of water present, those soils with higher organic contents actually have lower water potentials than the sandier soils with low organic contents. Thus although gravimetric water content may be high, the moisture is not actually easily available to the saprophytes on the litter. It is likely that the larger response of decomposition processes to moisture availability (Alexander 1977, Bunnel et al. 1977) is obscuring the effect of soil nutrient status. This design fault was not evident until after incubation was terminated. Further laboratory based, microclimatic decomposition studies should take this into account and attempt to provide a uniform water potential across all soils.

Conclusion

In summary, this laboratory based microcosm experiment demonstrated that rates of decomposition in the litter of five fynbos Biome ecosystems are substantially affected by litter quality. Sclerophyllous species' litter from low nutrient acidic fynbos systems exhibit lower decomposition rates than those of higher quality litter from nutrient rich systems. This difference is especially apparent between *L. laureolum* from a mountain fynbos system and *Diospyros whyteana* from afromontane forest. These results are typical of those reported in the literature and their implications for nutrient cycling in various ecosystems may be profound. It seems likely that the quality of litter produced by plants growing in soils of a particular nutrient status results in reinforcement of nutrient cycling patterns.

The effect of soil type on decomposition in this study was unexpected. It seems likely that this is a result of the short term nature of the experiment favouring fungal decomposition on acid soils. Varying water potentials due to differing organic content of the soil are likely to have compounded this effect. The result was that any effect that soil nutrient status may have had on litter decomposition was obscured. It is recommended that any future laboratory based, microcosm decomposition experiments take this effect into account. Finally, it seems that while these experiments are useful in comparing the effect of soil type and litter quality, extrapolation of results for comparison with field conditions is not possible.

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