Pergamon

Soil Biol. Biochem. Vol. 28, No. 10/11, pp. 1381–1388, 1996

0038-0717/96 $15.00 + 0.00

PII: S0038-0717(96)00158-7

DECOMPOSITION OF EUCALYPTUS LEAVES IN LITTER MIXTURES

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(Accepted 28 May 1996)

Summary—Leaf litter from *Eucalyptus globulus* was decomposed alone and in mixture with either oak (*Quercus petraea*), ash (*Fraxinus excelsior*) or birch (*Betula pendula*) leaf litter under laboratory conditions. Decomposition was monitored as CO_2 release and leaching of inorganic N over 13 weeks. At the end of the experiment, litters were separated into their species components and analyzed for mineral composition (K, Ca, Mg, P and N) and mass loss. Differences between expected and measured rates of decomposition were evaluated, based on a comparison between the results from the pure litters and the mixtures. Mixing eucalyptus litter with oak litter resulted in enhanced total CO_2 release from the litter mixture when compared with the pure components. Similar, but less marked, positive interactions were observed in mixtures with eucalyptus + birch and eucalyptus + ash. Decomposition of eucalyptus litter in the presence of the other litters also influenced N mineralisation, resulting in greater net N retention in the mixtures with eucalyptus + oak and eucalyptus + birch, but a decrease in mixture with ash. The results support the conclusion that the decomposition of litters in mixtures cannot be readily predicted from the behaviour of the component litters decomposing in isolation. We suggest that mixtures of eucalyptus with other litters could be one mechanism by which the high productivity rates of eucalyptus plantations may be maintained, and that manipulation of litter mixtures could assist in synchronising nutrient release and plant uptake. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

The management of litter mixtures provides an important means of manipulating soil organic matter development and nutrient release, yet has received little research attention (Fyles and Fyles, 1993). It has been suggested that nutrient release from rapidly decaying litter types can stimulate the decomposition of adjacent, more recalcitrant litter types (Seastedt, 1984) with, for example, Taylor *et al.* (1989a) attributing an acceleration of mass loss in *Populus–Alnus* mixtures to a transfer of nutrients from N-rich *Alnus* litter to *Populus* litter. Conversely, inhibitory compounds such as phenolics and tannins (Harrison, 1971; Dix, 1979; Swift *et al.*, 1979) could be expected to reduce the decomposition rates in certain litter combinations.

An increasing number of workers have reported on the effects of the litter of one tree species on the decomposition of litter from another (Seastedt, 1984; Carlyle and Malcolm, 1986; Klemmedson, 1987; Chapman *et al.*, 1988; Blair *et al.*, 1990), yet we still lack a theoretical framework for predicting these interactions (Ineson and McTiernan, 1992). Certain mixtures of litters have been shown to exhibit positive decomposition interactions, resulting in enhanced nutrient release (Carlyle and Malcolm, 1986; Chapman *et al.*, 1988), increased litter decay and increased respiration rates (Ineson and McTiernan, 1992). Chapman *et al.* (1988) found that although rates of respiration from the litter layer of *Picea abies* increased in mixture with *Pinus sylvestris*, a decrease was observed in mixtures with *Alnus glutinosa* and *Quercus petraea*. Fyles and Fyles (1993) suggested that litters have the potential to interact with positive or negative effects on decomposition rates and that interactions are not predictable from commonly measured litter quality properties.

Eucalyptus plantations have been associated with a reduction in populations of soil fauna and flora (Kardell *et al.*, 1986; Hingston *et al.*, 1989; Saxena, 1991; Bi *et al.*, 1992), the production of allelopathic compounds (Bernhard-Reversat, 1988; Bi *et al.*, 1992; Sanginga and Swift, 1992; Singh and Kohli, 1992), and anti-microbial effects (Della Bruna *et al.*, 1989; Della Bruna *et al.*, 1991). The slow rate of decomposition of eucalyptus forest litter, resulting in the storage of significant amounts of nutrients in the soil, has been recognised as a feature of this genus (Adams and Attiwill, 1986). Wood (1974) concluded that eucalyptus leaves decomposed more slowly than leaves of many European broad-leaved

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tree species, and highlighted the high initial polyphenolic content of the leaves. There are currently no data available on the decomposition of eucalyptus leaves in the presence of other litters and, in the current work, we investigated the possibility that some of the alleged negative effects of eucalyptus litter on soil biological activity would influence, or could be influenced by, the presence of other leaf litters.

The experimental approach involved comparison of decomposition rates of eucalyptus leaf litter when decomposed alone or in 50:50 mixtures with three other leaf litter species. This involved the establishment of control microcosms to assess the decomposition rates of litters when decomposed in isolation, and microcosms containing the 50:50 mixtures. In this way it was possible to compare 'expected' and 'observed' values for the decomposition characteristics of each of the mixtures (Chapman *et al.*, 1988; Blair *et al.*, 1990; Ineson and McTiernan, 1992).

MATERIALS AND METHODS

Preparation and watering of microcosms

Litter from pure stands of sessile oak (*Quercus petraea* Mattuschka (Liebl.)) from Gisburn, U.K. (Nat. Grid Ref. SD750585), common ash (*Fraxinus excelsior* L.) and silver birch (*Betula pendula* Roth.) from Grizedale forest, U.K. (Nat. Grid Ref. SD326915) and eucalyptus (*Eucalyptus globulus* Labill.) from Zas, Santiago de Compostela, Spain (UTM Grid Ref. 29TNH07) were collected from the forest floor immediately after leaf fall, taken to the laboratory and air-dried at room temperature. A sub-sample was sorted to remove debris, and petioles were also removed. The oak and ash leaves were cut into approximately 2 cm^2 pieces, while the birch leaves (minus petioles) were used whole. Samples of each leaf litter were retained for dry weight and initial nutrient content determinations (see below).

Each pure litter, 2.0 g, was added to microcosm chambers (Anderson and Ineson, 1982). The units, each with six replicates, formed control treatments containing pure ash (ASH), birch (BIR), eucalyptus (EUC) and oak (OAK) litter.

A similar series of microcosms were established containing the three mixtures of eucalyptus + oak (EUCOAK), eucalyptus + ash (EUCASH) and eucalyptus + birch (EUCBIR). Litter mixtures were prepared using 1 g of eucalyptus litter mixed with 1 g of oak, ash or birch, respectively, and the litters were thoroughly mixed to give maximum surface contact between the litters.

The litter in each microcosm was re-hydrated by the addition of 100 ml of distilled water, and soaked for 24 h, which served to leach out soluble tannins and readily-metabolizable materials (Anderson and Ineson, 1982). The litter was drained, and the first leachate discarded. Each microcosm was then inoculated with 1 ml of a coarsely-sieved suspension (1 mm mesh) of a macerate of fresh and partially decomposed litter in sterile, distilled water (Anderson and Ineson, 1982). The litter used for the inoculum was collected from the floor of a mixed deciduous–coniferous woodland in Lancashire, U.K.

The microcosms were kept in a water-cooled cabinet at 15°C. A randomised block design was used with one replicate of each pure and mixed treatment being placed on each of the cabinet's shelves. After 7 days, all of the microcosms were leached with 125 ml of distilled water, with leachates being retained for chemical analysis. Leaching was performed by repeated gentle immersion of the litter in the distilled water, draining under gravity, and re-application of the leachate to the surface of the litter. The litter was re-immersed three times on each sampling occasion, which ensured thorough equilibration of mineralised nutrients between the litter and the leachate (Anderson and Ineson, 1982). This procedure was repeated every 2 wk during the 13 week experiment.

Respiration measurements

Carbon dioxide evolution was monitored using an infra-red gas analysis (IRGA) system (Dursun *et al.*, 1993), on the day after leaching. For these measurements the microcosm inners were removed from the microcosms and placed into air-tight glass jars (500 ml), where they were flushed with CO_2-free air for 1 min. CO_2 evolution was then measured over the subsequent 4 h. All respiration and chemical analyses data are presented on a dry weight basis.

Chemical analyses of leachates

Shortly after collection, leachates were analysed for pH by using a Pye Unicam pH meter and combination electrode. Samples were then stored at 2°C and analysed for NH_4^+–N on a Technicon continuous flow autoanalyser using the salicylate-hypochlorite method, with nitroprusside as a catalyst (Gentry and Willis, 1988). Nitrate plus nitrite-N was also determined using a Technicon autoanalyser operating the hydrazine-sulphanilamide method (Allen, 1989).

Chemical analyses of litters

At the end of the experiment, the litter remaining in the microcosms was removed and carefully separated into the component litters, dried to constant weight at 80°C and analyzed for mineral composition. The pure litters, and samples of the original litter were analyzed in the same way.

Litter samples were ground in a freeze-mill (Spex 6700, Spex Industries Inc., U.S.A.) and H_2O_2–H_2SO_4 digests were performed on the four pure litters and the six separate components of the three combinations selected for terminal sampling. Three replicate digests per litter sample were performed. The digest solutions were analyzed for total-N, total-P, K, Ca and Mg. The Ca, Mg and K concentrations were determined using atomic absorption, total-N was determined by the salicylate-nitroprusside method (Berthelot reaction), and total-P by the molybdenum blue method.

Statistical analysis

The leachate concentrations for the pure litters and the mixtures were converted to equivalents g^{-1} dry weight of litter and mean values and standard errors of the means calculated. Values for pH were converted to H^+ ion concentrations and then treated as for the other leachate concentrations. Expected leachate concentrations and respiration rates were calculated as follows:

$$\text{Expected} = (\text{Observed pure litter} + \text{Observed pure eucalyptus litter})/2$$

Expected values were calculated from the data for the pure litters in the same experimental block, permitting the calculation of a mean and error term for the expected value for any mixture. Comparisons of observed and expected means were made using analyses of variance (ANOVA), using one-way ANOVA to compare mean nutrient contents.

According to the outcome of the ANOVA it was possible to classify litter mixture interactions in three ways: the simplest interaction occurred when the expected (see above) outcome from the mixture did not differ significantly ($P < 0.05$) from that actually observed, and this is referred to as no interaction. The remaining two possible interactions were positive and negative; the former being defined as when the measured release of an element was greater in the mixture than was expected from the behaviour of the component parts; 'negative interaction' was the reverse, with less release than anticipated. Correlation coefficients were computed between mass loss and initial chemical contents of the litters.

RESULTS

Litter mass loss

The litter mass losses observed during the 13 weeks of the experiment (Table 1), were greatest for ash (58%), and least for oak (28%). Eucalyptus and birch had similar, but intermediate weight losses.

Only two types of interaction were found for litter mass loss in mixtures; either a mixture showed a positive or non-significant interaction. Negative interactions, in which one litter inhibited the decomposition of another, were not observed (Table 1). Positive interactions appeared to occur for the decomposition of eucalyptus when in combination with ash (EUCASH) and birch (EUCBIR), with mass loss of eucalyptus increasing from 37 to 40%, yet these effects were not significant. Mass loss by eucalyptus litter in the presence of oak litter was very similar to eucalyptus decomposing alone (37%). In contrast, oak showed a significant increase in mass loss when in mixture with eucalyptus (Table 1). An apparent increase in the decomposition of ash (62%) in combination with eucalyptus was also observed (ash alone; 58%), but this difference was not significant. Birch mass loss failed to show any interactions.

Respiration

Respiration rates were highest during the first 2 wk of the study for all litter types, due to the large amounts of available C in the fresh litters, but these initial high rates decreased rapidly. CO_2 release rates over the entire experimental period differed significantly between litters. The highest respiration values were observed for ash litter, ranging between 1.0 and 4.2 ml 100 g^{-1} h^{-1} during the 13 week study; the lowest rates were for oak litter, with a range of values from 0.7–1.2 ml 100 g^{-1} h^{-1} (Fig. 1). Eucalyptus showed a high rate of respiration, close to that of ash (1.2–3.7 ml 100 g^{-1} h^{-1}), resulting in a significantly higher total CO_2 efflux than for oak or birch. CO_2 release from pure ash litter was slightly higher than for the eucalyptus litter during the first 9 wk of the study, but the situation

Table 1. Mass loss of leaf litter during the 13 week microcosm experiment, expressed as a percentage of the original dry weight. Values are means (n = 6), with standard deviations in brackets. Litter type codes are described in the text. Significant differences in mass loss of a component litter, when comparing pure and mixture treatments are shown (*p < 0.05)

Litter type		Mass loss (%)	
Component A	Component B	Component A	Component B
EUC	EUC	36.6 (2.0)	
OAK	OAK	27.8 (0.9)	
ASH	ASH	58.3 (1.4)	
BIR	BIR	35.6 (0.8)	
EUC	OAK	35.4 (1.7)	31.2 (1.4)*
EUC	ASH	40.4 (4.2)	62.0 (4.0)
EUC	BIR	40.3 (2.9)	34.4 (2.0)

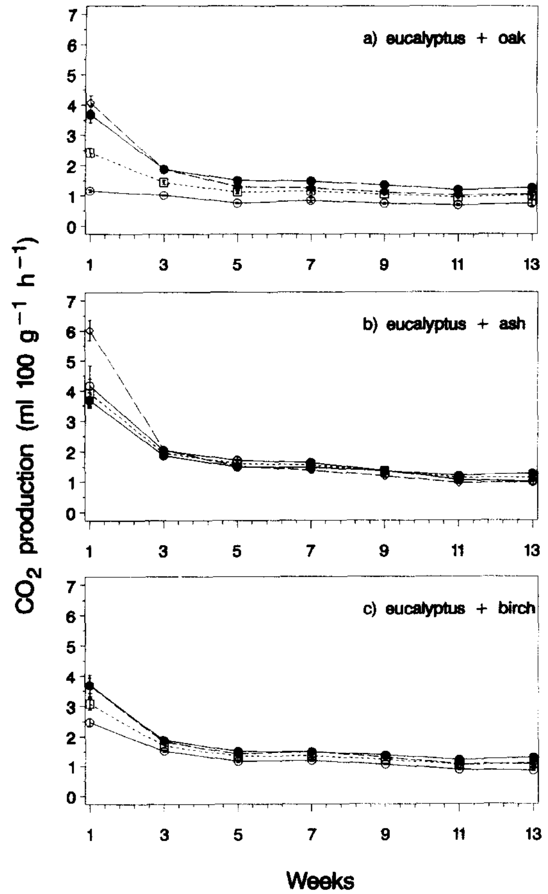

Fig. 1. Carbon dioxide evolution (ml CO_2 100 g^{-1} h^{-1}) from microcosms containing: (a) EUCOAK; (b) EUCASH and (c) EUCBIR litters. Pure eucalypt litter is shown as (●); pure oak, ash and birch litters as (○); observed values of the mixture as (◇) and the calculated expected values as (□). Values are means with standard errors, $n = 6$.

reversed after 9 weeks, with overall CO_2 losses showing no significant differences.

Two different interaction types (as defined above) were observed when pure litters and mixtures were compared; positive interaction and no interaction (Fig. 1). Again, as for mass loss, CO_2 release from all litter components was never slower when mixed with a second litter type than when in isolation. A marked positive interaction was seen for the EUCOAK mixture (Fig. 1 (a)), where the observed amount of CO_2 released significantly exceeded the expected amounts, during the earlier part of the experiment.

For the EUCASH mixture (Fig. 1(b)) an interaction was found only for week 1 when the observed value of the mixture significantly exceeded predicted values. A similar interaction was observed for the EUCBIR mixture (Fig. 1(c)).

Inorganic N

The highest amounts of NH_4^+ release were observed for the ash litter, ranging from 15 to 144 μg N g^{-1} 2 wk^{-1}, whereas no detectable NH_4^+ release was observed for either pure oak or pure birch litter throughout the entire experiment, suggesting total N retention by these two litters (Fig. 2). A small amount of NH_4^+ release was detected (0–14 μg N g^{-1} 2 wk^{-1}) for the eucalyptus litter.

The N release data for the litter mixtures show a positive interaction in the case of the EUCASH mixture (Fig. 2(b)), with observed N mineralization becoming significantly greater than expected after week 3, and remaining so until week 13. Little N mineralization was observed from either the EUCOAK or EUCBIR mixtures (Fig. 2(a) and (c),

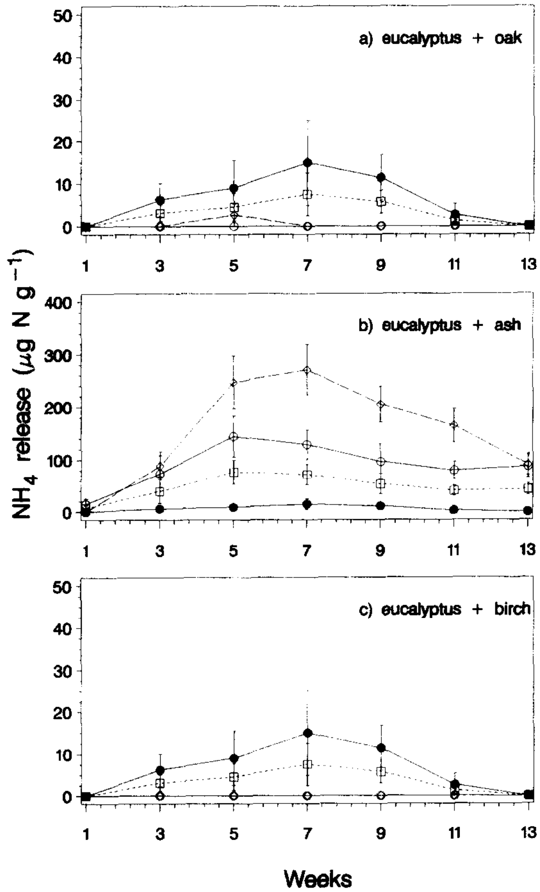

Fig. 2. Ammonium release (μg NH_4–N g^{-1} 2 $weeks^{-1}$) from microcosms containing: (a) EUCOAK; (b) EUCASH; (c) EUCBIR litters. Pure eucalypt litter is shown as (●); pure oak, ash and birch litters as (○); observed values of the mixture as (◇) and the calculated expected values as (□). Note the different scale for the EUCASH mixture. Values are means with standard errors, $n = 6$.

respectively) suggesting a considerable reduction in net N mineralisation when eucalyptus was combined with these litters. NO_3^- did not appear in any of the leachates from either pure or mixed litter types, during the entire experiment.

Hydrogen ions

Leachates from eucalyptus litter had the highest concentrations of H^+ ions (ranging from 120–290 ng g^{-1} 2 wk^{-1} during the 13 weeks of study), being consistently and significantly different from pure ash and birch litters (Fig. 3). The lowest H^+ release, *i.e.* highest leachate pH values, were observed for the ash litter microcosms [3–10 ng H^+ g^{-1} 2 wk^{-1}; Fig. 3(b)].

H^+ release from eucalyptus gradually increased during the course of the experiment with the lowest pH being observed at wk 9. This contrasted with the other pure litter types, in that they maintained a relatively constant leachate pH throughout the experiment.

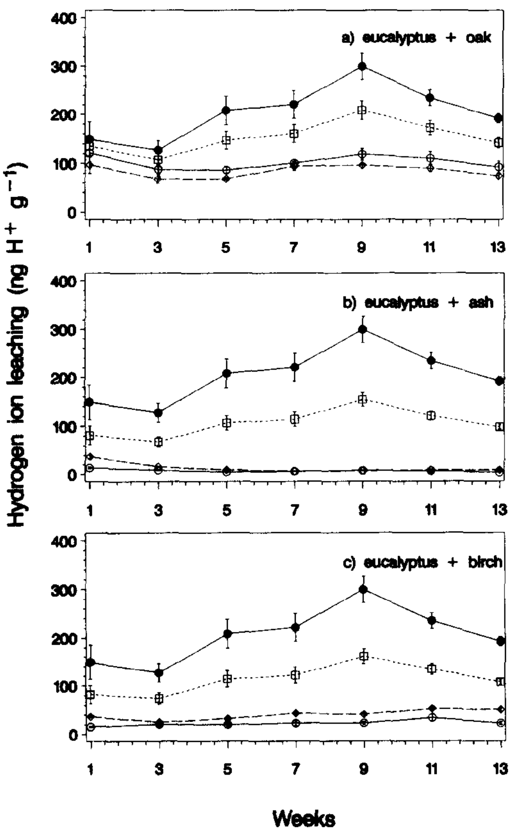

Fig. 3. Hydrogen ions release (ng H^+ g^{-1} 2 $weeks^{-1}$) from microcosms containing: (a) EUCOAK; (b) EUCASH; (c) EUCBIR litters. Pure eucalypt litter is shown as (●); pure oak, ash and birch litters as (○); observed values of the mixture as (◇) and the calculated expected values as (□). Values are means with standard errors, $n = 6$.

A significant reduction of leachate acidity in mixture, as compared to that of pure eucalyptus litter, was observed (Fig. 3). In the EUCOAK mixture this difference was significant after 3 wk, whereas it occurred for the EUCASH and EUCBIR mixtures throughout the experiment.

Mineral composition of the litters

Initial litter N content (Table 2) showed a strong correlation with mass loss (Table 1) ($r^2 = 0.967$, $P < 0.01$), indicating that litter N content was an important resource quality attribute, and could be used to predict decomposition rates in these systems. For example, oak litter, with the lowest initial N content, decomposed far more slowly than the ash litter and, moreover, calculations of the mean N content of the mixed litters enabled accurate predictions of mass loss in mixture (Fig. 4).

Magnesium also showed a strong linear relationship with mass loss ($r^2 = 0.951$, $P < 0.01$) with, again, the lowest initial content for oak (0.14%), and highest values were found for ash (0.44%). No strong correlations were found between decomposition rate and other initial litter mineral contents.

Table 2 identifies where significant differences in the elemental composition of the same litter in pure and mixed litters occurred, and does not provide a statistical comparison of initial and final concentrations for a given litter.

If the elemental changes for *pure* litters occurring during the course of the experiment are considered first, K appeared to be readily leached from all the litter types, giving lower ($P < 0.01$) contents of this cation at the end of the experiment in all the litters (Table 2). Calcium concentrations in the litters either remained around the initial values or increased slightly with time, with birch litter showing a significant increase ($P < 0.05$) during the experiment. No significant changes were found in total Ca contents in the eucalyptus, ash or oak litters. Litter N concentrations increased significantly in all litter types by the end of the experiment, whereas significant reductions in Mg contents were detected in oak ($P < 0.01$) and ash ($P < 0.01$), and for P in oak and birch litters.

The presence of another litter frequently affected the final nutrient content of the eucalyptus litter (Table 2); for example the final K content was always significantly higher ($P < 0.01$) in the eucalyptus litter decomposed in mixture, when compared to the pure eucalyptus litter. Similarly, final litter Ca content was generally higher in the eucalyptus when decomposed in mixture, with significant differences in the eucalyptus components of the EUCOAK ($P < 0.05$) and EUCASH ($P < 0.01$) mixtures.

The final elemental compositions of the other litter components of the eucalyptus mixtures were also frequently different from the respective pure treat-

Table 2. Chemical analysis of the litter at the beginning (initial) and end of the experiment. Values are given as mean percentage of dry weight (n = 6). Litter type codes are described in the text. Significant differences between the chemical composition of a component litter in pure and mixture treaments are shown (*p <0.05, **p <0.01)

Litter type	Component	Time	Elemental content (% dry weight)				
			K	Ca	Mg	P	N
EUC	EUC	Initial	0.08	0.5	0.18	0.06	1.3
EUC	EUC	End	0.06	0.6	0.17	0.08	1.9
EUCOAK	EUC	End	0.09**	1.0*	0.13**	0.06	1.5
EUCASH	EUC	End	0.07**	1.5**	0.15	0.06	1.6
EUCBIR	EUC	End	0.11**	0.8	0.16	0.06	1.4*
ASH	ASH	Initial	0.92	3.0	0.44	0.07	2.2
ASH	ASH	End	0.04	2.9	0.20	0.07	3.8
EUCASH	ASH	End	0.08	2.0**	0.19	0.08	3.4
BIR	BIR	Initial	1.10	1.0	0.20	0.22	1.4
BIR	BIR	End	0.15	1.4	0.19	0.10	1.8
EUCBIR	BIR	End	0.10**	1.1*	0.16	0.10	2.1*
OAK	OAK	Initial	0.31	1.9	0.14	0.05	1.0
OAK	OAK	End	0.05	2.1	0.11	0.02	1.2
EUCOAK	OAK	End	0.07*	2.0	0.15**	0.04**	1.5**

ments; for example, the birch component of the EUCBIR mixture contained significantly less K and Ca than the pure birch, whilst N behaved in exactly the opposite direction. The final concentrations of nearly all the elements tested were higher in the oak residues from mixture with eucalyptus, with the exception of Ca (Table 2).

DISCUSSION

The mass losses exhibited by the non-eucalyptus litters in our study fitted well with previous studies, in that the ash and birch litters decomposed rapidly, whilst the oak was much slower (Satchell and Lowe, 1967). However, the decomposition of the eucalyptus paralleled that of the birch litter in terms of mass loss, and did not confirm the reputation of eucalyptus as a recalcitrant litter (see the Introduction). The rate of decomposition of the eucalyptus fitted well with the overall relationship

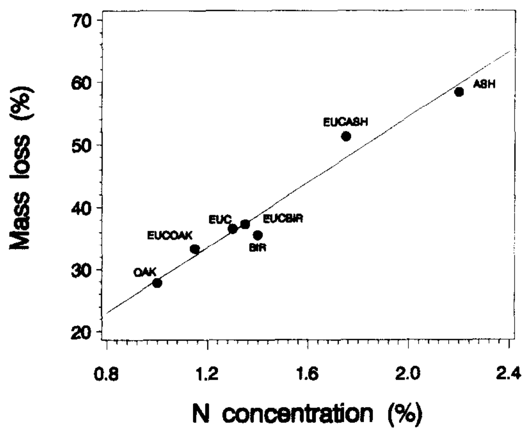

Fig. 4. Correlation between mass loss (%) and initial N content (%) in pure and mixed litters (r^2 = 0.97). Litter type codes are described in the text.

between initial N content and decomposition rates found across the four litters studied. The respiration data from the microcosms confirmed the order of decomposition of the four litters as ash > eucalyptus > birch > oak, corresponding well with the mass loss data.

Our work confirmed the generalisation that decomposition rates across a wide variety of litter types is related to initial N contents (Melillo *et al.*, 1982; Taylor *et al.*, 1989b), and that the significant but small increase in oak litter decomposition rates in the presence of eucalyptus was insufficient to modify this basic relationship (Fig. 4). Examination of Fig. 4 reveals that the mixed litters always fell above any line drawn between the two pure litters which comprised the mixture, suggesting that mass loss tended to be enhanced in mixture. However, the only significant change in mass loss resulting from mixture with eucalyptus was for oak, which showed enhanced decomposition. The effect of mixing with other litters, in terms of mass loss, confirmed an earlier observation that litters in mixtures rarely decompose more slowly in mixture than when in isolation, and frequently decompose faster (Ineson and McTiernan, 1992).

This interaction between oak and eucalyptus was confirmed by the CO_2 data, which showed that CO_2 production in the EUCOAK mixture initially far exceeded that expected; the mixture supported greater respiration than the eucalyptus alone, even though half of the material was oak, with its much lower basic respiration rate (Fig. 1(a)). Combining the mass loss data with those from the respiration studies suggests that the 'extra' C found in the respired CO_2 came from the oak litter. Similar, but more short-lived, interactions were apparent from the respiration data for other mixtures, but were not sufficiently large or long-termed to be reflected in respective mass losses. The respiration data demonstrated that the litter populations on the two litters interacted, and that these interactions were also reflected both in NH_4^+ leaching and total elemental compositions.

From the EUCOAK data (Fig. 2(a)), it can be seen that the pure eucalyptus litter reached a peak of N mineralisation by around week 7, at which time the pure oak litter failed to produce any detectable mineralised N. The expected NH_4^+ leachate concentrations arising from a 50:50 mix of these two litters should be intermediate between these values, but the actual amount of mineralised N was almost negligible throughout the experiment. Thus, either the presence of oak litter prevented the eucalyptus litter from releasing N, or the microflora on the oak litter retained N mineralised from the eucalyptus. The N concentration data presented in Table 2 clearly show that a gain in N concentration was found in the oak component of the EUCOAK mixture, supporting this second hypothesis. Budget calculations, taking into account both mass loss and changes in litter N content during the experiment, revealed that the oak component of the EUCOAK mixture actually gained N during the 13 wk of the study. This is in marked contrast to the N dynamics in the pure eucalyptus and oak litters. Similar conclusions can be drawn from the data for the EUCBIR mixture.

Microcosms containing the EUCASH mixture produced nearly twice as much mineral N as the pure ash microcosms, even though they contained half as much ash litter. The ash litter must have been responsible for producing this additional mineral N in the presence of eucalyptus litter, since the total amount of N in the eucalyptus component was very similar at the end of the experiment in all mixtures. In contrast, the ash component of the EUCASH mixture showed both increased mass loss and reductions in N content when compared with ash decomposing alone. Ineson and McTiernan (1992) demonstrated increased biological activity in mixed Norway spruce and oak litters, with associated increased N immobilisation. Our results agree, in that CO_2 efflux was greater in eucalyptus mixtures than in the equivalent pure oak and birch litters (after 7 wk). Therefore, the onset and duration of N mineralisation from decomposing litters can be modified by mixing with other litter types and offers the potential for synchronising nutrient mineralisation to plant uptake.

Although we do not have data for cation concentrations in litter leachates, the chemical analyses data presented in Table 2 support the conclusion that Ca and Mg moved between the litters. Significant decreases in the Mg content of eucalyptus decomposing in mixture with oak were mirrored by increases in the final Mg content of the oak litter; in the EUCASH mixture the eucalyptus showed an increase in total Ca content, whereas the ash lost significantly more Ca in the EUCASH treatment than when decomposing alone. These examples support the hypothesis that inter-specific movement of nutrients occurs in litter mixtures, apparently governed by nutrient gradients. The situation is analogous to that reported for the importance of mycorrhizal connections in transporting elements between higher plants (Read *et al.*, 1985), and we propose that fungal hyphae are the main agents linking resources of different qualities in our mixture experiments. This lends support to the suggestion (Wood, 1974) that the marked increases in total N content during the decomposition of eucalyptus leaves were due to N translocation by fungal hyphae.

Eucalyptus litter produced acidic leachates, and this was invariably modified by the addition of a second litter, with the leachates from mixed litters always being less acidic than expected values. The pH of the non-eucalyptus litter leachate dominated the resulting pH of leachates (Fig. 3), and this effect is believed to be due to the Ca contents of the litters used in the mixtures, with oak, birch and ash having initial Ca concentrations all greater than 1%, in comparison to the initial 0.5% concentration of the eucalyptus litter. This could have important implications for the development of soil faunal populations, and increases in faunal diversity have been demonstrated for certain litter combinations (Chapman *et al.*, 1988).

Although the above-ground interactions between tree species dominate the selection of mixtures in forest management, interactions below-ground may be of fundamental importance in maintenance of nutrient turnover (Brown, 1992). In highly-productive plantation forestry it becomes important to effectively manage soil development and nutrient cycling, and manipulation of litter decomposition processes may be necessary in order to maintain productivity (Adams and Attiwill, 1986). Our work suggests that mixtures of eucalyptus with other litters could be one mechanism by which the high productivity rates of eucalyptus plantations may be maintained, and that manipulation of litter mixtures could make an important contribution to synchronising nutrient release to plant uptake.

Acknowledgements—We wish to thank Dr A. Outeiro for statistical assistance. M. J. I. B. acknowledges financial support from Xunta de Galicia Research Grants Scheme, and P. I. would like to thank the European Community Environment Programme for funding aspects of this work.

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