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Litter decomposition by four functional tree types for use in silvopastoral systems

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Abstract

Litter fall and decomposition from trees in a silvopastoral system is considered to be an important factor contributing to soil quality. The hypotheses of this study are that different functional types of trees and seasonal differences in the growth of the trees affects litter quality and quantity and the rate of decomposition. Litter was collected in traps from four tree species representing four functional types, i.e. black alder (deciduous N-fixer), Tasmanian blackwood (evergreen N-fixer), red oak (deciduous non-N-fixer) and *Eucalyptus* (evergreen non-N-fixer). The rate of litter decomposition was measured using litter bags. A high rate of decay was linked to high amounts of microbial activity associated with the litter and this was affected by the differences in N and lignin content of the leaves. The leaf litter which exhibited the most rate of rapid decay and cycling of nutrients was that from the deciduous N-fixing tree species, which contained low amounts of lignin and C and high amounts of N. Tasmanian blackwood also produced N-rich litter, but the decay rate was retarded by higher contents of lignin. Non-N-fixing tree species produced leaf litter which decayed slowly due to both high contents of lignin and low amounts of N, regardless of whether the species were deciduous or evergreen. The initial lignin content and the lignin-to-N ratio in leaf litter emerge as likely controls of the rate of decay and therefore as predictors of the relative abilities of the different tree species to contribute nutrients to the pasture systems. These litter quality characteristics appear to be independent of the functional type categories. Seasonal effects on leaf litter quantity and quality were not as important as the over-riding chemical differences between tree species. A mixture of litter types could be used to manipulate the timing of nutrient release to benefit pasture growth.

1. Introduction

Grassland farming is maintained in New Zealand through the application of fertilizer and the behavior of the grazing animal. Biodiversity of species has been reduced to a few key productive economic species and regeneration of woody species has been suppressed. This allows energy and nutrient flows to be channelled into a narrow range of plant and animal products. While this may satisfy the economic component of sustainable production systems, it may not satisfy the biological component. Increasing the biodiversity of grassland ecosystems through introduction of trees is likely to have many benefits to the farming system, i.e. stabilizing soil, providing shelter and shade to animals (Gregory, 1995), diversification of income through tree products (Young, 1991) and enhancing soil fertility (Young, 1986; White, 1987; Arshad and Coen, 1992; Gregorich et al., 1994). Our paper focuses on the contribution that different functional types of tree make to nutrient cycling via the litter fall pathway.

The two main factors affecting pasture in a silvopastoral system are light i.e. photosynthesis and supply of C and nutrient supply and transformations. This influenced our choice of tree functional types in this study, i.e. deciduous versus evergreen from a light perspective and N-fixer versus non-N-fixer from a nutrient perspective. The species selected as examples of these four functional types were black alder (*Alnus glutinosa* (L.) Gaertner) for the N-fixing deciduous type, Tasmanian blackwood (*Acacia melanoxylon* (R. Br)) for the evergreen N-fixing type, red oak (*Quercus rubra* L.) for the deciduous non-N-fixing type and eucalyptus (*Eucalyptus nitans)* for the evergreen non-N-fixing

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functional type. Nutrient flow is influenced by the timing, quantity, quality and decomposition rate of litter, all of which are determined by the functional tree type. Quantity of litter entering the system varies from a pulse to continuous fall throughout the year depending on the species. High quality litter (high N, low lignin) will decay and release nutrients quickly whereas that of low quality (low N, high lignin) will decay slowly (Swift et al., 1979). Most New Zealand pasture is in nitrogen deficit. *Trifolium repens* is the major legume used to provide N to the system. Nitrogen-fixing trees may augment this nitrogen. We have concentrated on measuring the N, C and lignin components of leaf litter as they influence decomposition and release of N (Melillo et al., 1982; Berg and Staaf, 1981; Berendse et al., 1987). Microbial activity will also assist in comparing rates of decomposition from the different functional types (Anderson and Domsch, 1978; Visser and Parkinson, 1992; Wardle, 1993).

We investigated the suitability of different functional tree types to contribute to nutrient input e.g. N from N-fixing and non-N-fixing trees and the role of lignin in the supply of nutrients from deciduous versus evergreen types, in a silvopastoral system. This was done by quantifying leaf litter fall, chemical characteristics and decomposition rate.

2. Methods

2.1. Site description

The four tree species we selected were present in small stands planted for aesthetic purposes at Horotiu (E 175° 10′: S 37° 41′), north of Hamilton, New Zealand. The oak trees were planted in 1990 and the other three species were planted in 1988. The planting densities ranged from alder at 3000 stems ha^{-1} (sph) in a 90 m^2 area, Tasmanian blackwood at 1350 sph in 252 m^2 area, eucalyptus at 3500 sph in a 125 m^2 area and a stand of eight oaks at 2000 sph. These trees had not been pruned or thinned. The understorey vegetation was predominantly unimproved, heavily shaded pasture with a high content of buttercup (*Ranunculus repens* L.). The average rainfall for the district was 120 mm per month. Average temperature for 1995 was 9°C in winter, 13°C, in spring, 18°C in summer and 15°C in autumn (NIWA, 1994, 1995).

2.2. Measurement of the litter fall

Litter was collected fortnightly, over a 14 month period (February 1994–April 1995), from six cone-shaped traps strung randomly between the tree canopies for each tree type. These traps were made from 1 mm mesh fiberglass cloth. The 50 cm diameter trap openings were between 1.5 and 2 m above the ground. Only the leaf portion of the litter was collected, oven dried at 70°C overnight, then weighed. To calculate the quantity of litter per unit area the weight of litter present in each litter trap was divided by the total area of the trap and converted to a per hectare basis.

2.3. Measurement of litter decomposition

Leaf litter was collected from the ground around each litter trap site for subsequent measurement of decomposition rate. Entire, fresh litter was preferentially collected to ensure that all species had leaves in similar condition. Leaf litter from the evergreen trees was collected and laid down in three seasons: winter (June 1994), spring (September 1994) and summer (February 1995). This was done to check for any seasonal differences in leaf characteristics and decomposition rate. The single pulse of litter produced by deciduous trees was laid down in winter. All leaf material was dried in an oven overnight at 80°C to standardize the moisture content of the litter.

Decomposition was evaluated using the litter bag technique (Swift et al., 1979; Wardle et al., 1993). Litter decomposition bags (10×20 cm) were constructed from fiberglass 1 mm mesh cloth. Six grams of dried, intact leaf litter was placed in each bag. The bags were pinned to the ground under the trees from where the litter was collected. The pasture at these sites was not grazed, but was kept clipped to an approximate height of 5 cm, to reduce variation in the microclimate of the ground cover tier which might otherwise have created variation in the decomposition environment.

One litter bag from each replicate block for each tree species was sampled at approximately 8 week intervals. Harvest of the winter set of bags covered a 48 week period. A greater number of bags from evergreen trees were laid in the spring and summer allowing sampling to continue for 72 and 56 weeks respectively. Litter weight was recorded for all replicates each time litter bags were harvested. Upon collection all soil and roots adhering to the litter were removed, and the litter dried at 80°C for at least 15 h prior to weighing.

The total content of N and C for litter was measured for a composite dried sample for each treatment at each harvest. The measurements were made with a Europa Scientific elemental analyzer with a GC (Anca SL) using the dry combustion DUMAS method (Bremner and Mulvaney, 1982; McGill and Figueiredo, 1993) and was coupled to a mass spectrometer for element detection.

Lignin was determined using a modification of the approach of Cunniff (1995). Lignin determinations were made on a dried 1 g subsample from the com-

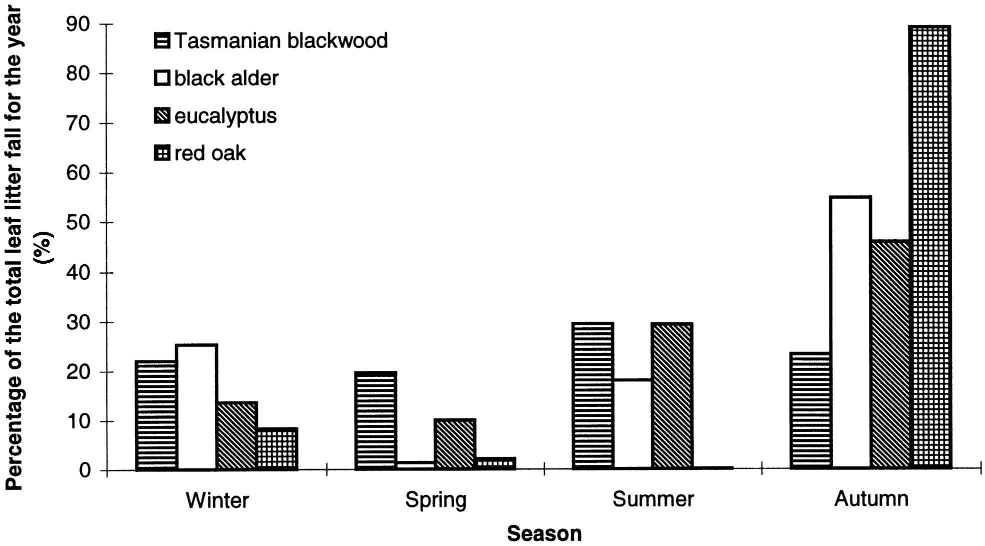

Fig. 1. Leaf litter component from six traps for each species at Horotiu presented as a percentage of the total fall throughout one year.

bined replicates of the litter bags at each harvest. The acid detergent fibre assay was used to determine the lignocellulose content, and the cellulose was then removed by a lignin determination assay. The lignin content was calculated as a percentage of the total sample weight.

The activity and relative biomass of decomposer microorganisms on the leaf litter was estimated by measuring the evolution of CO_2 from incubated subsamples. Microbial activity was measured using undried leaf litter from each harvest. Two subsamples of leaf litter were placed in 169 ml air tight containers, one with glucose addition at 10,000 μg g^{-1} litter and one without. The difference in CO_2–C concentration between 1 and 4 h incubations was determined with an infrared gas analyzer. Measurements from the container without glucose represented the basal respiration (BR) of the microorganisms present and those from the container with glucose represented substrate induced respiration (SIR). The ratio of BR to SIR was used as a relative measure of the microbial metabolic quotient (MQ), which is inversely related to microbe efficiency in conserving carbon sources (Sparling, 1992; Wardle, 1992).

2.4. Calculations

Decay rate constants were calculated for each functional type. For each litter type, regression was used to relate the log of the weight to time, and the slopes of these relationships were used to determine the decay constants. These decay constants were then analyzed by linear regression to test whether there were significant differences between species, seasons or planting densities. The changes in time of MQ, C-to-N ratio, lignin-to-N ratio, weight, C, N and lignin content were analyzed by a mixed model smoother Flexi (Upsdell, 1994). The means over the different planting densities for each species and time point are plotted in Fig. 2 together with the estimated value and 95% confidence band for the predicted curve.

3. Results

3.1. Litter fall pattern and chemical quality

Leaf drop occurred throughout the year for all species with the deciduous trees and eucalyptus demonstrating a pulse in leaf fall during autumn early winter (Fig. 1). In contrast the Tasmanian blackwoods shed leaves evenly throughout the year. Alder and oak shed 3920 and 660; Tasmanian blackwood and eucalyptus shed 3280 and 6040. During the peak period of litter fall the N-fixers typically had a much higher N content than did the non-N-fixers (Table 1). Litter C content was similar (48%) across functional types. Alder had the lowest lignin content (19.8%) and Tasmanian blackwood the greatest (34.9%). The N-fixers had a low C-to-N ratio and low lignin-to-N ratio compared with the non-N-fixers (Table 1). Alder had a lignin-to-N ratio which was half of that of Tasmanian blackwood. Seasonal differences in N, C and lignin content were minimal for both Tasmanian blackwood and eucalyptus and the results across season are therefore presented across the whole year.

3.2. Decomposition

Alder had a significantly ($P < 0.01$) faster decay rate ($k = 0.0368$) than the other tree types, with half the original weight being lost after 17 weeks (Table 2,

Table 1
Initial concentrations of N, C, lignin and the ratio of initial C to initial N and initial lignin to initial N for each of the functional types

Species	Initial concentration (%)			%C-to-%N (initial)	%lignin-to-%N (initial)
	C	N	Lignin		
Alder	46.2	2.43	19.8	19.0	8.1
Oak	49.2	0.71	26.2	69.3	36.8
Eucalyptus	51.3	0.66	25.3	77.7	38.3
Tasmanian blackwood	47.6	1.77	34.9	26.9	19.7

Fig. 2). Oak, eucalyptus and Tasmanian blackwood did not reach their half life during the period of sampling but it was predicted to be 96, 116 and 124 weeks, respectively. Half the C present in alder disappeared within the first 10 d of decomposition, and thereafter the rate of disappearance continued slowly (Fig. 2). Alder had a significantly ($P < 0.01$) faster decay rate of C ($k = 0.052$) compared with the other tree types (Table 2).

Alder released N faster ($P < 0.01$) than the other tree types, with less than 0.1% remaining at the end of the 48 week sampling. In contrast there was little disappearance of N in Tasmanian blackwood litter (Fig. 2). Both oak and eucalyptus accumulated N (Table 2), with the N content of oak doubling over the 48 week sampling (Fig. 2). Some N accumulated in eucalyptus litter but there was a lesser amount in Tasmanian blackwood litter.

Half of the lignin present in the alder litter had disappeared by 12 d and less than 1% lignin remained at the end of the sampling. Little lignin reduction occurred in the other tree types (Table 2). There was a slight lignin accumulation at the start of the sampling, with oak and eucalyptus followed by little change (Fig. 2).

The microbial metabolic quotent (MQ) associated with alder declined after 32 weeks and rose slightly (Fig. 2). A similar trend was noted for Tasmanian blackwood leaf litter but the sampling ended before confirmation of a rise in MQ was measured. The decrease in MQ for oak and eucalyptus litter was not as rapid as for the N-fixing tree leaf litter.

The oak and eucalyptus lignin-to-N ratio declined steadily, in contrast to that of alder which steadily increased and Tasmanian blackwood which remained constant. The C-to-N ratio for all functional types followed similar patterns of reduction despite starting from different initial quantities. The decay rate constants for weight were regressed against the initial litter quality variables (C, N, lignin, C-to-N, lignin-to-N) in an attempt to use initial values as a predictor of weight loss. Initial lignin accounted for 27% of the overall variance associated with weight loss. Neither C, N nor C-to-N ratio contributed to the overall variance of weight loss as the F ratio was less than 1. The lignin-to-N ratio accounted for 0.4% of the total variation in weight loss. This was increased to 8% by using the log(lignin-to-N) ratio and to 44% if the log(lignin) and log(N) variables were used independently without their coefficients being forced to be the same in absolute value but opposite in sign.

4. Discussion

The main differences between deciduous and evergreen species was in the patterns of litterfall rather than in terms of decomposition or litter quality. Litter of N-fixers did not necessarily have a higher decomposition rate despite having a high N concentration

Table 2
Decay rate constants and standard errors ($n = 16$) for weight, N, C and lignin for each functional type, calculated from the slope of log(weight) versus time

Species	Weight	C	N	Lignin
Alder	0.0368 (0.0025)	0.052 (0.0027)	0.0446 (0.0029)	0.0385 (0.0029)
Oak	0.0070 (0.0025)	0.009 (0.0027)	−0.0119 (0.0029)	−0.0022 (0.0029)
Eucalyptus	0.0081 (0.0014)	0.009 (0.0016)	−0.0048 (0.0017)	0.0000 (0.0017)
Tasmanian blackwood	0.0066 (0.0007)	0.008 (0.0008)	0.0006 (0.0008)	0.0022 (0.0008)
Significance	*	*	*	*

*Treatment (species) effects are significant at $P = 0.05$ following one-way ANOVA.

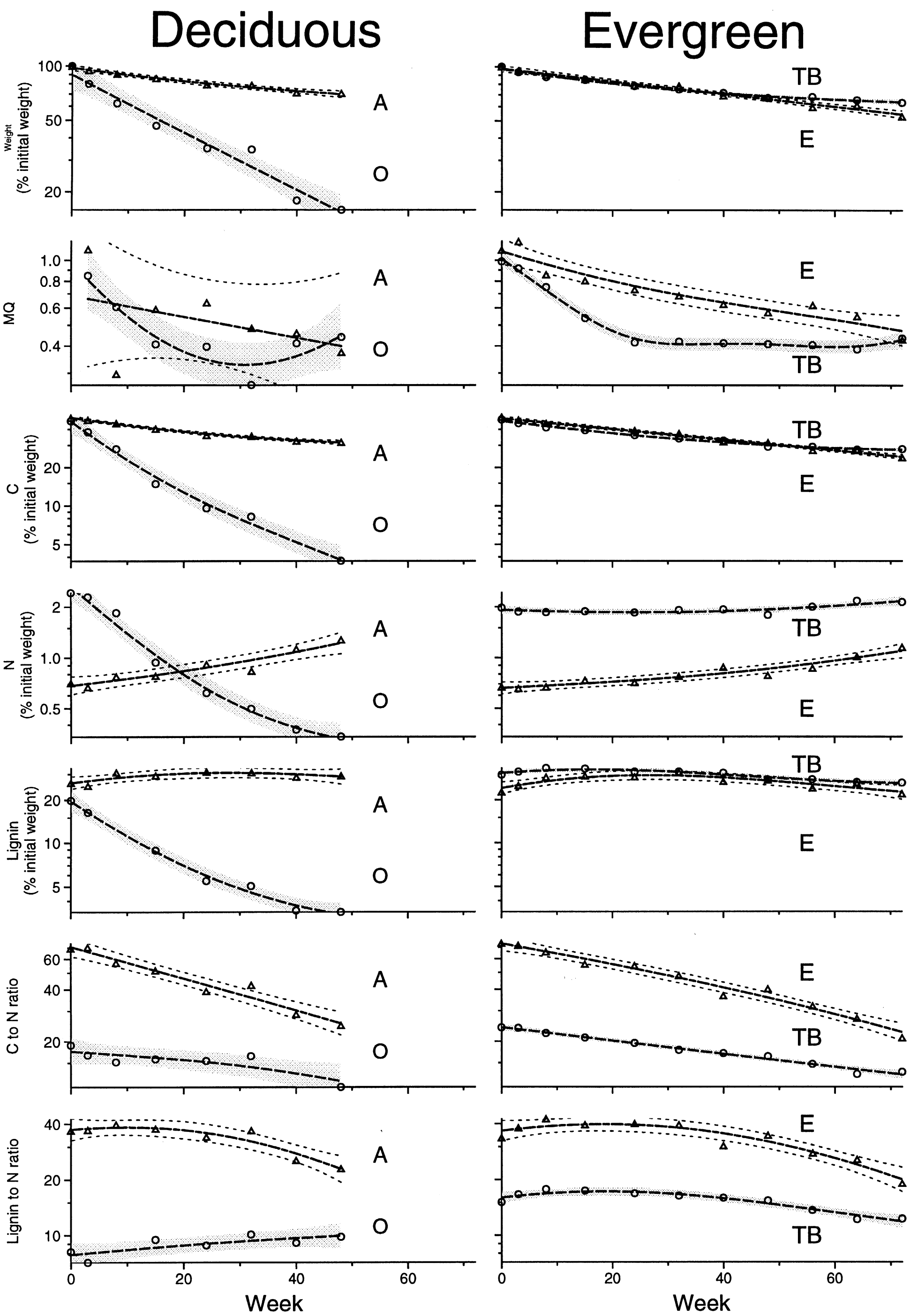

Fig. 2. Decay rates for weight, N, C and lignin as a percentage of the initial weight of leaf material and the metabolic quotient, C-to-N ratio and Lignin-to-N ratio over the sampling period. Red oak, △; black alder, •; eucalyptus, △; Tasmanian blackwood ○. The dotted lines are the confidence limits associated with the lines fitted using FLEX1 (Upsdell, 1994).

therefore the concept of this group as a functional type with regard to decomposition was not upheld. Chemical components of leaf litter were better predictors of nutrient release than was broad functional type classification. Of the chemical components measured in our study, lignin values were the best for predicting the decay rate of litter. Previous investigators have used the lignin-to-N ratio to determine decomposition and nutrient release (Melillo et al., 1982). We suspect that they may have found a better relationship if they had regressed litter decay with both lignin and 1/N without forcing the coefficients of lignin and 1/N to be the same such as occurs when the lignin-to-N ratio is used. Over half the percentage variation in decay rate of weight was unaccounted for. There is usually a rapid loss of soluble sugars followed by polysaccharides, cellulose, hemicellulose and finally lignin (Swift et al., 1979). Polyphenolic compounds and nutrient elements e.g. P, Ca, Mg, etc. may all also influence the rate of decomposition (Swift et al., 1979; Edmonds, 1980). We did not measure these components. Moisture and temperature also influence decomposition (Meentemeyer, 1978; Swift et al., 1979; Edmonds, 1980) although in this study the patterns and rates of nutrient release were similar across seasons.

The MQ for a particular tree species is a reflection of the chemical composition of the litter. Litter with large amounts of lignin coupled with low relative amounts of N typically bear a stressed microbial community (Hobbie, 1992) and a high MQ, reflective of a lack of response to the addition of glucose, as demonstrated by oak and eucalyptus. The rapid decline in the MQ of litter from N-fixers represented a rapid colonization of new leaf litter by microbes. A stable phase followed when competition for resources was high. The increase in MQ for alder litter after the stable phase indicated a shift from domination by competitive to stress tolerator microbes which increased in the litter as resources were depleted (Wardle, 1993). The more advanced stage of microbe community development observed in the alder litter can be interpreted as an indication of faster decay rates which arise when the chemical quality of the litter is amendable to decomposition. The quality of eucalyptus and oak litter as a medium for microbial activity was poor and it provided a nutrient-stressed environment for microbes after the soluble sugars were used up in the early phases. This resulted in a much higher MQ than that recorded for other litter types throughout the decomposition process and appears to be associated with a slower decay rate.

A change in litter N over time was evident particularly for alder in which there was a rapid release without a period of initial accumulation, unlike the other species. A release of N occurred at a C-to-N ratio of 19 which corresponded to 2.4% N, and this is consistent with the studies of Bocock (1964) and Mulder et al. (1969). The relative increase of N in decomposing litter has been frequently recorded (e.g. Bocock, 1964; Edmonds, 1979, 1980). Accumulation occurred at N contents of 0.7%, which is similar to other reported studies (Bocock, 1964; Berg and Staaf, 1981). There are many reported reasons for the accumulation of N, none of which were tested in this work but a net increase could indicate an uptake of N from the environment. Studies on sessile oak have shown atmospheric precipitation, insect frass and tree canopy plant material to be a source of N (Bocock, 1964). Occasionally fungal hyphae were observed on the decomposing litter and they may have translocated N from the surrounding environment such as was observed by Berg and Soderstrom (1979) with pine needle litter.

The lack of N release from Tasmanian blackwood, which had a relatively high initial concentration of N, may be due to its high lignin content (35%). Data exists which suggests that lignin products serve as a sink for accumulated N (Berg and Staaf, 1987). Coldwell and Delong (1950) found release of N from litter with a low lignin content (15%) but accumulation in those with higher content (30%). The expected input of N into the soil system from leaf litter which accumulates N will therefore not commence rapidly but will act as a sink with a slow release pattern. This may be of benefit to a pasture system in which growth is slowing down at the time of peak deciduous litter fall and which is therefore unable to fully utilize N rapidly released from a species such as alder. A mixture of litter types with different release patterns should ensure minimal leaching from the system. Other litter components which were caught in the traps were catkins, bark and twigs. Although no chemical analysis was done on this litter it can be expected that it would have a high lignin content and therefore act as sink for N. Therefore planting mixtures of trees or having different pruning managements would be beneficial for manipulating the timing of nutrient release so as to benefit pasture growth. This management technique has been successful with matching trees with cropping systems (Young, 1991).

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