

Short-term and long-term effects of tannins on nitrogen mineralisation and litter decomposition in kauri (*Agathis australis* (D. Don) Lindl.) forests

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Abstract Kauri (*Agathis australis* (D. Don) Lindl.) occurs naturally in the warm temperate forest of northern New Zealand where it grows mixed with angiosperm tree species. Below mature kauri trees thick organic layers develop in which large amounts of nitrogen are accumulated. This nitrogen seems to be inaccessible to plants. While litter quality can explain the low decomposition rate below kauri, it is not known what causes the accumulation of nitrogen. We hypothesised that kauri tannins reduce nitrogen mineralisation and litter decomposition below kauri. We further hypothesised that high tannin concentrations in the soil would increase the availability of dissolved organic nitrogen relative to the availability of inorganic nitrogen. To test these hypotheses a laboratory incubation was carried out for 1 year. Purified tannins of kauri and of two other common New Zealand tree species were added to samples of the soil organic layer from under a kauri tree. The results suggest

that during the first month of incubation the added tannins reduced nitrogen availability by sequestering proteins or by stimulating nitrogen immobilisation. In the long-term, the reduced nitrogen release, which was found following tannin addition, seems attributable to the complexation of proteins by tannins. It further appeared that the addition of tannins did not change the ratio of dissolved organic nitrogen to inorganic nitrogen in the long-term. We conclude that the effect of kauri tannins on nitrogen release offers a good explanation for the accumulation of nitrogen below kauri trees.

Keywords Decomposition · Kauri (*Agathis australis*) · Nitrogen mineralisation · Tannin

Introduction

The New Zealand kauri tree (*Agathis australis* (D. Don) Lindl.) can be regarded as a long-lived pioneer. It establishes early in the succession in relatively open “pioneer” conditions, but trees can live for more than 1,000 years (Ogden and Stewart 1995). Kauri occurs naturally in the warm temperate forest of northern New Zealand where it grows mixed with angiosperm tree species. Below mature kauri trees very thick organic layers develop, attaining a thickness of 2 m or more near the trunk of the tree (Silvester and Orchard

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1999). The organic layer contains large amounts of nitrogen—up to 0.65 kg N/m^2 —that seem to be inaccessible to plants (Silvester 2000) and it is assumed that the thick organic layer leads to podzolisation of the underlying soil (Swindale 1957; Jongkind and Buurman in press).

The accumulation of organic matter below kauri can at least partly be explained by its litterfall. Kauri leaves have a thick and extremely heavy cuticle (Barton 1982). Kauri leaf litter accounts for only about 35% of kauri litterfall; over 40% is made up of woody material like cones, branches, and bark (Enright 1999; Silvester and Orchard 1999). One way that plants can affect nitrogen mineralisation is by the production of polyphenols. Earlier studies indicate that polyphenols of kauri play a role in the podzolisation process under kauri (Bloomfield 1957). Phenolics are chemically defined as compounds that possess an aromatic ring bearing a hydroxyl substituent, including their functional derivatives. Polyphenols have several or many phenolic hydroxyl substituents (Waterman and Mole 1994). The most abundant polyphenols of woody plants are condensed tannins. Tannins—polyphenolic compounds ranging in molecular weight between 500 Da and 3,000 Da—are present in plant cells in vacuoles, cell walls and in the intercellular spaces (Hättenschwiler and Vitousek 2000; Kraus et al. 2003a). They can leach from plant tissue (Hernes et al. 2001) and thus reach the soil.

Nitrogen availability and litter decomposition can be reduced in several ways by polyphenols. Polyphenols, and especially those of relatively high molecular weight like tannins, have the ability to sequester proteins in complexes that are resistant to decomposition. Polyphenols may also inhibit microbial activity by being toxic or by interacting with microbial exoenzymes. Further, especially the compounds of low molecular weight, may act as a carbon source for the growth of microbes, which can lead to the immobilisation of nitrogen. Polyphenols may also reduce decomposition by themselves being resistant to decomposition, or by coating other compounds (Field and Lettinga 1992; Hättenschwiler and Vitousek 2000; Kraus et al. 2003a).

In this study we tested four hypotheses. The first was that polyphenols of kauri reduce nitro-

gen mineralisation. The second was that polyphenols of kauri reduce litter decomposition. Since especially large polyphenol molecules like tannins are able to sequester proteins, we focussed on tannins. Northup et al. (1995, 1998) suggest that polyphenols in plant litter can benefit the plants by altering the availability of dissolved organic nitrogen (DON) and inorganic nitrogen. This would be beneficial for those plants that are able to take up the organic nitrogen (for instance, via ectomycorrhizae). We therefore tested a third hypothesis: a high tannin concentration of kauri litter results in greater availability of dissolved organic nitrogen (DON) relative to the availability of inorganic nitrogen. Previously, we measured the tannin concentration in the foliage of a number of common plant species of the mixed forest of northern New Zealand, and it appeared that the gymnosperm rimu (*Dacrydium cupressinum*) has similar tannin concentrations as kauri (Verkaik and Berendse, unpublished data). Further, it is known that the decomposition of kauri foliage is not extremely slow compared to the decomposition of foliage of New Zealand species like rewarewa (*Knightia excelsa*) or silver tree fern (*Cyathea dealbata*) (Enright and Ogden 1987). However, especially kauri is known for its extreme accumulation of organic material and nitrogen. Our fourth and final hypothesis was that kauri tannins have stronger effects on nitrogen mineralisation and litter decomposition than the tannins of other common New Zealand tree species.

To study the effects of tannins, we purified tannins of kauri and of two other common New Zealand tree species and added them to material from the organic layer of the kauri forest. The experiment was run for a year to study long-term effects.

Material and methods

Tannin purification

To obtain purified tannins we used the methods of Schimel et al. (1996) and Yu and Dahlgren (2000). We collected samples of about 400 g fresh green leaves from kauri, (*Agathis australis*

(D. Don) Lindl.), the gymnosperm rimu (*Dacrydium cupressinum* Lambert) and the angiosperm rewarewa (*Knightia excelsa* R. Br.) at three sites in the Waitakere Ranges in April and May 2003. The leaves were dried, ground, and stored in a freezer. The ground material was washed three times with methylene chloride and extracted three times with 80% aqueous acetone. After each washing or extraction the plant material was separated from the solvent using vacuum filtration. The acetone extractable fraction was roto-evaporated to remove the acetone, and the residue was washed with hexane. The water fraction was concentrated on a roto-evaporator and freeze-dried. The resulting powder was redissolved in 50% aqueous methanol and mixed through a slurry of sephadex LH-20 and 50% aqueous methanol. This slurry was applied to a glass funnel and eluted with 50% aqueous methanol until only low concentrations of polyphenols were detected in the effluent using the Folin–Ciocalteu method (Waterman and Mole 1994). The sephadex was washed with 80% aqueous acetone to remove the tannin and the eluate was then roto-evaporated and freeze-dried to obtain a powder of purified tannin.

Design of the experiment

The purified tannins were added to samples from the organic layer from under a kauri tree. In May 2003 we collected a sample of 6 kg of the humus and fermentation layer at one site in the Waitakere Ranges (NZMS 260-Q11: 498687). The material was air-dried, transported to the Netherlands, stored for about 9 months in the dark at room temperature, sieved (2 mm) and then sub-samples of 5 g were put in Petri dishes 92 mm in diameter and 15 mm deep, 3 ml demineralised water was added and the dishes were pre-incubated in the dark at 25°C. After 2 weeks, the five treatments were started. All the Petri dishes received 2 ml demineralised water; for the control treatment, this was the only addition. To distinguish between the process of sequestering of proteins by tannins and the immobilisation of nitrogen by microbes, one treatment was the addition of 0.1 g cellulose per dish (20 mg/g organic material). The other treatments consisted

of the addition of 0.1 g tannins from kauri, rimu or rewarewa per dish (20 mg/g organic material). After the additions the Petri dishes were sealed with Para film and incubated in the dark at 25°C. Every month the incubated Petri dishes were aerated by lifting-off their covers, were brought back to their starting weight by adding demineralised water and were then resealed. Batches of five Petri dishes per treatment (but 10 dishes from the control) were removed from incubation for analysis at various intervals: after 2 days (referred to as $t = 0$), after 1 month and after 1 year.

Measurements

After collection of the dishes, the fresh weight of the organic material in each Petri dish was measured, the moisture content was measured in a sub-sample, and then the dry weight was calculated. The C and N concentrations of the organic material were measured with an element analyser (Fison instruments EA 1108) in dried (30°C) samples that had been pulverised with a ball mill. The moisture content (drying at 105°C) and ash content (loss on ignition) were determined and the results of all measurements were corrected for moisture and ash content. Sub-samples of the organic material were extracted with 1 M KCl and the pH of the extracts was measured. The mineral nitrogen concentrations were measured with a segmented flow analyser (Skalar, SAN plus system, the Netherlands), and the organic nitrogen concentration was determined using the method of Yu et al. (1994). Pulverised samples of the organic material collected 2 days after tannin addition (at $t = 0$) were extracted with 50% aqueous acetone (50 mg of sample in 10 ml solvent, following Yu and Dahlgren 2000). In these extracts polyphenol concentrations were measured colorimetrically by the Folin–Ciocalteu method (Waterman and Mole 1994) and using tannic acid (Sigma–Aldrich) as standard.

Statistical analyses

All statistical analyses were conducted with the SPSS statistical package for Windows (12.0.1). ANOVAs with Tukey tests (significance set at 0.05) with treatment as fixed factor were used to

test for differences in polyphenol concentration, nitrogen concentration, C:N ratio, N loss, and mass loss between the different treatments. Before running each ANOVA the homogeneity of variance was tested; if variances were not equal, a non-parametric test was used. The non-parametric Kruskal–Wallis test was performed to compare more than two treatments, while the Mann Whitney test was used to compare two treatments.

Results

At the start the polyphenol concentrations in the Petri dishes to which rimu and rewarewa tannins had been added were as low as the concentration in the control Petri dishes (Table 1). Only in the Petri dishes to which kauri tannins had been added was the concentration higher than the control, but at 15 mg/g it was still lower than the added 20 mg/g. At the start and during the experiment, the pH-KCl was low in all treatments (Table 1). During the experiment, in all treatments inorganic nitrogen was mainly present as ammonium and the concentration of nitrate was

always less than 0.1% of the ammonium concentration (data not shown).

After 1 month's incubation, the inorganic nitrogen in the organic material of the control had increased, but the inorganic nitrogen in the kauri tannin and rimu tannin treatments had decreased (Fig. 1). The amount of inorganic nitrogen in the cellulose and rewarewa tannin treatments had not changed (Fig. 1). After 1 month, the amount of DON had decreased in all treatments, and this decrease was larger in the kauri and rimu tannin treatments than in the other treatments (Fig. 1). After 1 year, the organic material in all treatments had released inorganic nitrogen and DON (Fig. 2). Whereas the cellulose treatment had released the same amounts of inorganic nitrogen and DON as the control, the tannin treatments all had released smaller amounts of inorganic nitrogen and DON (Fig. 2). After one-month incubation, due to the release of inorganic nitrogen in the control, the ratio of DON to inorganic nitrogen was significantly lower in the control than in the other treatments (Fig. 3). In the long-term, the ratios of DON to inorganic nitrogen were similar in all treatments (Fig. 3).

Table 1 pH in the KCl extract, polyphenol concentration (mg/g), C:N ratio, extractable inorganic nitrogen (the sum of $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$, in $\mu\text{g/g}$ dry weight) and dissolved

organic nitrogen ($\mu\text{g/g}$ dry weight) at the start of the experiment in the different treatments. Row values followed by different letters differ significantly ($P < 0.05$)

	Control	Cellulose	Kauri tannins	Rimu tannins	Rewarewa tannins
PH-KCl	2.7a	2.7a	2.7a	2.7a	2.7a
Polyphenol concentration	7.6a	4.7a	15.1b	6.6a	7.2a
C:N ratio	31.4a	32.8b	32.1ab	32.2ab	31.9ab
Inorganic nitrogen	489a	460a	481a	473a	459a
DON	383d	362ab	370bc	379cd	356a

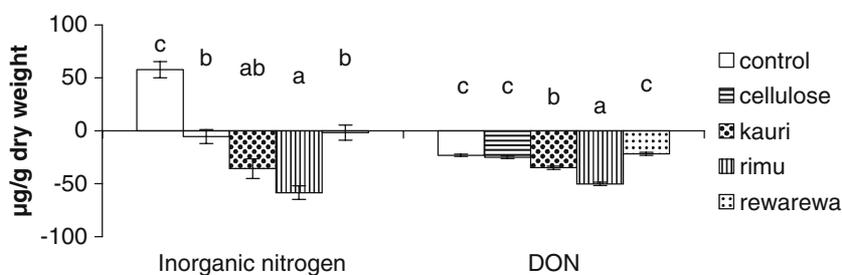


Fig. 1 The difference ($\pm\text{SE}$; in $\mu\text{g/g}$ dry weight incubated material) between the initial and the 1-month values for extractable inorganic nitrogen ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$) or

dissolved organic nitrogen. Different letters indicate significant differences ($P < 0.05$) between treatments

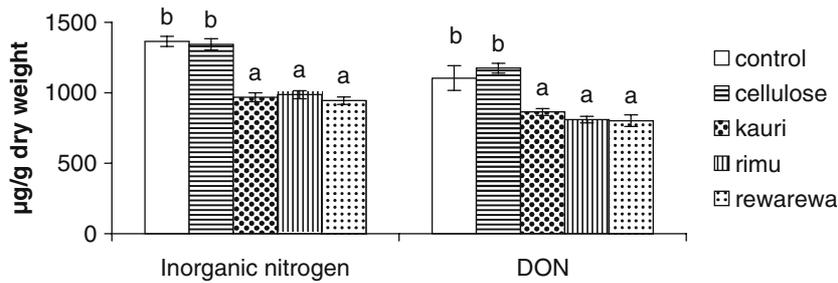


Fig. 2 The difference (\pm SE; in $\mu\text{g/g}$ dry weight incubated material) between the initial and the 1-year values for extractable inorganic nitrogen ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$) or

dissolved organic nitrogen. Different letters indicate significant differences ($P < 0.05$) between treatments

Fig. 3 The ratio (\pm SE) of DON to inorganic nitrogen (the sum of $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$) at the start, after 1-month and after 1-year incubation. Different letters in the same incubation period indicate significant differences ($P < 0.05$) between treatments

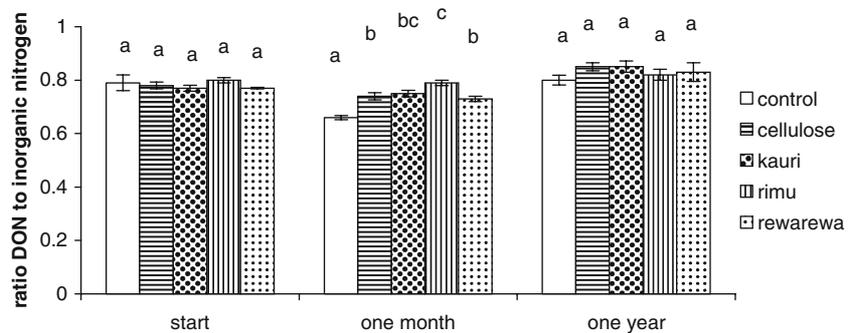
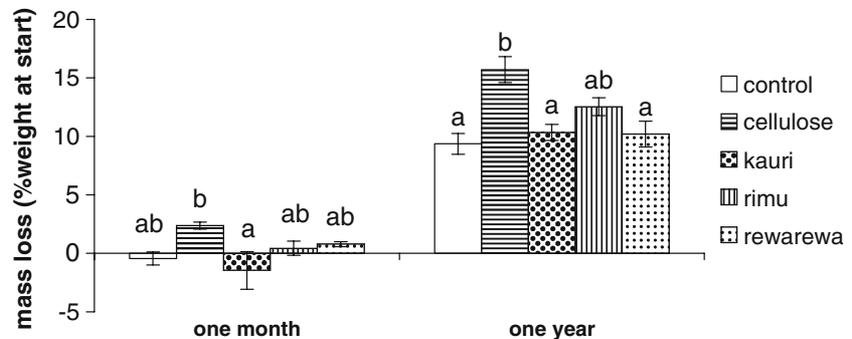


Fig. 4 Mass loss (\pm SE, as % of weight at the start) after 1-month and after 1-year of incubation. Different letters in the same incubation period indicate significant differences ($P < 0.05$) between treatments



After 1 month and also after 1 year of incubation, mass loss in the control was similar to the mass loss in the tannin addition treatments (Fig. 4). After 1 month of incubation, the addition of cellulose had brought about greater mass loss compared to the addition of kauri tannins (Fig. 4), while after 1 year the mass loss in the cellulose addition treatment was greater than the mass loss in the control and in treatments with kauri and the rewarewa tannin additions (Fig. 4).

Discussion

Nitrogen mineralisation

Since kauri tannin addition resulted in a reduction of net nitrogen release compared to the control (Figs. 1, 2), our first hypothesis, that kauri tannins can reduce nitrogen mineralisation is confirmed. The results indicate that the added kauri tannins were not toxic for microorganisms, since adding a

toxic compound would have inhibited microbial activity and reduced mass loss (Kraus et al. 2003a).

The tannin fraction, which we purified is dominated by high molecular weight tannins (Fierer et al. 2001). Research suggests that, besides being able to sequester proteins, these tannins might also act as a C source, stimulating nitrogen immobilisation (Kraus et al. 2004). In our study we used cellulose for comparison, and the treatment with this compound showed a different response than the addition of kauri tannins. Just as in the study done by Schimel et al. (1996), the cellulose in our study probably acted as a temporary substrate for the microbial population, thereby stimulating nitrogen immobilisation compared to the control 1 month after incubation (Fig. 1). Compared to the control the cellulose treatment increased mass loss (Fig. 4), probably because of the larger microbial population, which was present. On the short-term the kauri tannin treatment however, showed no effect on mass loss (Fig. 4), suggesting that in this treatment nitrogen immobilisation was not as important as in the cellulose treatment. Still, the addition of kauri tannins caused a larger decrease of DON availability than the addition of cellulose (Fig. 1). Also on the long-term both compounds acted differently, with cellulose stimulating mass loss and the tannin addition showing a larger reduction of nitrogen availability (Figs. 2, 4).

It is commonly found that tannins, especially tannins with high molecular weight, have the ability to complex proteins (e.g., Bradley et al. 2000; Fierer et al. 2001; Kraus et al. 2004). Kauri tannins appear to have this ability too (Jongkind, unpublished data), and therefore we assume that the reduction of DON availability following kauri tannin addition is mainly attributable to the complexation of proteins by kauri tannins. A reduced availability of DON would decrease nitrogen mineralisation, reducing the release of inorganic nitrogen. In addition, the ongoing consumption of inorganic nitrogen by the microbial population would further reduce the availability of inorganic nitrogen. Both processes can explain the reduced availability of inorganic nitrogen following kauri tannin addition (Fig. 1).

One month after incubation the difference in nitrogen release (the sum of inorganic nitrogen

and DON) between the control and the kauri tannin addition was only 0.1 mg/g (Fig. 1), but during the incubation in the following 11 months this increased to 0.64 mg/g (Fig. 2). Our results therefore indicate that the complexation of proteins by tannins can require a long time period.

Litter decomposition

Our results did not confirm the hypothesis that added tannins reduced litter decomposition. Decomposition was probably carbon limited in our experiment, as indicated by the stimulation of mass loss by cellulose addition (Fig. 4). The extra mass that the cellulose treatment lost compared to the control exceeded the mass of the added cellulose. After 1 year, the cellulose treatment had lost 6.3% more mass than the control (Fig. 4) but the mass of the cellulose treatment at the start (0.1 g cellulose out of 5.1 g dry weight) only comprised 2% of cellulose. Presumably the addition of cellulose fuelled an increase of the microbial population, which then decomposed more soil organic matter than the microbial population of the control.

One of the ways tannins can reduce litter decomposition is by complexing proteins and extracellular enzymes of microbes (Kraus et al. 2003a). The kauri tannins we used appear to be able to complex proteins too (see discussion above), and one might expect that therefore they would also be able to complex extracellular enzymes. Both processes would result in a reduction of litter decomposition after tannin addition. However, we found no reduction of mass loss after tannin addition (Fig. 4). Fierer et al. (2001) reported similar findings. They added balsam poplar (*Populus balsamifera*) tannins to soil organic material of balsam poplar vegetation and to soil organic material of alder (*Alnus tenuifolia*) vegetation. In both soil types the high molecular weight tannins complexed proteins. The soil respiration, however, was only reduced in the alder soil material and not in the poplar soil material. Fierer et al. (2001) suggested that the microbes in the poplar soil material, which are naturally exposed to high tannin inputs, are adapted to high tannin concentrations. Therefore they will not be inhibited as strongly as the microbes in the alder

soil material, which are not normally exposed to high tannin inputs. The same argument could be used to explain our results: the soil below kauri trees is naturally exposed to high tannin inputs and therefore the microbial population will be adapted to high tannin concentrations.

Dissolved organic nitrogen

The results after one-month incubation confirm the hypothesis that tannins change the availability of DON relative to inorganic nitrogen, but the results also show that in the long-term the ratio of DON to inorganic nitrogen did not change (Fig. 3). In a tannin addition experiment, which was run for 10 weeks, Bradley et al. (2000) found no shift in the ratio of DON to inorganic nitrogen either. However, they found no effect of tannin addition on the DON concentration, whereas in our study the DON concentration was even lowered by the addition of tannins (Fig. 2). In the study done by Bradley et al. (2000) the concentration of DON was very low compared to the concentration of inorganic nitrogen, probably because of the pre-treatment leaching in their experiment. In our experiment the DON concentration was similar to the concentration of inorganic nitrogen (Table 1, Fig. 3) and both the DON and the ammonium release were reduced by tannin addition (Fig. 2). As a result, the ratio of organic to inorganic nitrogen was not changed in the long-term.

Kauri tannins versus tannins of other species

The hypothesis that kauri tannins show a stronger effect on nitrogen mineralisation than tannins of other species was not confirmed, since the effect of kauri tannins on the availability of inorganic nitrogen was similar to the effects of rewarewa tannins or rimu tannins (Fig. 1). However, after one-month incubation the effect on DON availability was larger in the kauri tannin treatment than in the rewarewa tannin treatment. Other studies have also found that purified tannins of different species act differently (e.g., Kraus et al. 2003b), and differences in tannin structure appear important. Since the short-term effects of rewarewa tannin addition, on nitrogen availability and mass loss, were similar to the effects of

cellulose addition (Figs. 1, 4), we are not able to indicate if these short-term effects of rewarewa tannins were due to complexation or to immobilisation. It appears that the rimu tannins not only reduced nitrogen availability by immobilisation but also by the complexation of proteins in the short-term, since the rimu tannin treatment showed a larger decrease of nitrogen availability than the cellulose treatment but showed a similar mass loss. In the long-term, the effects on nitrogen release and mass loss were similar for the three tannin additions and differed from the cellulose treatment (Figs. 2, 4), suggesting that in the long-term the complexation of proteins by tannins is the main process affecting nitrogen availability.

Two days after tannin addition, the polyphenol concentrations for all three kinds of tannins were low compared to the added quantities of 20 mg/g (Table 1). Similar results have been found in other studies. Schofield et al. (1998) added purified sorghum tannins to soil samples and used a variety of extraction solutions, but were unable to measure any of the added tannins. Two weeks after the addition of tannins to humus Bradley et al. (2000) did not detect any tannin in the humus leachates. These studies and our findings show that the added tannins quickly become unavailable for extraction, indicating that the tannins bind to the substrate. Although these tannins are unavailable for extraction, the results show that they can still influence nitrogen mineralisation.

Nitrogen accumulation in kauri forest

In our study the effects of kauri tannins on nitrogen availability were assessed under laboratory conditions. In kauri forest the effects of tannins might be different, due to for instance the presence of soil mesofauna or to fluctuating environmental conditions (Kraus et al. 2003a). However, our study shows that potentially kauri tannins have a large effect on nitrogen availability. One year after the start of the experiment the difference in nitrogen release (the sum of inorganic nitrogen and DON) between the control and the kauri tannin addition was 0.6 mg nitrogen (Fig. 2). This suggests that 20 mg of kauri tannins can sequester 0.6 mg nitrogen. In kauri forest the annual leaf litterfall is 54–277 g/m² (Enright 1999;

Silvester and Orchard 1999), which, given the tannin concentrations measured in another study (Verkaik and Berendse, unpublished data) gives an input of about 6–33 g kauri tannins/m² y¹. If these kauri tannins complexed nitrogen to the same extents as they did in our experiment, this would result in a nitrogen sequestration of 0.18–0.99 g nitrogen/m² y¹. During the 600–700 years' lifetime of a kauri tree (Ahmed and Ogden 1987), a sequestration of 0.09–0.5 kg nitrogen/m² would be possible which is comparable to the amount of nitrogen in the organic layer of a mature kauri forest (Silvester 2000).

The purified tannins of the other two species had similar long-term effects on nitrogen release as did kauri tannins (Fig. 2). This emphasises that also other tree species in New Zealand kauri forest have the ability to sequester proteins. We propose that the exceptional accumulation of nitrogen under kauri can be explained by the combination of the high attainable age of kauri and by its ability to occupy certain positions in the landscape for several generations of trees—a possible time span of thousands of years (Ogden and Stewart 1995).

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