

## Kauri trees (*Agathis australis*) affect nutrient, water and light availability for their seedlings

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**Abstract:** Plants can change the soil that they grow on, for example by producing litter. If litter characteristics are such that their effect on the soil increases a plant's fitness, a positive feedback can develop between the plant and the soil. Several studies indicate that New Zealand kauri trees (*Agathis australis*) lower the availability of nutrients in the soil beneath their crown. Low nutrient availability would be positive for the survival of kauri seedlings as they are known to use nutrients more efficiently than angiosperm species. We tested the hypotheses that nutrient availability is lower and light availability is higher beneath kauri trees than beneath the surrounding angiosperm vegetation. We determined the availability of nutrients (using leaf nutrient concentrations as a proxy), soil moisture, and light in both situations. As a reference we did the same measurements in tea tree vegetation (*Leptospermum scoparium* and *Kunzea ericoides*) where kauri seedlings were abundant. The availability of nitrogen, phosphorus and calcium was lower under kauri than in the surrounding vegetation. Further, in a dry period the availability of water in the organic layer surrounding the kauri trunk was lower than in the mineral soil further away from the kauri trunk. We suggest that periodic drought explains why the density of kauri seedlings under mature kauri trees is less than in tea tree vegetation. Kauri seedlings are more tolerant of drought and low nutrient availability than other tree seedlings and we conclude that the conditions under mature kauri give kauri seedlings an advantage over seedlings of other tree species. The low nutrient availability under mature kauri trees supports the idea of a positive soil–plant feedback driven by poor decomposability of kauri litter.

**Keywords:** *Agathis australis*; kauri; New Zealand; nutrient availability; light availability; soil moisture; plant–soil interactions

## Introduction

Plants can influence soil properties in many ways, e.g. via their roots through nutrient uptake, root exudates and dead roots, or via their litter (e.g. Hobbie 1992; Binkley 1995; Knops et al. 2002; Prescott 2002). The influence that plants have on soil properties can feed back on their growth (e.g. Berendse 1994; Northup et al. 1995). Binkley and Giardina (1998) reviewed the literature and found examples of tree species that had a positive influence on their own fitness via their effects upon the soil, as well as examples of species that had a negative fitness effect. An example of a positive soil–plant feedback is the mosaic of patches dominated by hemlock (*Tsuga canadensis*) or sugar maple (*Acer saccharum*) in forest in the north-eastern United States (Binkley & Giardina 1998). The mosaic pattern appears to result from the influence that these species have, via the soil, upon each others seedlings (Frelich et al. 1993). Positive soil–plant feedback

interactions are probably important in the dynamics of natural ecosystems (Binkley & Giardina 1998; Van Breemen & Finzi 1998).

The New Zealand kauri tree (*Agathis australis*) is an interesting species with which to study soil–plant feedbacks, because it has a huge effect upon the soil. Kauri forests in northern New Zealand are mixed forests of angiosperm and gymnosperm tree species. Under mature kauri trees, a thick layer of organic material develops (Silvester & Orchard 1999), which leads to increased weathering of the underlying mineral soil (Swindale 1957; Beveridge 1977; Jongkind & Buurman 2006). The organic layer under old kauri trees may contain up to 0.65 kg m<sup>-2</sup> nitrogen, which is largely inaccessible to plants (Silvester 2000). High concentrations of polyphenols in kauri litter might be responsible for the accumulation of nitrogen in the organic layer below kauri, because they can bind proteins and decrease the rate of N mineralisation (Verkaik et al. 2006). It has further been suggested

that the high polyphenol content of kauri litter leads to the remarkable podzolisation under old kauri trees (Bloomfield 1953).

High densities of kauri seedlings are often found in tea tree vegetation, dominated by *Leptospermum scoparium* or *Kunzea ericoides*, suggesting that the conditions in tea tree vegetation are favourable for kauri regeneration (Mirams 1957; Bielecki 1959; Ecroyd 1982). However, on closer observation it appears that kauri also regenerates in stands of mature kauri trees, though at a lesser density (Ahmed & Ogden 1987; Ogden et al. 1987; Ogden & Stewart 1995). Kauri seedlings have low nutrient requirements (Peterson 1962; Silvester 2000) and it is thought that kauri seedlings are better able to compete with faster growing angiosperm seedlings on sites of low fertility than on sites of higher fertility (Pook 1979; Burns & Leathwick 1996). Therefore, a decrease in nutrient availability caused by the accumulation of kauri litter will improve the conditions for kauri regeneration relative to other species. Kauri seedlings are more light demanding than angiosperm seedlings (Pook 1979), and since the understorey vegetation and tree canopy under kauri trees are generally more open than the surrounding forest (Bielecki 1979), this might add to the relative advantage of kauri seedlings growing under mature kauri trees.

As part of a bigger research project on soil–plant feedbacks in kauri forest, we have investigated the conditions for kauri regeneration under mature kauri trees. We have tested the following hypotheses: (1) light intensity will be higher under kauri than in the surrounding angiosperm vegetation, and (2) nutrient availability will be lower under kauri than in the surrounding angiosperm vegetation. To evaluate the site conditions relative to the conditions in the tea tree vegetation, where kauri seedlings are abundant, we tested the hypothesis that (3) environmental conditions under kauri are more similar to the conditions in the tea tree vegetation than are conditions in the surrounding vegetation.

## Methods

### Outline

To test the hypotheses we established five plots under the crown of different mature kauri trees ('kauri plots'), five plots just outside the crown of these kauri trees ('angiosperm plots') and five plots in tea tree vegetation ('tea tree plots'). In all plots we measured soil water availability, light availability, and thickness of the organic layer. As an indication of differences in nutrient availability in the soil, we compared nutrient concentrations in the leaves of the shrub species

hangehange (*Geniostoma rupestre* var. *ligustrifolium*), which is common to all plots.

### Study areas

The plots measured 100 m<sup>2</sup> and were all situated in the Waitakere Ranges in New Zealand. We selected five mature kauri trees with diameters ranging from 1.1 to 2.3 m on different locations where there was no sign that kauri had ever been logged. One tree was situated on a slope in the Nihotupu area (E2650640, N6470128, 220 m a.s.l), two trees were situated on the same ridge in the Huia area (E2649758, N6469038, 120 m a.s.l and E2649790, N6469069, 140 m a.s.l) and two trees were situated on two different slopes in the Cascades area (E2645802, N6477703, 100 m a.s.l and E2645279, N6478133, 180 m a.s.l). Under the crown of each of these kauri trees one kauri plot was laid out. In the vegetation dominated by angiosperm trees surrounding each kauri tree we selected an angiosperm plot. This plot was chosen to adjoin the edge of the kauri crown and was situated within 30 m distance from the kauri trunk. These angiosperm plots were selected to have the same inclination and orientation as the kauri plots and were not covered by the crown of a mature kauri tree. At one location, where the angiosperm vegetation bordering the kauri tree did not have the same topography as the kauri tree, we situated the angiosperm plots nearby, on the same topography as the original kauri tree, and next to another mature kauri tree. In addition we selected five tea tree plots in secondary forest where kauri seedlings were abundant, one in the Nihotupu area (E2650805, N6469962, 220 m a.s.l), two in the Huia area (E2649817, N6468660, 20 m a.s.l and E2649672, N6468492, 40 m a.s.l) and two in the Cascades area (E2645800, N6477496, 120 m a.s.l and E2645846, N6477633, 120 m a.s.l).

### Nutrient concentration in hangehange leaves

To compare the nutrient availability in the plots, we determined the nutrient concentration in the leaves of the shrub hangehange, which occurred in all plots. At the end of October 2004 in each plot three replicate samples were collected. For each sample leaves were collected from five to seven shrubs that had a height of 0.7–2.5 m. Only leaves with a length more than 4 cm were picked and per shrub three branches were sampled. From each branch we picked two young leaves, light green coloured on a yellowish petiole, and two older, dark green leaves. The leaves were air- and oven-dried in New Zealand, weighed, transported to The Netherlands, where they were dried again (48 h, 35°C), ground, and analysed. The ground material was digested with sulphuric acid, salicylic acid, hydrogen peroxide and selenium (Temminghoff et al. 2000) and the concentrations of nitrogen, phosphorus, potassium,

calcium, magnesium and sodium in the digest were determined spectrophotometrically (Skalar, SAN plus system or AAS).

### Soil moisture availability

To compare soil moisture availability in the plots, we determined the actual soil water content ( $w$ ), the average bulk density ( $\rho$ ) and the water content at pF 4.2 ( $w_{pF4.2}$ ) and calculated the available volumetric soil water content (as:  $(w - w_{pF4.2}) \times \rho$ ). In 2002 the water content was measured three times in the kauri and the tea tree plots. In 2003 the water content was measured three times in all plots. For each measurement we took in each plot six soil samples at 0–7.5 cm depth and six soil samples at 7.5–15 cm depth, using an auger. Depth was measured from the top of the litter layer. Within each sample we measured the thickness of the litter layer (L), the fermentation-plus-humus layer (F+H), and the mineral layer. In each sample the mass water content ( $w$ ) was determined, by drying and weighing:

$$w = \frac{\text{mass of wet soil} - \text{mass of dry soil}}{\text{mass of dry soil}}$$

The dry bulk density of the soil ( $\rho$ ) was determined as the average of six samples per plot taken with an auger with known volume. The mass water content of these samples at permanent wilting point ( $w_{pF4.2}$ ) was determined with a pressure membrane apparatus (Pearcy et al. 1989). Near the kauri trunks the mineral (clay) soil was mostly covered with a thick organic layer, dominated by humified material, while further from the trunk only a thin layer of undecomposed litter was present. As a result, some of the samples of the kauri plots were dominated by organic material while others were dominated by clay soil. The samples of the angiosperm and tea tree plots consisted mainly of mineral soil (clay). We determined the wilting point of three organic samples and three mineral samples from the kauri plots, of two mineral samples from the angiosperm plots, and of two mineral samples from the tea tree plots. In the statistical analyses of the samples from the kauri plots we separated the samples dominated by organic material ( $F+H > 3.5$  cm) and samples dominated by mineral (clay) material ( $F+H \leq 3.5$  cm).

### Light measurements

We determined canopy openness and photon flux density in the plots using an MZ-50 Pentax camera with a fisheye lens (Sigma 8 mm, f4) that was levelled with a bubble level at 0.75 m above the ground. Photos were taken in May and June 2002 in the kauri and tea tree plots and in September 2004 in the angiosperm plots. In each plot we took 10 photos, evenly distributed over

the plot, under an evenly overcast sky, using the half-automatic mode of the camera and the timed shutter release. Shutter speed was set on 1/125, or slower under low light conditions. We used Ilford ISO 125 black and white films. The images were scanned with a Nikon LS-2000 film scanner, saved in BMP format, and converted (in Adobe Photoshop) to a grey-scale image with a bit depth of eight bits.

To calculate canopy openness and photon flux density, the images were analysed with Winphot 5 (Ter Steege 1996). Using the manual threshold of the program, each image was converted twice to black and white pixels and the average value of the two threshold values was used (Englund et al. 2000). To calculate photon flux density at 0.75 m height we selected nine days in the growing season. Latitude was set at  $-36.5$ , longitude at  $-174.30$ , time zone at 12 and altitude at 100. Transmission of red, transmission of far red, the red far-red ratio, diffuse part, and tau were set at the default values of 0.05, 0.45, 1.20, 0.15, and 0.60 respectively. For each day we set the sun fraction at 50, used the standard overcast sky type and included diffuse canopy light.

### Organic layer thickness and kauri diameter

The thickness of the organic layer (litter layer + fermentation layer + humus layer) was measured in each plot using an iron rod of 0.7-cm diameter (Silvester & Orchard 1999). To estimate organic layer thickness we probed with the iron rod on about 30 different positions in each plot, through the softer organic layer until the harder mineral layer was reached. We verified this method several times, by removing, by hand or with an auger, the organic layer from the mineral soil. The diameter of kauri trees (mature trees and 'rickers' or poles) in the plots was measured at 1.3 m height.

### Statistical analyses

Statistical analyses were conducted with the SPSS statistical package for Windows (12.0.1). ANOVA with Tukey tests (significance level set at 0.05) were performed to test for differences in soil water availability, canopy openness, and photon flux density between the three plot types. Homogeneity of variance was tested before each ANOVA, and when the variances were not equal Kruskal–Wallis tests were used. Differences in soil water availability between the kauri and angiosperm plots and between the samples from kauri plots dominated by organic material or clay were tested with a paired-sample  $t$ -test. Differences in thickness of the organic layer were tested with the Kruskal–Wallis test, since the variances of the different groups were not homogenous. Differences in nutrient concentrations between the kauri and angiosperm plots were tested with a paired non-parametric test (Wilcoxon), while

other differences in nutrient concentrations were tested with a *t*-test. To evaluate the relation between organic layer thickness and other site conditions, Spearman correlations were calculated for the data of the kauri and angiosperm plots.

## Results

### Site conditions

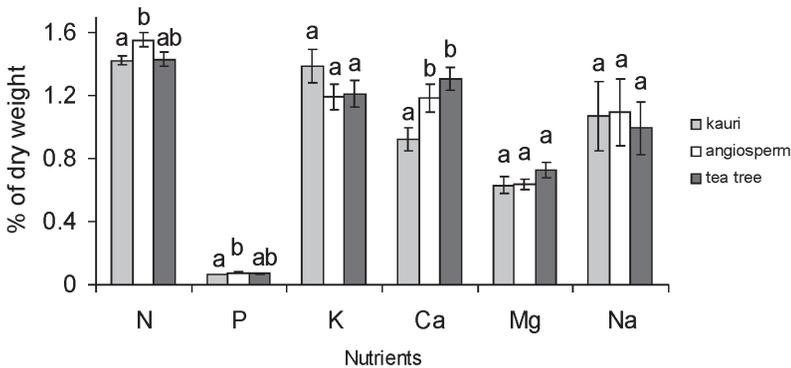
Nutrient concentrations in hangehange leaves differed between the angiosperm and kauri plots. Nitrogen, phosphorus and calcium concentrations were lower in the kauri plots (Fig. 1). We found no significant differences between nutrient concentrations of hangehange leaves in the angiosperm and tea tree plots. Also, the nutrient concentrations of hangehange leaves in the kauri and tea tree plots were similar, except for the calcium concentration, which was higher in the tea tree plots than in the kauri plots (Fig. 1). The average weight per leaf was similar for the kauri and angiosperm

plots (data not shown). But the leaves collected in the tea tree plots weighed less than the leaves of the kauri plots, while the leaves of tea tree and angiosperm plots had similar weights (data not shown).

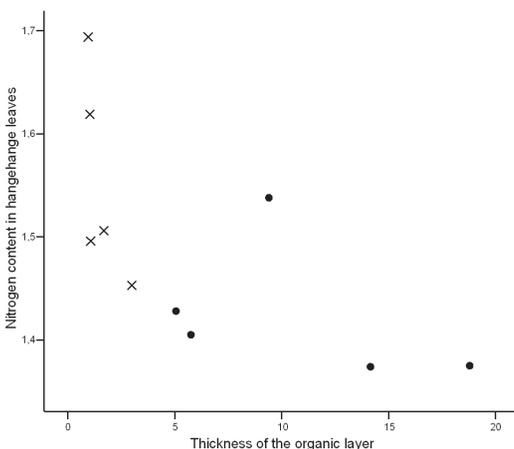
The organic layer in the kauri plots was thicker than those in the angiosperm and tea tree plots (Table 1). The light conditions at 0.75 m were not different between the three plot types (Table 1). Also, for five of the six soil moisture measurements the available volumetric water content did not differ between the plot types. Only for the measurement in April 2002, at 7.5–15 cm depth, the samples from the kauri plots dominated by organic material were dryer than the samples from the kauri plots dominated by clay and the samples from the tea tree plots (Table 2).

### Correlations

Thickness of the organic layer and kauri diameter were positively correlated (Table 3) suggesting that organic material accumulates with the increasing age of the kauri tree. It appeared that the thickness of the organic layer



**Figure 1.** Mean nutrient concentrations in hangehange leaves (% of dry weight) collected in kauri, angiosperm and tea tree plots in the Waitakere Ranges, northern New Zealand. Error bars indicate SE and different letters indicate significant differences ( $P < 0.05$ ) between plot types.



**Figure 2.** Relationship between organic layer thickness (cm) and the nitrogen concentration in hangehange leaves (% of dry weight) in kauri (•) and angiosperm (×) plots in the Waitakere Ranges, northern New Zealand ( $r = 0.749$ ,  $P = 0.006$ ).

**Table 1.** Mean ( $\pm$  SE) light availability parameters and organic layer thickness in three plot types in the Waitakere Ranges, northern New Zealand (2002–2003). Column values followed by different letters are significantly different ( $P < 0.05$ ).

	Canopy openness (%)	Photon flux density (mol m <sup>-2</sup> day <sup>-1</sup> )	Organic layer thickness (cm)
Kauri	10.2 $\pm$ 1.3 <sup>a</sup>	3.59 $\pm$ 0.29 <sup>a</sup>	10.6 $\pm$ 2.6 <sup>a</sup>
Angiosperm	8.2 $\pm$ 0.5 <sup>a</sup>	3.20 $\pm$ 0.27 <sup>a</sup>	1.5 $\pm$ 0.4 <sup>b</sup>
Tea tree	9.1 $\pm$ 0.9 <sup>a</sup>	3.84 $\pm$ 0.56 <sup>a</sup>	2.4 $\pm$ 1.1 <sup>b</sup>

**Table 2.** Available soil moisture content (% of soil volume) at two different depths in three plot types in the Waitakere Ranges, northern New Zealand. For the kauri plots a distinction was made between samples dominated by organic material or by clay. Column values followed by different letters are significantly different ( $P < 0.05$ ).

Date of measurement	13–21 January 2002		4–7 February 2002		16–18 April 2002		26 March–3 April 2003		28 April–1 May 2003		26–31 May 2003	
	0–7.5	7.5–15	0–7.5	7.5–15	0–7.5	7.5–15	0–7.5	7.5–15	0–7.5	7.5–15	0–7.5	7.5–15
Kauri plots – organic	24.9 <sup>a</sup>	29.4 <sup>a</sup>	13.1 <sup>a</sup>	13.5 <sup>a</sup>	11.1 <sup>a</sup>	13.3 <sup>a</sup>	15.2 <sup>a</sup>	23.6 <sup>a</sup>	13.3 <sup>a</sup>	18.7 <sup>a</sup>	23.3 <sup>a</sup>	46.3 <sup>a</sup>
Kauri plots – clay	29.9 <sup>a</sup>	32.9 <sup>a</sup>	11.3 <sup>a</sup>	21.4 <sup>a</sup>	11.0 <sup>a</sup>	23.2 <sup>b</sup>	11.6 <sup>a</sup>	27.0 <sup>a</sup>	11.2 <sup>a</sup>	23.0 <sup>a</sup>	21.0 <sup>a</sup>	29.8 <sup>a</sup>
Angiosperm plots	-	-	-	-	-	-	15.6 <sup>a</sup>	26.4 <sup>a</sup>	18.0 <sup>a</sup>	26.3 <sup>a</sup>	27.4 <sup>a</sup>	31.9 <sup>a</sup>
Tea tree plots	29.2 <sup>a</sup>	31.6 <sup>a</sup>	15.9 <sup>a</sup>	20.4 <sup>a</sup>	13.1 <sup>a</sup>	20.2 <sup>b</sup>	15.1 <sup>a</sup>	21.9 <sup>a</sup>	14.7 <sup>a</sup>	20.9 <sup>a</sup>	21.9 <sup>a</sup>	26.2 <sup>a</sup>

**Table 3.** Coefficients of correlation between vegetation parameters and thickness of the organic layer ( $n = 10$ ). \*  $P < 0.05$ , \*\*  $P < 0.01$ . The correlations of K-concentration, Mg-concentration and Na-concentration in hangechange leaves with the other parameters were not significant.

	Organic layer thickness	Photon flux density	Canopy openness	Kauri diameter	N-conc.	P-conc.	Ca-conc.	Leaf-weight
Thickness of organic layer	1.000	0.552	<b>*0.661</b>	<b>**0.912</b>	<b>**−0.794</b>	<b>**−0.863</b>	−0.612	0.224
Photon flux density	0.552	1.000	<b>*0.673</b>	0.459	−0.273	−0.350	−0.200	0.091
Canopy openness	<b>*0.661</b>	<b>*0.673</b>	1.000	0.472	<b>*−0.709</b>	<b>*−0.650</b>	−0.382	0.430
Kauri diameter	<b>**0.912</b>	0.459	0.472	1.000	<b>*−0.692</b>	<b>**−0.800</b>	<b>*−0.653</b>	−0.071
N-concentration	<b>**−0.794</b>	−0.273	<b>*−0.709</b>	<b>*−0.692</b>	1.000	<b>**0.875</b>	<b>*0.685</b>	−0.103
P-concentration	<b>**−0.863</b>	−0.350	<b>*−0.650</b>	<b>**−0.800</b>	<b>**0.875</b>	1.000	0.513	−0.094
Ca-concentration	−0.612	−0.200	−0.382	<b>*−0.653</b>	<b>*0.685</b>	0.513	1.000	−0.030
Leaf-weight	0.224	0.091	0.430	−0.071	−0.103	−0.094	−0.030	1.000

correlated positively with canopy openness too (Table 3). We did not find a correlation between organic layer thickness and the available volumetric soil water content at any of the measuring dates (data not shown). The results further suggest that plots with a thick organic layer had a lower nitrogen and phosphorus availability, since the nitrogen and phosphorus concentrations in the hangechange leaves correlated negatively with thickness of the organic layer (Table 3, Fig. 2). The nitrogen and phosphorus concentrations also correlated negatively with canopy openness (Table 3). No correlations

were found between light conditions and leaf weight, nor between leaf weight and nutrient concentration (Table 3).

## Discussion

### Light and soil moisture availability

The canopy photographs that we took to test if light availability is higher below the kauri crown than just outside the crown (hypothesis (1)) were taken in autumn

2002 in the kauri and tea tree plots, and in spring 2004 in the angiosperm plots. Although these photographs were not taken in the same season, we still think that they allow comparison of the light conditions in the plots, since the temperate forest in New Zealand is evergreen, the photographs were taken on overcast days, and light intensity was not measured directly but computed from the photographs. The results of these computations (Table 1) do not support our first hypothesis. However, we frequently observed a strong light intensity gradient from the darker edge of the kauri crown to the more open area near the kauri trunk. Comparison of the light conditions close to the kauri trunks with those further from the trunks would probably have shown significant differences. The positive correlation we found between canopy openness and thickness of the organic layer (Table 3) also indicates that with increasing age of a kauri tree its litter accumulates on the soil, and simultaneously the combined canopy of the kauri tree and its understorey shrubs and trees becomes more open.

Our soil moisture measurements show that in April 2002 the organic soil under the kauri crown was dryer than the surrounding clay under the kauri crown (Table 2). Though soil moisture was not measured in the angiosperm plots in April 2002, data (Verkaik, unpublished) suggest that during dry periods the organic layer under the kauri crown is also dryer than the clay soil under the surrounding angiosperm vegetation.

Our first soil moisture measurement (in the third week of January 2002) was conducted after a rainy December and a rainy start of January, when the soil was saturated with water (mean ( $\pm$ SE) daily rainfall over 6 weeks before measurement =  $9.3 \pm 2.0$  mm). At that time the available water contents of the organic soil and the clay soil under kauri were similar (Table 2), indicating that it is not the difference in soil material that causes the difference in water availability later in the season. The soil moisture measurement of April 2002 was preceded by a relative dry period (mean ( $\pm$ SE) daily rainfall over 2 weeks before measurement =  $1.6 \pm 0.9$  mm), and because such dry periods are common in the Waitakere Ranges almost every year, we suspect the organic layer under mature kauri trees is frequently much dryer than the clay soil under the surrounding vegetation. Kauri trees probably transpire more strongly than the surrounding vegetation, since their crowns emerge above the main canopy where they are exposed to sun and wind. As the fine roots of kauri are concentrated in the organic layer (Ecroyd 1982), we propose that the uptake of water by kauri roots causes the periodical dryness of the organic layer under kauri trees.

### Nutrient availability

The low nutrient concentrations in the leaves of hangehange shrubs below kauri crowns (Fig. 1) offer some support for the second hypothesis that nutrient availability beneath mature kauri trees is lower than beneath surrounding angiosperm trees. However, an alternative explanation for the lower nutrient concentration in these hangehange leaves could be that light availability is higher below kauri than outside the kauri crown. More light might stimulate the growth of hangehange, thereby diluting the concentrations of nitrogen and phosphorus in its leaves. However, differences in light availability between plot types were not significant (Table 1). Further, under field conditions nitrogen concentrations are often found to be higher in sun leaves than in shade leaves (Meletiou-Christou et al. 1994). We also found no correlation between the weight of the hangehange leaves and canopy openness or photon flux density (Table 3). The weight of the leaves also did not correlate with any of the measured nutrient concentrations in these leaves (Table 3). Therefore we think that the lower nitrogen and phosphorus concentrations in the hangehange leaves below kauri compared with just outside the kauri crown do indeed show that nutrient availability is lower under the crown. This finding suggests that kauri lowers nutrient availability in the soil (e.g. Bieleski 1959; Ecroyd 1982) and that kauri forest can be regarded as a mosaic of site fertility (Ogden & Stewart 1995).

The negative correlations between nutrient concentrations in hangehange leaves and thickness of the organic layer (Table 3, Fig. 2) might be explained by the immobilisation of nutrients in the organic layer (Enright & Ogden 1987; Silvester 2000; Verkaik et al. 2006). Another explanation might be the strong weathering or podsolisation of the mineral soil beneath kauri trees (Bloomfield 1953; Wells & Northey 1985; Jongkind & Burman 2006).

### Are conditions under kauri favourable for kauri seedlings?

Our measurements suggest that the environmental conditions for seedlings under mature kauri trees are characterised by a relatively high light intensity, low nutrient availability, and periodical dryness (Tables 1 & 3, Fig. 1). With regard to the light and nutrient conditions, the kauri plots are more similar to the tea tree vegetation where kauri seedlings are abundant, than to the angiosperm plots. A main difference between the kauri plots and the tea tree plots is that during dry periods the organic layer under kauri is dryer than the clay soil under tea tree (Table 2). We propose that periodical dryness is a main cause for the relative scarcity of kauri seedlings under mature kauri compared with the tea tree vegetation, since young kauri seedlings are susceptible to low soil moisture availability (Mirams 1957).

In the long run, however, periodical dryness of the soil may be an advantage to kauri, because, when they grow older, kauri seedlings can tolerate drought better than many other species (Bielecki 1959; Barton 1982; Stephens et al. 1999). The nutrient-poor conditions we found beneath the kauri crown can also be an advantage for kauri seedlings competing with angiosperm seedlings, since compared with other species kauri seedlings have relatively low nutrient requirements (Peterson 1962). On sites of higher soil fertility kauri seedlings are often out-competed by faster growing angiosperm seedlings (Pook 1979; Bond 1989; Burns & Leathwick 1996). Since nutrient availability appears to be lowered by the influence of kauri trees, a positive feedback between kauri and the soil might be present.

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## References

- Ahmed M, Ogden J 1987. Population dynamics of the emergent conifer *Agathis australis* (D. Don) Lindl. (kauri) in New Zealand I. Population structures and tree growth rates in mature stands. *New Zealand Journal of Botany* 25: 217–229.
- Barton IL 1982. An investigation of aspects of the physiology and ecology of kauri (*Agathis australis* Salisb.). Unpublished MSc thesis, University of Waikato, Hamilton, New Zealand. 214 p.
- Berendse F 1994. Litter decomposability: a neglected component of plant fitness. *Journal of Ecology* 82: 187–190.
- Beveridge AE 1977. Notes on the silviculture of kauri. In: Chavasse CGR ed. *New Zealand Institute of Foresters, Forestry handbook 1977*. Pp. 125–130.
- Bielecki RL 1959. Factors affecting growth and distribution of kauri (*Agathis australis* Salisb.). *Australian Journal of Botany* 7: 252–294.
- Bielecki RL 1979. Kauri forest. In: *New Zealand trees, conifers*. Auckland and London, Collins Nature Heritage Series. Pp. 18–28.
- Binkley D 1995. The influence of tree species on forest soils: processes and patterns. In: Mead DJ, Cornforth IS eds *Proceedings of the Trees and Soil Workshop, 28 February–2 March 1994*, Lincoln University, New Zealand. Pp. 1–33.
- Binkley D, Giardina C 1998. Why do tree species affect soils? The warp and woof of tree–soil interactions. *Biogeochemistry* 42: 89–106.
- Bloomfield C 1953. A study of podsolisation. Part II. The mobilization of iron and aluminium by the leaves and bark of *Agathis australis* (kauri). *Journal of Soil Science* 4: 17–23.
- Bond WJ 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnean Society* 36: 227–249.
- Burns BR, Leathwick JR 1996. Vegetation-environment relationships at Waipoua Forest, Northland, New Zealand. *New Zealand Journal of Botany* 34: 79–92.
- Ecroyd CE (compiler) 1982. *Biological flora of New Zealand 8. Agathis australis* (D. Don) Lindl. (Araucariaceae) Kauri. *New Zealand Journal of Botany* 20: 17–36.
- Englund SR, O'Brien JJ, Clark DB 2000. Evaluation of digital and film hemispherical photography and spherical densitometry for measuring forest light environments. *Canadian Journal of Forest Research* 30: 1999–2005.
- Enright NJ, Ogden J 1987. Decomposition of litter from common woody species of kauri (*Agathis australis* Salisb.) forest in northern New Zealand. *Australian Journal of Ecology* 12: 109–124.
- Freligh LE, Calcote RR, Davis MB, Pastor J 1993. Patch formation and maintenance in an old-growth hemlock–hardwood forest. *Ecology* 74: 513–527.
- Hobbie SE 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* 7: 336–339.
- Jongkind AG, Buurman P 2006. The effect of kauri (*Agathis australis*) on grain size distribution and clay mineralogy of andesitic soils in the Waitakere Ranges, New Zealand. *Geoderma* 134: 171–186.
- Knops JMH, Bradley KL, Wedin DA 2002. Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecology Letters* 5: 454–466.
- Meletioui-Christou MS, Rhizopoulou S, Diamantoglou S 1994. Seasonal changes of carbohydrates, lipids and nitrogen content in sun and shade leaves from four Mediterranean evergreen sclerophylls. *Environmental and Experimental Botany* 34: 129–140.
- Mirams RV 1957. Aspects of the natural regeneration of the kauri (*Agathis australis* Salisb.). *Transactions of the Royal Society of New Zealand* 84: 661–680.
- Northup RR, Yu Z, Dahlgren RA, Vogt KA 1995. Polyphenol control of nitrogen release from pine

- litter. *Nature* 377: 227–229.
- Ogden J, Stewart GH 1995. Community dynamics of the New Zealand conifers. In: Enright NJ, Hill RS eds *Ecology of the Southern conifers*. Melbourne, Melbourne University Press. Pp. 81–119.
- Ogden J, Wardle GM, Ahmed M 1987. Population dynamics of the emergent conifer *Agathis australis* (D. Don) Lindl. (kauri) in New Zealand II. Seedling population sizes and gap-phase regeneration. *New Zealand Journal of Botany* 25: 231–242.
- Pearcy RW, Ehleringer J, Mooney HA, Rundel PW 1989. *Plant physiological ecology: field methods and instrumentation*. New York, Chapman and Hall.
- Peterson PJ 1962. Mineral nutrition of *Agathis australis* Salisb., the kauri. Part I. Effects of deficiencies of essential elements of the growth and foliar mineral composition of seedlings. *New Zealand Journal of Science* 5: 141–164.
- Pook EW 1979. Seedling growth in tanekaha (*Phyllocladus trichomanoides*): effects of shade and other seedling species. *New Zealand Journal of Forestry Science* 9: 193–200.
- Prescott CE 2002. The influence of the forest canopy on nutrient cycling. *Tree Physiology* 22: 1193–1200.
- Silvester WB 2000. The biology of kauri (*Agathis australis*) in New Zealand II. Nitrogen cycling in four kauri forest remnants. *New Zealand Journal of Botany* 38: 205–220.
- Silvester WB, Orchard TA 1999. The biology of kauri (*Agathis australis*) in New Zealand. I Production, biomass, carbon storage, and litterfall in four forest remnants. *New Zealand Journal of Botany* 37: 553–571.
- Stephens DW, Silvester WB, Burns BR 1999. Differences in water-use efficiency between *Agathis australis* and *Dacrycarpus dacrydioides* are genetically, not environmentally, determined. *New Zealand Journal of Botany* 37: 361–367.
- Swindale LD 1957. The effect of kauri vegetation upon the development of soils from rhyolite and olivine basalt. *New Zealand Soil News* October (5): 164–166.
- Temminghoff EJM, Houba VJG, Van Vark W, Gaikhorst GA 2000. *Soil and plant analysis procedures. Part 3: plant analysis procedures*. The Netherlands, Wageningen University, Sub-Department of Soil Quality.
- Ter Steege H 1996. Winphot 5; a programme to analyze vegetation indices, light and light quality from hemispherical photographs. Georgetown, Guyana, Tropenbos Guyana Reports 95-2, Tropenbos Guyana Programme.
- Van Breemen N, Finzi AC 1998. Plant–soil interactions: ecological aspects and evolutionary implications. *Biogeochemistry* 42: 1–19.
- Verkaik E, Jongkind AG, Berendse F 2006. Short-term and long-term effects of tannins on nitrogen mineralisation and litter decomposition in kauri (*Agathis australis* (D. Don) Lindl.) forests. *Plant and Soil* 287: 337–345.
- Wells N, Northey RD 1985. Strengths of a densipan, humus-pan and clay-pan in a spodosol developed under kauri (*Agathis australis*) and the implications for soil classification. *Geoderma* 35: 1–13.

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