Site conditions affect seedling distribution below and outside the crown of kauri trees (*Agathis australis*)

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Abstract: It has been suggested that plants can change soil characteristics via their litter to favour their own species. The New Zealand kauri tree (*Agathis australis*) presents an interesting case for studying such a positive feedback between plant and soil because it has a huge impact upon the soil. We hypothesised that, under mature kauri trees, compared with sites outside the projection of the crown, seedlings of angiosperm trees are relatively rare, while kauri seedlings are relatively common, due to the poor soil conditions and the higher light intensity. We counted seedlings under and outside the crowns of kauri trees and correlated the presence of these seedlings to measured site conditions. The results confirm the hypotheses and indicate that the establishment of kauri seedlings is favoured by the open canopy and high light intensities below kauri. The low nutrient availability under kauri appears to be unfavourable for the survival of angiosperm seedlings but not for the survival of kauri seedlings. Since the lower nitrogen availability under kauri is due to sequestration of nitrogen in the organic layer under kauri, a positive feedback between kauri and the soil is likely.

Keywords: *Agathis australis*; kauri; New Zealand; plant competition; seedling survival; plant–soil feedback

Introduction

Many studies show that plant litter can change the characteristics of the soil that plants are growing on (e.g. Van Breemen 1993; Binkley 1995; Wardle 2002). It has been suggested that these changes can be beneficial to the species concerned (Van Breemen & Finzi 1998). A positive feedback might develop between plants and soil, whereby plants produce litter that enhances their competitive dominance (e.g. Frelich et al. 1993; Berendse 1994; Northup et al. 1998; Clark et al. 2005). Binkley and Giardina (1998) suggested a study of sites where a second generation of trees grows on sites influenced by the first generation would yield insight into the relative importance of such positive feedbacks for trees. The New Zealand kauri tree (*Agathis australis*) seems an appropriate species to test these ideas, because of its huge impact on the soil (e.g. Swindale 1957; Silvester 2000; Jongkind & Buurman 2006).

Kauri occurs in the warm temperate forest on the North Island of New Zealand. Kauri forest can be regarded as a vegetation mosaic consisting of patches dominated by kauri trees and patches dominated by other species (Cockayne 1921; Halkett & Sale 1986; Ogden & Stewart 1995; Burns & Leathwick 1996). On places where forest has disappeared through disturbance like logging, a cyclone or a landslide, patches of tea tree vegetation (*Leptospermum scoparium* and *Kunzea ericoides*, both Myrtaceae) establish. In this tea tree vegetation many kauri seedlings can often be found (Mirams 1957; Bieleski 1959). When enough kauri seedlings have established, they will eventually replace the tea trees. The kauri will form a forest of poles or 'rickers', and when the leading kauri poles are well above their associates, kauri will develop an open spreading crown above the canopy of the other species, and a relatively even aged stand of mature kauri will develop (Burns & Smale 1990; Ogden & Stewart 1995). When the initial cohort of kauri dies it is potentially replaced by a second cohort of kauri, but this cohort will be less synchronous and dense than the first (Ogden 1985). Many of the gaps created by the death of mature kauri trees are requisitioned by faster growing angiosperm species (Enright et al. 1993). However, gap-phase regeneration of kauri does occur, especially on sites of low fertility where young kauri trees compete most successfully with angiosperm species, and on sites where disturbance is frequent (Ogden et al. 1987; Ogden & Stewart 1995). The low-fertility and high-disturbance sites, like ridge-crests, can

thus be regarded as the centre of the kauri niche from which, following large-scale landscape disturbances, kauri expands across the landscape (Ogden & Stewart 1995; Enright et al. 1999).

In a previous study in the kauri forests of the Waitakere Ranges (Verkaik & Braakhekke 2007) we have measured site conditions in plots situated right below the crown of mature kauri trees and in plots just outside their crown projections. The results of that study indicated that nitrogen and phosphorus availability are lower under than outside the kauri crown. The results also indicated that, during dry periods, water availability is less in the thick organic layer under the kauri crowns than in the surrounding clay soil. It further appeared that, as the kauri trees grow older, the organic layer gets thicker and the canopy of the vegetation becomes more open. Since kauri seedlings need high light intensities (Pook 1979; Wright 1993) and probably can stand dry and nutrient-poor conditions better than many angiosperm species (Bieleski 1959; Verkaik et al. in press) the results suggest that, compared with the conditions outside the kauri crown, the conditions under the kauri crown are relatively favourable for the growth of kauri seedlings, and unfavourable for the growth of angiosperm seedlings (Verkaik & Braakhekke 2007).

In the present study we focused on the distribution of seedlings and hypothesised that (1) due to the poor soil conditions under kauri, seedlings of angiosperm tree species are rare under kauri compared with sites just outside the crown of kauri and (2) due to the openness of the canopy, kauri seedlings are relatively common under kauri trees compared with sites just outside the crown of kauri trees. To test these hypotheses, we counted seedlings of tree and shrub species in plots under five kauri trees and just outside the crowns of these kauri trees. As a reference we also counted seedlings in plots in tea tree vegetation where kauri seedlings were abundant. We analysed the relationships between seedling densities and several site conditions that were measured by Verkaik and Braakhekke (2007).

Methods

Site conditions

The plots measured 100 m^2 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. 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. Five plots were situated near these plots, with the same inclination and orientation, but just outside the projection of the kauri crown, in vegetation dominated by angiosperm tree species (the 'angiosperm plots'). These angiosperm plots were bordering the edge of the kauri crowns and were situated within 30 m distance from the kauri trunk. 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 and E2645846, N6477633, both 120 m a.s.l).

A detailed description of the methods used to measure the site factors and of the results is given in Verkaik & Braakhekke (2007). We determined plant available soil water as the actual volumetric soil water content minus the water content at the permanent wilting point. In 2002 available soil water was determined three times, but only in the kauri and tea tree plots, while in 2003 it was determined three times in all plots. To compare nutrient availability in the plots we measured the nutrient concentration of leaves of the shrub species hangehange (*Geniostoma rupestre* var. *ligustrifolium*), which was common to all plots. Light availability (photon flux density at ground level and canopy openness) in the plots was determined using hemispherical photographs (Sigma 8 mm f4 fisheye lens, MZ 50 Pentax camera). The thickness of the organic layer in the plots was measured by probing with an iron rod through the soft organic layer down to the harder clay layer underneath.

Number of seedlings

In each plot we counted seedlings of trees, shrubs, and tree ferns while seedlings of vines were not counted. Seedlings of shrubs were only counted as long as they were still mostly unbranched. The seedlings were divided in three size classes: class 1 from 0 to 10 cm, class 2 from 10 to 30 cm, and class 3 from 30 to 100 cm. The survival rate of seedlings from size class 1 to size classes 2 and 3 was calculated by expressing the seedling numbers in the latter classes as a percentage of the number in class 1. The seedlings in the kauri and tea tree plots were counted in January 2002 and those in the angiosperm plots in September 2004. Despite this difference in sampling date, we think that for several reasons (see discussion) the data can still be used to test the hypothesis.

Most seedlings could be identified, at least to genus level. We did not distinguish between *Nestegis montana* and *N. lanceolata* seedlings in classes 1 and 2, although most were probably *N. lanceolata* seedlings since mature *N. lanceolata* plants were far more abundant than mature *N. montana*. Neither did we distinguish

between the *Coprosma* species in classes 1 and 2, except for the species *C. lucida* and *C. grandifolia*. Most of those undetermined *Coprosma* seedlings were probably *C. arborea* since this species was by far the most common in the vegetation. We did not distinguish between *Melicytus macrophyllus* and *M. ramiflorus* seedlings. In some plots a small number (at most 5−10) of the smallest seedlings remained undetermined.

We calculated the number of 'non-gymnosperm seedlings' by including seedlings of the following species: *Beilschmiedia tarairi, B. tawa, Coprosma arborea, Corynocarpus laevigatus, Cyathea dealbata, Dicksonia squarrosa, Dysoxylum spectabile, Elaeocarpus dentatus, Hedycarya arborea, Hoheria populnea* var. *populnea, Kunzea ericoides, Knightia excelsa, Litsea calicaris, Melicytus* spp., *Myrsine australis, M. salicina, Nestegis lanceolata, Pittosporum tenuifolium, Pseudopanax arboreus, P. crassifolius, Quintinia serrata, Rhopalostylis sapida, Schefflera digitata, Leptospermum scoparium* and *Vitex lucens*. Since this group includes tree ferns as well as angiosperm seedlings, we will use the term 'non-gymnosperm seedlings' throughout the text.

Analyses

To calculate canopy openness and photon flux density, the hemispherical photographs were analysed with Winphot 5 (Ter Steege 1996). All statistical analyses were conducted with the SPSS statistical package for Windows (12.0.1). Differences in seedling numbers between kauri and angiosperm plots were tested with the paired non-parametric Wilcoxon test, and differences in seedling numbers between tea tree and kauri plots and tea tree and angiosperm plots were tested with the non-parametric Mann–Whitney test. To evaluate the relationships between the site factors and the presence or survival of the seedlings Spearman correlations were calculated for the data of all the plots, for the data of the combinations of two plot types (kauri and tea tree plots, kauri and angiosperm plots, and angiosperm and tea tree plots), and for the three individual plot types.

Results

Number of seedlings

The absolute numbers of non-gymnosperm seedlings of the height classes 1, 2 and 3 were not significantly different between the kauri, angiosperm and tea tree plots (Table 1). Kauri seedlings of height classes 2 and 3, however, were more common in tea tree plots than in kauri or angiosperm plots (Table 1).

Figure 1 illustrates seedling survival from class 1 to classes 2 and 3. The survival of non-gymnosperm seedlings to class 2, calculated by expressing the seedlings of class 2 as a percentage of the seedlings in
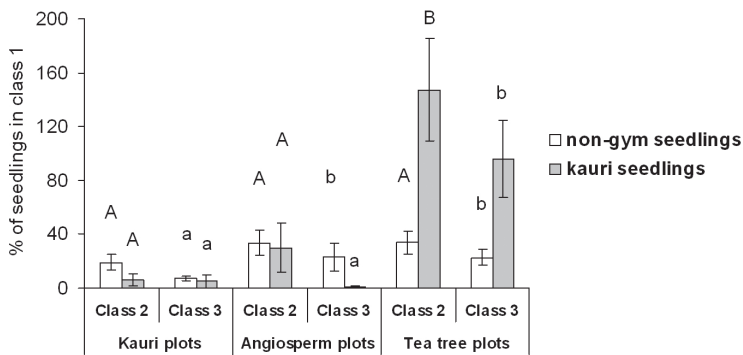
Figure 1. Survival of kauri and non-gymnosperm seedlings from size class 1 to size classes 2 or 3. Different upper-case letters indicate significant differences between bars in survival to size class 2 and different lower-case letters indicate significant differences between bars in survival to size class 3 ($P < 0.05$). Error bars indicate SE.

Table 1. Mean number of seedlings (± SE) within three height classes in three plot (100 m^2) types at study sites within the Waitakere Ranges, northern New Zealand.
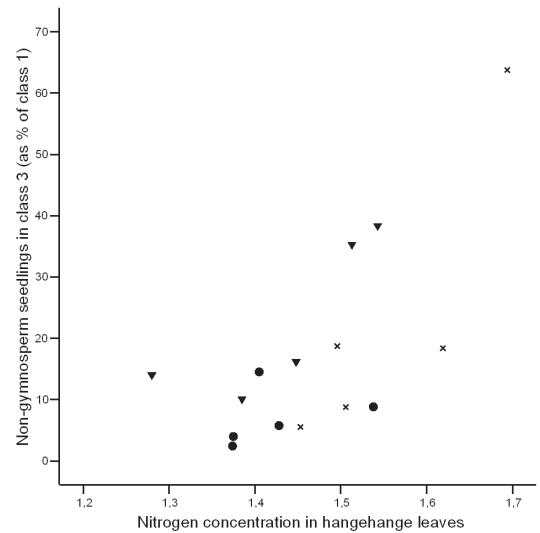
Height class (1–3)	Non-gymnosperm seedlings			Kauri seedlings		
	0–10 cm	10–30 cm	30–100 cm	0–10 cm	10–30 cm	30–100 cm
Kauri	379.6 ± 66.0	60.6 ± 9.8	22.6 ± 4.1	17.4 ± 6.5	1.8 ± 1.6	0.6 ± 0.6
Angiosperm	236.4 ± 59.9	62.6 ± 13.3	35.0 ± 7.7	12.8 ± 7.6	2.4 ± 1.4	0.4 ± 0.9
Tea tree	292.7 ± 59.4	94.8 ± 26.6	65.2 ± 19.3	36.8 ± 20.1	38.7 ± 14.8	17.9 ± 2.8

class 1, was not different between the kauri, angiosperm and tea tree plots. The survival of non-gymnosperm seedlings to class 3, calculated by expressing the seedlings of class 3 as a percentage of the seedlings in class 1, was significantly lower in the kauri plots than in the angiosperm and tea tree plots. The survival of kauri seedlings to classes 2 and 3 was not different between the kauri and angiosperm plot, but in the tea tree plots survival of kauri was significantly higher. In the angiosperm plots survival to class 3 was lower for kauri seedlings than for non-gymnosperm seedlings. In kauri plots these numbers were about equal, suggesting that the conditions under mature kauri trees to survive to size class 3 are equally favourable for kauri seedlings as for angiosperm seedlings.

Correlations between site conditions and seedling numbers

Differences in nutrient availability appear to be important for non-gymnosperm seedlings, since the absolute number of seedlings of class 3 correlated positively with the nitrogen concentration in hangehange leaves (Table 2). Also, the survival of non-gymnosperm seedlings to class 2 and 3 correlated positively with the nitrogen concentration in hangehange leaves (Table 2, Fig. 2). Further, the absolute numbers of non-gymnosperm seedlings of classes 2 and 3 correlated positively with the phosphorus concentration in hangehange leaves when the data of kauri and tea tree plots were merged (Table 3). The survival of non-gymnosperm seedlings to class 2 also correlated positively with the nitrogen concentration in the hangehange leaves when the data

of kauri and tea tree plots were merged (Table 3). These results suggest that the non-gymnosperm seedlings are hampered by low nutrient availability under kauri.

Figure 2. Correlation between nitrogen concentration in hangehange leaves (% of dry weight) and the survival of non-gymnosperm seedlings to size class 3 (non-parametric, $r = 0.646$, $P = 0.009$), for the kauri plots (●), the angiosperm plots (×) and the tea tree plots (▼).

Table 2. Non-parametric correlations between site conditions and the absolute number and survival of kauri and non-gymnosperm seedlings in the Waitakere Ranges. Data of all plot types ($n = 15$). * $P < 0.05$, ** $P < 0.01$.

	Species	Organic layer thickness	Photon flux density	Canopy openness	N concentration hangehange	P concentration hangehange	Kauri diameter
Numbers							
Class 1	Non-gym	0.171	0.132	0.143	−0.343	−0.081	0.383
Class 2	Non-gym	*−0.530	−0.191	−0.150	0.242	0.358	−0.307
Class 3	Non-gym	**−0.749	−0.291	−0.443	*0.520	0.496	−0.472
Survival							
Class 1 to class 2	Non-gym	*−0.525	−0.257	−0.229	*0.568	0.373	*−0.520
Class 1 to class 3	Non-gym	**−0.736	−0.282	−0.371	**0.646	0.433	**−0.653
Numbers							
Class 1	Kauri	0.245	0.404	*0.617	−0.410	−0.455	0.168
Class 2	Kauri	−0.329	0.142	0.191	−0.091	−0.157	−0.304
Class 3	Kauri	−0.271	0.261	0.033	−0.045	−0.287	−0.288
Survival							
Class 1 to class 2	Kauri	*−0.560	−0.062	−0.069	0.135	0.028	−0.476
Class 1 to class 3	Kauri	−0.380	0.250	−0.068	0.068	−0.218	−0.341

The absolute numbers of non-gymnosperm seedlings of the classes 2 and 3 correlated negatively with thickness of the organic layer and so did the survival of non-gymnosperm seedlings to class 2 and 3 (Table 2). Three of these four negative correlations were also found when, to eliminate possible effects of the observation date, the data of the angiosperm plots were left out of consideration (Table 3). This suggests that a thick organic layer hampers the survival of non-gymnosperm seedlings.

The absolute number of kauri seedlings of class 1 correlated positively with canopy openness for all the plots (Table 2), as well as for the kauri plots and tea tree plots only (Table 3). We also found negative correlations between kauri diameter and the number of kauri seedlings (Table 3). This suggests the establishment of kauri seedlings is favoured by open conditions. The survival of kauri seedlings to size classes 2 and 3 correlated negatively with thickness of the organic layer (Tables 2 & 3). The absolute number and survival of kauri seedlings did not correlate with the nitrogen concentration or phosphorus concentration in hangehange leaves, which suggests that nutrient availability is not an important factor for kauri seedlings.

Sites with more available soil moisture appear to have fewer small non-gymnosperm seedlings, since we found negative correlations between the absolute number of non-gymnosperm seedlings of class 1 and soil moisture availability in the upper soil layer for the measurements of March 2003 and May 2003 (Table 4, data of the kauri and the angiosperm plots together). These negative correlations were also found when the data of the kauri plots and the angiosperm plots were analysed separately (data not shown). The survival of non-gymnosperm seedlings to size class 2 was correlated positively to soil moisture availability in March 2003 (Table 4). A positive correlation was also found when data of the tea tree and kauri plots were analysed separately (data not shown). There was no relationship between survival of non-gymnosperm seedlings to size class 3 and soil moisture availability, which suggests that soil moisture availability is less important for the survival of larger seedlings.

We found positive correlations between soil moisture availability in March 2003 and the absolute number of kauri seedlings of class 2 (Table 4). Further, we found positive correlations between the survival of kauri seedlings to class 2 and soil moisture availability in March 2003 (both soil layers) and April and May 2003 (deeper soil layer; Table 4). These positive correlations were also found when the data of the kauri plots and the angiosperm plots were analysed separately (not shown). However, we found no correlation between soil moisture availability and the number and survival of kauri seedlings to class 3. This suggests that for kauri, as for non-gymnosperm species, soil moisture is more relevant to the smallest seedlings than to seedlings of more than 10 cm height.

Discussion

Methodology

Seedling densities in the plots will depend on the date of observation. The results will therefore be affected by

Table 3. Non-parametric correlations between site conditions and the absolute number and survival of kauri and non-gymnosperm seedlings at sites within the Waitakere Ranges. Data of the kauri and tea tree plots only (*n* = 10). * *P* < 0.05, ** *P* < 0.01.

	Species	Organic layer thickness	Photon flux density	Canopy openness	N concentration hangehange	P concentration hangehange	Kauri diameter
Numbers							
Class 1	Non-gym	0.127	−0.091	−0.115	−0.188	0.213	0.331
Class 2	Non-gym	*−0.723	−0.492	−0.468	0.517	*0.673	−0.546
Class 3	Non-gym	**−0.818	−0.200	−0.418	0.503	*0.652	*−0.707
Survival							
Class 1 to class 2	Non-gym	−0.588	−0.152	−0.176	*0.636	0.317	*−0.650
Class 1 to class 3	Non-gym	**−0.818	−0.079	−0.188	0.588	0.335	**−0.869
Numbers							
Class 1	Kauri	0.304	0.480	**0.790	−0.377	−0.407	0.078
Class 2	Kauri	−0.485	0.166	0.141	0.080	0.006	*−0.690
Class 3	Kauri	−0.557	0.244	−0.125	0.269	−0.113	**−0.774
Survival							
Class 1 to class 2	Kauri	*−0.669	−0.018	−0.104	0.288	0.093	**−0.785
Class 1 to class 3	Kauri	*−0.719	0.206	−0.325	0.557	0.094	**−0.832

Table 4. Non-parametric correlations of the absolute number and survival of kauri seedlings and non-gymnosperm seedlings with soil moisture availability in the Waitakere Ranges measured three times in 2003 at two depths. Data of the kauri and angiosperm plots only ($n = 10$). * P <0.05 level, ** P <0.01.

| | | March 2003 | | April 2003 | | May 2003 | |
		0–7.5 cm	7.5–15 cm	0–7.5 cm	7.5–15 cm	0–7.5 cm	7.5–15 cm
Numbers							
Class 1	Non-gym	*−**0.636**	−0.127	−0.576	−0.079	**−0.867**	−0.236
Class 2	Non-gym	−0.067	0.097	−0.219	−0.298	−0.426	−0.365
Class 3	Non-gym	0.127	0.042	−0.079	−0.285	−0.006	−0.212
Survival							
Class 1 to class 2	Non-gym	***0.636**	0.382	0.455	0.079	0.552	0.067
Class 1 to class 3	Non-gym	0.467	0.067	0.345	−0.139	0.539	−0.042
Numbers							
Class 1	Kauri	0.225	0.067	0.231	0.201	0.316	0.316
Class 2	Kauri	***0.701**	***0.785**	0.474	0.454	0.259	0.629
Class 3	Kauri	0.415	0.182	−0.061	−0.216	0.242	0.216
Survival							
Class 1 to class 2	Kauri	***0.808**	***0.925**	0.614	*0.653	0.356	*0.743
Class 1 to class 3	Kauri	0.415	0.182	−0.061	−0.216	0.242	0.216

the different dates on which the seedlings were counted in the angiosperm plots on the one hand and the kauri and tea tree plots on the other hand. However, seedlings in kauri forest generally have a slow growth rate. For seedlings between 10 and 30 cm in height in kauri forest an average growth rate of only 5.4 mm yr^{-1} was reported (Gillman & Ogden 2001). In an old secondary kauri stand, kauri seedlings of 1.4-m height appeared to have a mean age of 40 years (range 30–56 years) (Burns & Smale 1990). Because of these slow growth rates it is likely that each height class we distinguished contained seedlings that germinated during a number of years. The slow growth rate makes our method more robust to the differences in sampling date. This was confirmed by the fact that most significant correlations between site conditions and seedling density were also found when we analysed the data from the different observation dates separately (see below).

Non-gymnosperm seedlings

The observation that the survival of non-gymnosperm seedlings to class 3 is lower under mature kauri trees than in the angiosperm vegetation outside the projection of the kauri crowns (Fig. 1) supports the hypothesis that seedlings of non-gymnosperm species are hampered under mature kauri. Also the correlation tests suggest conditions under kauri are not favourable for the growth and survival of non-gymnosperm seedlings. Both the absolute number of non-gymnosperm seedlings of class 3 and the survival of non-gymnosperm seedlings of class 2 and 3 correlated negatively with thickness of the organic layer (Table 2). These correlations were also found when the data of the angiosperm plots were

omitted from the analysis to rule out a possible effect of the observation date (Table 3).

One explanation for the negative correlation between survival of non-gymnosperm seedlings and organic layer thickness can be the low availability of nutrients in the organic layer of the kauri plots. Nitrogen and phosphorus concentrations in hangehange leaves were lower under kauri than outside the crown of kauri and correlated negatively with organic layer thickness (Verkaik & Braakhekke 2007). The positive correlations we found between nitrogen and phosphorus concentrations in the hangehange leaves and the presence or survival of non-gymnosperm seedling (Tables 2 & 3, Fig. 2) suggest these seedlings are hampered by nutrient deficiency. These correlations were also found when the data of the angiosperm plots were omitted from the analysis in order to eliminate a possible effect of differences in observation date (Table 3).

An additional explanation for the negative correlation between survival of non-gymnosperm seedlings and organic layer thickness might be variation in seedling mortality due to litterfall. In kauri forest macro-litterfall poses a threat to the survival of seedlings. Litterfall of kauri, tree ferns and nīkau palm (*Rhopalostylis sapida*) especially can damage and kill seedlings (Gillman & Ogden 2001, 2005; Gillman et al. 2004). Although the angiosperm plots contained tree ferns (*Cyathea dealbata* and *Dicksonia squarrosa*) and nikau palm, damage to seedlings due to litterfall might be higher in the kauri plots, since these plots were established beneath the crown of kauri trees and contained in addition some tree ferns (*Cyathea dealbata*).

Kauri seedlings

The hypothesis that light conditions under kauri are favourable for kauri seedlings is supported by part of the results. The number of kauri seedlings of height class 1 correlated positively to canopy openness (Table 2) and this positive correlation was also found when the data of the angiosperm plots were left out of consideration to rule out a possible effect of observation date (Table 3). There are more studies suggesting that high light intensities favour the growth of kauri seedlings (Bieleski 1959; Pook 1979; Ogden et al. 1987; Wright 1993).

Since the density of kauri seedlings is generally much higher in secondary forest dominated by tea tree than under mature kauri trees (Mirams 1957), we have included the tea tree plots as a reference in our study to get an indication of the conditions that are optimal for kauri regeneration. The density of kauri seedlings of classes 2 and 3 (Table 1) as well as survival from class 1 to classes 2 and 3 (Fig. 1) were indeed lower in the kauri plots than in the tea tree plots.

There are several explanations for the lower survival of kauri seedlings below kauri than below tea tree. The positive correlations between soil moisture availability and the survival of kauri seedlings to class 2 (Table 4) indicate that the smaller kauri seedlings are susceptible to drought, as suggested earlier by Mirams (1957). Since nutrient and light availability in the kauri and tea tree plots are similar, while soil moisture availability is lower in the kauri plots (Verkaik & Braakhekke 2007), we think that the lower density and survival of small kauri seedlings under mature kauri trees is due to periodical drought. When the kauri seedlings grow taller they will be better resistant to drought (Bieleski 1959; Barton 1982; Stephens et al. 1999).

A second explanation for the lower survival of kauri seedlings below kauri than in tea tree vegetation might be seedling mortality due to macro-litterfall (Gillman & Ogden 2001, 2005). Although the tea tree plots also contained species whose litterfall can damage seedlings, such as tree ferns (*Dicksonia squarrosa*, *Cyathea dealbata, C. medullaris*), nīkau palm and sometimes a ricker of kauri, the seedlings in the kauri plots were probably exposed to higher rates of macro-litterfall since all kauri plots were established beneath the crowns of mature kauri trees.

A positive feedback between kauri and the soil?

Compared with tea tree vegetation, mature kauri stands normally contain low numbers of kauri seedlings. However, successful regeneration of kauri within stands of mature kauri does occur. This is indicated by the presence of several hundreds of established kauri seedlings and saplings per hectare in stands of mature kauri forest (Ogden et al. 1987) and by the observation that in many mature kauri stands kauri trees of all diameter classes are present (Ahmed & Ogden 1987). Regeneration in stands of mature trees is important for the survival of the species, since it enables kauri to occupy low-fertility and high-disturbance sites for some generations and await large-scale disturbances after which it can spread across the landscape (Ogden 1985; Ogden & Stewart 1995).

For kauri seedlings conditions might be more favourable beneath kauri than in angiosperm vegetation just outside the kauri crown. Beneath mature kauri, the survival of kauri seedlings and non-gymnosperm seedlings did not differ significantly from each other, while in the angiosperm plots just outside the kauri crown, the survival of kauri seedlings was less than the survival of non-gymnosperm seedlings (Fig. 1). We suspect that outside the kauri crown, where nutrient availability is higher and light intensity lower, kauri seedlings lose the competition for light from the faster growing angiosperm seedlings, as suggested for gymnosperm species in general (Bond 1989) and for kauri specifically (Pook 1979; Burns & Leathwick 1996; Verkaik et al. in press). Under kauri, the kauri seedlings appear better able to compete with angiosperm seedlings since the latter seem to be hampered by low nutrient availability. Since the low nutrient availability under mature kauri is caused by the slow decomposition rate of kauri litter and the consequent sequestration of nutrients in the organic layer (Silvester 2000; Verkaik et al. 2006), we conclude that a positive feedback between kauri and the soil might be present.

Acknowledgements

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