

Tree fern trunks facilitate seedling regeneration in a productive lowland temperate rain forest

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Abstract Seedling regeneration on forest floors is often impaired by competition with established plants. In some lowland temperate rain forests, tree fern trunks provide safe sites on which tree species establish, and grow large enough to take root in the ground and persist. Here we explore the competitive and facilitative effects of two tree fern species, *Cyathea smithii* and *Dicksonia squarrosa*, on the epiphytic regeneration of tree species in nutrient-rich alluvial forests in New Zealand. The difficulties that seedlings have in establishing on vertical tree fern trunks were indicated by the following observations. First, seedling abundance was greatest on the oldest sections of tree fern trunks, near the base, suggesting that trunks gradually recruited more and more seedlings over time, but many sections of trunk were devoid of seedlings, indicating the difficulty of establishment on a vertical surface. Second, most seedlings were from small-seeded species, presumably because smaller seeds can easily lodge on tree fern trunks. Deer browsing damage was observed on 73% of epiphytic seedlings growing within 2 m of the ground, whereas few seedlings above that height were browsed. This suggests that tree ferns provide refugia from introduced deer, and may slow the decline in population size of deer-preferred species. We reasoned that tree ferns would compete with epiphytic seedlings for light, because below the tree fern canopy photosynthetically active radiation (PAR) was about 1% of above-canopy

PAR. Frond removal almost tripled %PAR on the forest floor, leading to a significant increase in the height growth rate (HGR) of seedlings planted on the forest floor, but having no effects on the HGRs of epiphytic seedlings. Our study shows evidence of direct facilitative interactions by tree ferns during seedling establishment in plant communities associated with nutrient-rich soils.

Keywords Facilitation · Keystone species · Quantile regression · New Zealand

Introduction

During regeneration in productive forests, competitive interactions between seedlings and established plants are assumed to predominate, whereas facilitative interactions are not thought to be common or important (Holmgren et al. 1997). Competition is thought to predominate because the forest floor is deeply shaded by established plants, so small seedlings are limited by light (Canham et al. 1994; Metcalfe and Grubb 1995). Canopy trees typically intercept around 95–99% of incoming photosynthetically active radiation (PAR), and dense understorey plants, such as ferns, bamboos and palms may intercept a further 50% (Harmon and Franklin 1989; Denslow et al. 1991; George and Bazzaz 1999; Wang and Augspurger 2004; Coomes et al. 2005). In addition, trees can exert other negative effects on species regeneration, by competing for soil nutrients (Coomes and Grubb 2000), providing shelter for herbivores and granivores (Wada 1993) and releasing allelochemicals (Horsley and Marquis 1983).

Facilitation, on the other hand, is widely recognized as being important in xeric, low-nutrient and high-altitude habitats (Bertness and Callaway 1994; Callaway 1995). For example, during plant regeneration in arid and semi-arid

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ecosystems, mature individuals improve the establishment of young plants growing around them by providing shade that reduces plant and soil temperatures (i.e. “nurse plant effect”) (Turner et al. 1966; Franco and Nobel 1989). Similarly, in alpine and subalpine areas, young plants can benefit from being protected from wind and wind-blown snow and ice by adult plants (Bonde 1968; Carlsson and Callaghan 1991). In contrast, only indirect facilitation (sensu Levine 1999) has been considered as important for regeneration success in tall forests, whereby one species is less affected by competition from the understorey layer than another and is thereby given a comparative advantage (Pages and Michalet 2003). For example, in temperate forests in Japan, the regeneration of *Picea glehnii* is strongest in locations with a dense understorey of bamboo (*Sasa* species), whereas *Abies sachalinensis* has greater success when bamboo is absent (Takahashi 1997). The explanation is that *P. glehnii* establishes well on dead logs and thereby escapes competition with *Sasa*, whereas *A. sachalinensis* establishes on the ground where it is outcompeted by the bamboo when it is present, so the bamboo indirectly facilitates the regeneration of *Picea* (Takahashi 1997).

Traditionally the nature of plant interactions in high and low productive habitats have been considered as competitive and facilitative respectively; however, this does not provide a complete picture as even nurse-plant interactions can become negative (Flores-Martinez et al. 1998). Recent studies have stressed the complexity of plant interactions by showing that the interplay between facilitation and competition is dynamic and the strength and direction of plant interactions are not strictly defined for a given plant community (Bertness and Hacker 1994; Callaway and Walker 1997; Maestre and Cortina 2004). In this paper, we investigate the facilitative effect of tree ferns on tree regeneration in a nutrient-rich lowland temperate rain forest in New Zealand, and in particular we test for direct facilitative effects. Very few seedlings of any species are found growing on the floors of these forests (Coomes et al. 2005), because of deep shading by trees and ferns and herbivory by invasive deer and pigs. Elevated surfaces provide important sites for tree regeneration (Ogden 1971). For example, Coomes et al. (2005) found that 99% of tree seedlings were restricted to elevated surfaces in an alluvial forest in southern New Zealand. The authors showed that about 60% of adult trees within a 2-km² area had started life as epiphytes on tree fern trunks. It seems that tree ferns facilitate regeneration of certain species as many seedlings are observed to establish as epiphytes on tree fern trunks, and then grow large enough to take root and persist independently of the tree fern (Pope 1926; Wardle 1963; Veblen and Stewart 1980; Newton and Healey 1989; Coomes et al. 2005; Fig. 1).



Fig. 1 A 5-m-tall *Weinmannia racemosa* sapling which established epiphytically on the trunk of a *Dicksonia squarrosa* tree fern in an alluvial forest in southern New Zealand. Mature trees of this species are often observed to have a tree fern trunk buried in their trunks, indicating their epiphytic origins

Here we explore the facilitative and competitive effects of two tree fern species, *Cyathea smithii* and *Dicksonia squarrosa* (henceforth referred to by genus only), on the regeneration of tree species. Specifically, we test the hypotheses that:

1. *Dicksonia* supports more, and taller, seedlings than *Cyathea* tree ferns of comparable size, because *Cyathea* individuals retain a pendulous skirt of dead fronds that stifles seedling establishment on the trunk (Page and Brownsey 1986).
2. Considering that the age of tree fern trunks increases with distance from the tree fern crown (D), seedling abundance (SA) will be linearly related to D , and seedling height (SH) will be exponentially related to D . This is because seedlings have had longer to establish towards the base of the trunks and will be taller than those in younger sections of the tree fern trunk.
3. Tree ferns facilitate regeneration by providing establishment sites above the deer browse layer.
4. Tree ferns have a negative effect on growth and survival of seedlings on the forest floor, because of the deep shade cast by their fronds.

We test these hypotheses using an observational study of SA, height and browsing damage on 109 living and 46 dead tree fern trunks, and by conducting an experiment to investigate the effects of frond removal on the growth of seedlings planted on the forest floor and on those naturally occurring epiphytic seedlings. In addition, we estimated the growth rate of seedlings and tree ferns, in order to explore the conditions under which seedlings are most likely to overtop their hosts.

Materials and methods

Study site

The study site was situated in lowland temperate rain forests in the southwest of the South Island, New Zealand, in the Waitutu Ecological Region of Fiordland National Park (46.4°S, 167.2°E, McEwen 1987). All the work was conducted in forests growing on nutrient-rich alluvial soils, which are regularly refreshed by the alluvial deposits from two main rivers, the Waitutu and the Wairaurahiri. The forest is composed of a mixture of evergreen coniferous and angiosperm trees, and has a fern-dominated understorey. Two species of angiosperms, *Nothofagus menziesii* (Nothofagaceae) and *Weinmannia racemosa* (Cunoniaceae) dominate the canopy. The conifers *Dacrydium cupressinum* and *Podocarpus hallii* (Podocarpaceae) are occasionally present. Common understorey angiosperms include small trees of *Pseudowintera colorata* (Winteraceae), *Fuchsia excorticata* (Onagraceae), *Griselinia littoralis* (Griselinaceae) and several species of *Raukaua* (Araliaceae). A characteristic feature of these alluvial forests is a dense fern understorey, dominated by the crown fern, *Blechnum discolor*, and the tree ferns *Cyathea smithii* and *Dicksonia squarrosa*.

Observational study of seedlings on tree fern trunks

An initial survey of seedling occurrence was made by line-intersect sampling, in January 2002. Nine parallel transects, each 1–1.5 km long, were established every 500 m in two forest patches along a 13-km stretch of the Waitutu River. These ran from the river to the bottom of the steep escarpment of the marine terraces; the river flowed approximately south, and transects were oriented east–west, perpendicular to the river. Any tree fern between 0.50 and 6 m height that was within 2 m of the transect line was identified by species. Where possible, tree ferns were tagged at breast height (1.35 m), otherwise immediately below the crown. Five tree ferns taller than 6 m were excluded from the study because tree fern bases can be quite unstable, making it impossible for us to climb them without the risk of them toppling. Trunks of dead tree ferns found within 2.5 m of

each transect line were tagged and their length was measured.

The trunk of each tree fern was vertically divided into 50-cm segments, and the mid-point of each section marked with a nail to indicate the height at which light measurements were to be taken. For each of these sections, all tree seedlings greater than 5 cm tall that were growing on the tree fern trunk were identified to species, and their heights and basal diameters were measured. It was noted whether each seedling had been browsed by deer, indicated by a sharp cut in the apical stem. Seedlings that were less than 5 cm tall were counted by species. Any seedlings with interconnected roots were counted only once. The same method was used to sample tree seedlings on every fallen tree fern trunk found within 2.5 m of each transect line.

We characterized light environments for all fallen and standing tree ferns along each transect. Measurements of PAR within the forest were made using a quantum sensor (LI-1905B; Licor, Neb.) under uniformly cloudy conditions, and expressed as a percentage of the “above-canopy PAR” which was simultaneously recorded using a second quantum sensor that had been placed in a nearby forest clearing. For standing tree ferns, PAR was measured on the north, south, east and west side of each 50-cm segment, at the mid-point height of the segment, and at about 5 mm away from the stem. The mean of these four readings was used to calculate the percentage PAR transmission (%PAR). For fallen tree ferns, PAR was recorded on top of the trunk, within each of the 50-cm segments.

The relationship between total number of seedlings on a tree fern trunk and fern height was determined using quantile regression (quantreg package in R), which allows regression lines to be fit to the upper boundary of a bivariate dataset as well as through the centre of the relationship (Cade and Noon 2003). This approach was used because the bivariate plot appeared wedge-shaped, with much greater variance in number of seedlings for large tree ferns. This could suggest that tree fern height only limits seedling numbers when other (unquantified) factors are no longer limiting, and so defining the upper boundary relationship is important (Cade and Noon 2003). For similar reasons, the relationship between SA (i.e. number of seedlings within 50-cm segments), and *D* was analysed by the same approach. To determine whether other factors influenced SA, we added the following terms into the quantile regression model: tree fern species, tree fern height and %PAR.

We used least-square regression analyses to test increases in log-mean SH as a function of tree fern height and tree fern species. Similarly, we tested whether epiphytic SH was exponentially related to *D* by least-square linear regression (lm routine in R), with log (SH) as the response variable, excluding seedlings that had been

browsed from this analysis. Distances from the tree fern top, tree fern species, and light values (%PAR) were included as explanatory variables in these analyses. In all the analyses, a full model was fitted to the data and then reduced to a minimal adequate model by removing terms sequentially, starting from the highest-order interaction terms, and using ANOVA to test for statistical significance of each term (Crawley 2002).

The extent to which standing tree ferns provide a site safe from browsing was quantified by comparing the proportion of seedlings that had been browsed in 50-cm segments up the stems of upright tree ferns, and comparing these proportions with those found in 50-cm segments of fallen ferns. Additionally, we evaluated how the height-to-diameter ratio varied between seedlings on fallen ferns and seedlings on the lower 2 m of standing tree ferns (<2 m). These were analysed using χ^2 -tests.

Competitive effects of tree ferns

The effect of tree fern shading on seedling growth was tested by a manipulation experiment in which seedlings of dominant canopy species were planted into soil on the forest floor under tree fern canopies and under tree ferns from which fronds had been removed. The experiment used a split-plot design with tree fern species as the main factor and tree species as the split-plot effect. In January 2003, sixteen plants each of *Cyathea* and *Dicksonia* were selected (average height 3.2 ± 0.4 m) and for each species eight tree ferns were randomly assigned the frond-removal treatment and the remaining eight retained as controls. Any ground vegetation beneath the crown of each tree fern was removed and a 1.5-m-tall enclosure was constructed around this area using fish netting (mesh size = 5 cm), to protect transplanted seedlings from deer and pigs. For the frond-removal treatment, each frond was cut at its base with secateurs. PAR transmission to the forest floor was measured on overcast days, both before and after frond removal. Measurements were taken at three distances from the tree fern trunk (at the base of the trunk, halfway between the trunk and the projected crown, and at the edge of the projected crown) along lines oriented north, east, south and west from the trunk. PAR measurements are expressed as a percentage of above-canopy PAR, as described in previous sections. The effect of frond removal on %PAR was tested by ANOVA.

Four tree species were chosen for the seedling transplant experiment; *Raukaua simplex*, *N. menziesii*, *Prumnopitys ferruginea*, and *W. racemosa*. Seedlings of at least 5 cm height were excavated from forests close to the study site. In January 2003, two seedlings of each species were transplanted into the soil within each of the 32 fenced enclosures using a randomised design with a minimum of 30-cm

spacing between individuals. Prior to planting, height from the root collar to the apical tip of each seedling was measured with a tape measure and a paint spot used to mark the root collar for subsequent remeasurements. The total number of leaves was counted and leaves were marked with spots of white paint. In April 2004, planted seedlings were manually harvested and carried to the laboratory where SH was measured from the white mark and relative height growth rate (HGR) was calculated as $[\ln(\text{final height}) - \ln(\text{initial height})]/\text{time}$. HGR data were analysed by linear mixed-effect models (the *lme* function in R), with frond-removal treatment, tree species, and tree fern species as fixed effects, and the identity of each tree fern as a random effect. This type of model gives identical results to conventional split-plot ANOVA when there are no missing data, but has distinct advantages when data are missing due to seedling mortality. Leaf production was assessed by counting the number of new leaves on each seedling produced from January 2003 to March 2004, and was analysed using a mixed-effects model which included initial number of leaves as a covariate. A χ^2 -test on counts of seedlings that were alive and dead was used to determine whether frond removal and tree fern species had any effect on seedling survival.

In addition to the planting experiment, all naturally occurring epiphytic seedlings found on experimental tree ferns were tagged and their height and number of leaves were recorded at the start of the experiment. At the end of the experiment, the heights of these seedlings were remeasured, and HGRs calculated. Variation in HGR with respect to treatment and tree fern species was tested with linear models.

Comparison of tree fern and seedling growth rates

We calculated tree fern height growth by estimating the number of fronds produced each year and measuring the number of frond scars per centimetre of trunk height. In January 2002, the height (to the base of the crown) and number of fronds of 18 *Cyathea* and 20 *Dicksonia* individuals of various sizes were recorded. All fronds were marked with coloured plastic tags. These individuals were revisited after 1 and 2 years. At each visit, the number of new fronds was counted and new tags added to these fronds, to calculate the annual rate of frond production. The number of frond scars within a 40-cm band placed in the middle of the trunk was counted on trunks of *Cyathea* and *Dicksonia* individuals and these data were used to convert annual frond production into height growth. The %PAR immediately above the 38 tree ferns was characterized using the procedure described previously. The relationship between height growth and light was modelled with a Michaelis–Menten function (using the *nls* function in R). To evaluate

whether tree ferns grew faster than seedlings of tree species, we compared the mean HGR of seedlings with the tree ferns. We used the light-growth functions to estimate HGR for stems growing in deep shade (2.5% PAR) and small gaps (5% PAR), assuming that tree ferns reach a constant rate of height growth once crowns reach full size. This was compared with tree SH growth, which we assumed to increase exponentially with height. Seedling HGRs of 5- and 30-cm-tall seedlings were calculated by taking their mean relative growth rates [$1/x (dx/dt)$, where x is height] and multiplying them by 5 and 30.

Results

Observational study of seedlings on living tree fern trunks

Epiphytic seedlings were more common on *Dicksonia* than on *Cyathea* trunks: they were found on 85% of *Dicksonia* trunks but only 55% of *Cyathea* trunks (Table 1). The total number of seedlings on tree fern trunks depended on the height of the fern (Fig. 2, left panel): most short ferns (<2 m in height) had no epiphytic seedlings on them, particularly in the case of *Cyathea*, whereas some of the larger tree ferns had over 50 seedlings on them. The average rate of increase in seedling number with tree fern height was greater for *Dicksonia* than for *Cyathea* (Fig. 2, left panel). However, the slope of the 95th quantile line was similar for the two fern species (Fig. 2, left panel). As hypothesized, mean SH increased exponentially with tree fern size, and the regression relationship did not differ between *Cyathea* and *Dicksonia* (Fig. 2, right panel).

SA increased from the top to the base of standing tree ferns (Fig. 3a, b). The median regression line fitted to SA vs. D had an intercept that did not differ significantly from

zero, and the slope of the relationship was greater for *Dicksonia* than for *Cyathea* (Fig. 3a, b). In contrast, the slopes of the 95th quantile lines were not statistically different from one another (Fig. 3a, b). SA was not correlated with %PAR, neither in the case of *Cyathea* ($F_{1,358} = 0.31$, $P = 0.57$) nor *Dicksonia* ($F_{1,364} = 0.64$, $P = 0.42$), even though the upper sections of *Cyathea* and *Dicksonia* received higher %PAR than lower sections (Table 1). SH (excluding browsed seedlings) was unrelated to D (Fig. 3c, d) or %PAR (Spearman rank correlation $r \geq 0.5$; $df = 44$; $P = 0.07$).

Deer browsed heavily on seedlings within 2 m of the ground, with $73 \pm 10\%$ of seedlings showing signs of damage, but seedlings higher up the trunk escaped browsing (Fig. 4a). Browsed seedlings showed lower height-to-diameter ratios, so the average height-to-diameter ratio of seedlings within 2 m of the ground was significantly less than that of seedlings above the browsing layer (Table 1).

Comparison of seedlings on living and fallen tree ferns

Seedlings were much more common on fallen than on standing tree ferns: when all species were considered together, there were 3 times as many seedlings on fallen as on standing tree ferns, and the differences would have been even greater if seedling density had been calculated on a per unit area basis, rather than per unit length, given that only the upper surface of fallen ferns is available for colonization (Table 1). For almost all species, SA was greater on fallen than on standing tree ferns (Table 2), presumably reflecting that horizontal surfaces are easier for seedling establishment than vertical ones. Fallen tree fern trunks did not provide establishment sites for a significantly greater diversity of tree species: of the 18 species found growing on tree fern trunks, 17 were found on fallen and 15 on

Table 1 Summary of the attributes of tree ferns, and their associated epiphytic seedlings, sampled from alluvial forests in southern New Zealand. Within a row, different letters indicate significant differences

Tree fern species	Live, standing tree ferns		Dead, fallen tree ferns
	<i>Cyathea smithii</i>	<i>Dicksonia squarrosa</i>	Unknown
Sample size	61	48	26
Length of trunk (m)	2.6 ± 0.018	3.4 ± 0.21	4.4 ± 0.34
No. ferns with epiphytic seedlings	34	41	26
Median number of seedlings per trunk	1	10	44
%PAR (<2 m from base) ^a	0.99 ± 0.29 a	0.96 ± 0.55 a	1.11 ± 0.02 b
%PAR (>2 m from base)	3.40 ± 0.41 a	3.59 ± 0.74 a	
Seedling height (<2 m from base)	20.49 ± 3.62 a	20.50 ± 1.41 a	11.32 ± 0.55 b
Seedling height (>2 m from base)	25.58 ± 10.34 a	36.01 ± 4.18 b	
H-to-D ratio (<2 m from base)	56.6 ± 4.1 a	61.2 ± 9.7 a	43.5 ± 5.8 b
H-to-D ratio (>2 m from base)	123 ± 16.4 a	118 ± 14.1 b	

^a <2 m from base represents epiphytes growing in the browse tier

among tree ferns ($P < 0.01$), tested by Student's t -tests of values shown (mean \pm 1 SE). %PAR Percentage above-canopy photosynthetically active radiation, H-to-D height-to-diameter

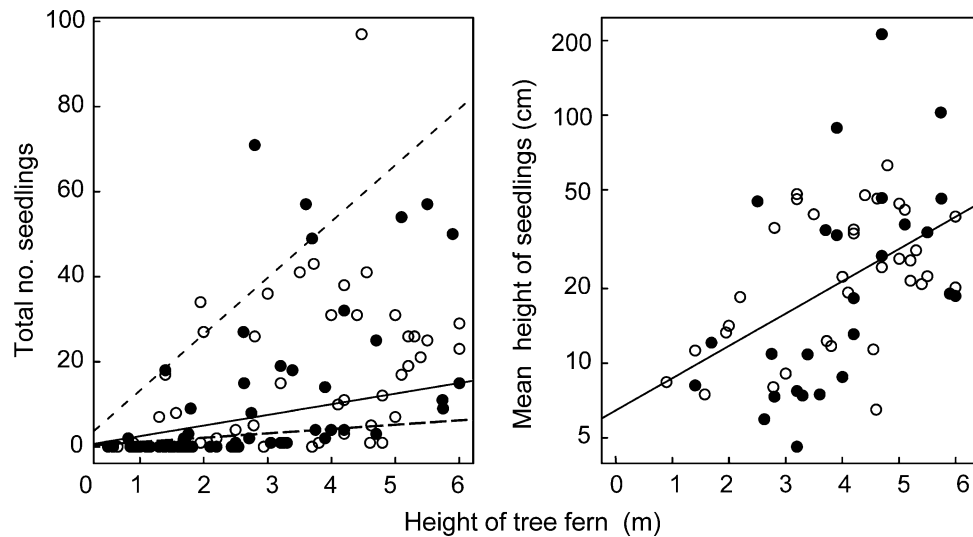
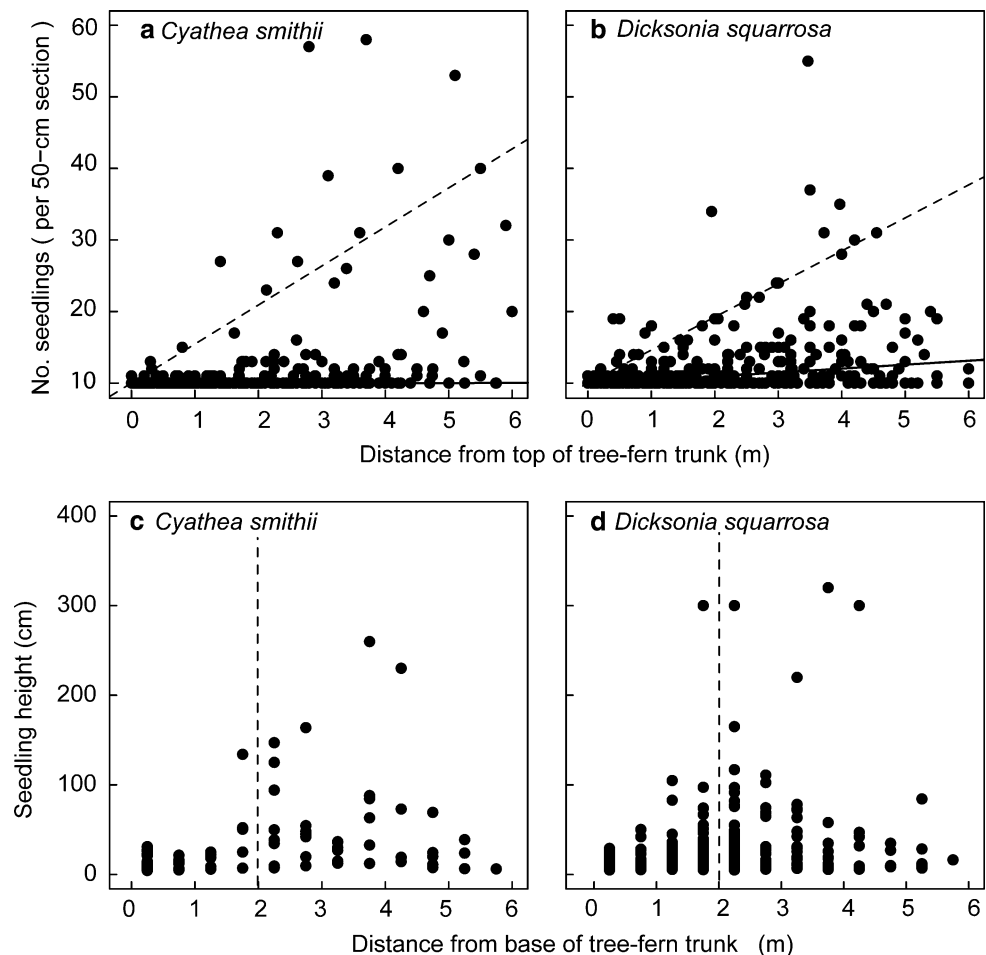


Fig. 2 Number of epiphytic seedlings growing on trunks of *Cyathea* (filled circle) and *Dicksonia* (open circle) in relation to tree fern height (left panel), and the mean height of seedlings (excluding those browsed by deer) in relation to tree fern height (right panel). Left panel The 50th quantile lines have slopes of 3.65 ± 0.76 for *Dicksonia* and 1.06 ± 0.61 for *Cyathea* (dashed lines) (significantly different,

$t = 4.1, P < 0.01$). In contrast the slopes of the 95th quantile lines were 12.1 ± 4.7 for *Dicksonia* and 13.2 ± 3.7 for *Cyathea* (not significantly different, $t = 0.32, P > 0.1$), and the common regression line is shown as a dotted line. Right panel The least-squares regression relationship did not differ between tree fern species ($F_{2,57} = 1.12, P = 0.33$), and the line is given by $\log(\text{seedling height}) = 0.58 + 0.18(\text{tree fern height})$

Fig. 3 Number of seedlings growing epiphytically on tree fern trunks (per 50-cm segment) as a function of distance along the trunk from the top towards the base (a, b), and seedling height of individual seedlings as a function of distance from the top (c, d). a, b The 50th quantile lines (solid lines) have slopes of 0.27 ± 0.081 for *Dicksonia* and 0.00 ± 0.03 for *Cyathea* (significantly different, $t = 5.4, P < 0.01$). The slopes of the 95th quantile lines (dotted lines) were 4.61 ± 0.65 for *Dicksonia* and 5.45 ± 1.31 for *Cyathea* (not significantly different, $t = 1.64, P > 0.1$). The relationships given in c and d were not statistically significantly ($F_{1,96} = 3.2, P = 0.07$ and $F_{1,325} = 0.63, P = 0.42$, respectively)



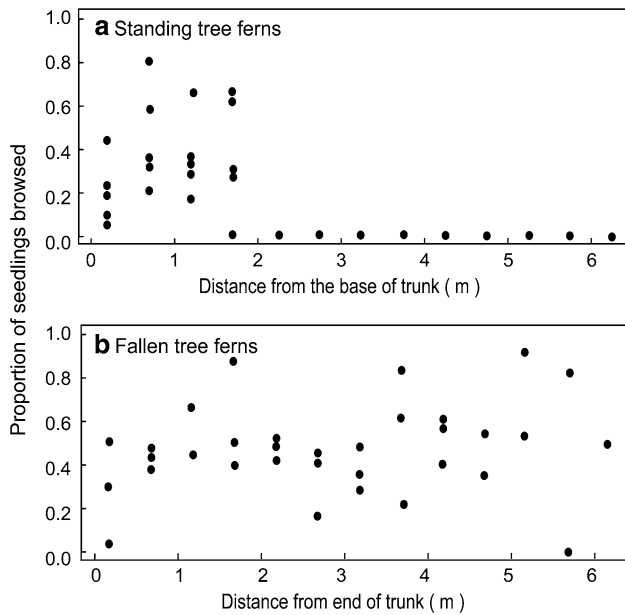


Fig. 4 The proportion of seedlings (within 50-cm segments of tree fern trunks) that had been browsed, in relation to the distance from the base of standing (a) and fallen tree ferns (b). Proportion of browsed seedlings is higher on fallen tree ferns than on lower sections (i.e. <2 m) of standing tree ferns (0.49 ± 0.03 vs. 0.35 ± 0.07 , $\chi^2 = 32$, $df = 6$, $P < 0.0001$). The proportion does not decrease along tree fern trunks ($F_{1,8} = 0.29$, $P = 0.26$)

standing tree fern trunks. The 18 species found on tree fern trunks included species that comprised 98% of the basal area of the alluvial forest (Table 2). Seedlings of *Metrosideros umbellata* and *Nothofagus solandri* var. *cliffortioides* were found on fallen tree fern trunks, even though these are not present as adult trees in the alluvial forests, and must have dispersed hundreds of metres from neighbouring sites.

On trunks of fallen tree ferns, SA did not vary with distance from either of the trunk ends ($F_{1,247} = 0.18$, $P = 0.67$); this lack of correlation may indicate that many of the seedlings on fallen trunks established after the fern fell over. Neither did we find a relationship between SH and distance from ends ($F_{1,242} = 1.70$, $P = 0.19$). The mean %PAR measured on fallen tree ferns was very low and similar to that measured at the base of standing tree ferns (Table 1). There was no correlation between SA and %PAR ($F_{1,246} = 2.51$, $P = 0.11$) or mean SH per 50-cm vertical segment and %PAR ($F_{1,1} = 0.11$, $P = 0.74$). Mean SH on fallen ferns was lower than the mean SH of those growing in the lower 2 m of standing tree fern trunks (Table 1). This could be because the proportion of browsed seedlings on fallen tree ferns was higher than on standing tree ferns (Fig. 4), and this proportion did not decrease along fallen tree ferns (Fig. 4b).

Table 2 Attributes of woody species growing epiphytically on 109 standing and 26 fallen tree ferns sampled from alluvial forests in southern New Zealand

Species ^a	Family	Seed size (mm)	Basal area (cm ² m ⁻²) ^b	Total number of seedlings	Seedlings m ^{-1c}	
					Fallen	Standing
<i>Weinmannia racemosa</i>	Cunoniaceae	1.1–1.5	21.351	1,910	6.42	3.50
<i>Griselinia littoralis</i>	Griselinaceae	4.2	4.36	280	2.20	0.08
<i>Raukaua simplex</i>	Araliaceae	3	0.036	117	0.23	0.27
<i>Nothofagus menziesii</i>	Fagaceae	4.5–6.3	24.118	114	0.91	0.02
<i>Coprosma foetidissima</i>	Rubiaceae	5.5–7.5	0.07	101	0.78	0.03
<i>Fuchsia excorticata</i>	Onagraceae	0.61	2.54	34	0.25	0.02
<i>Carpodetus serratus</i>	Carpodetaceae	1.17	4.053	29	0.21	0.02
<i>Prumnopitys ferruginea</i>	Podocarpaceae	11–17	0.445	22	0.19	0.00
<i>Pseudowintera colorata</i>	Winteraceae	2.6–3.6	0.179	14	0.12	0.00
<i>Coprosma rotundifolia</i>	Rubiaceae	4	0.318	12	0.08	0.01
<i>Coprosma ciliata</i>	Rubiaceae	4	0.012	11	0.09	0.002
<i>Nothofagus solandri</i> ^d	Fagaceae	5	0	11	0.09	0.00
<i>Myrsine australis</i>	Myrsinaceae	3	0.115	8	0.01	0.02
<i>Dacrydium cupressinum</i>	Podocarpaceae	4	4.061	4	0.03	0.002
<i>Schefflera digitata</i>	Araliaceae	2–3	0.212	4	0.00	0.01
<i>Coprosma rigida</i>	Rubiaceae	8–12	0.08	3	0.03	0.00
<i>Melicytus ramiflorus</i>	Violaceae	5	0.86	3	0.02	0.003
<i>Metrosideros umbellata</i>	Myrtaceae	7	0	3	0.00	0.01
<i>Aristotelia serrata</i>	Elaeocarpaceae	3–4	0.012	2	0.02	0.00
<i>Raukaua edgerleyi</i>	Araliaceae	3	0.621	2	0.00	0.01

^a Species names are from the New Zealand Plant Names Database (<http://nzflora.landcare-research.co.nz>)

^b Basal areas are from permanent plots in the study area, and provide an indication of the relative abundance of the species as adults (Coomes et al. 2005)

^c Calculated as either total number of seedlings divided by total length of 26 fallen tree ferns or the total height of 109 standing tree ferns

^d var. *cliffortioides*

Effects of frond removal on seedling growth and mortality

Removing tree fern fronds significantly increased the HGR of seedlings planted on the forest floor, but did not affect HGR of epiphytic seedlings (Fig. 5a). Frond removal resulted in a 320% increase in %PAR reaching the forest floor, which led to a significant increase in HGR (Fig. 5a) and in leaf production (Fig. 5b) of planted seedlings. However, HGRs of epiphytic seedlings were not affected by frond removal (Fig. 5a), perhaps because frond removal led to only a small increase in the %PAR reaching these seedlings (from 3.6 to 4.3%PAR). HGR of epiphytic seedlings was greater on *Dicksonia* than on *Cyathea* (0.70 ± 0.03 vs. 0.46 ± 0.01 cm year⁻¹, $F_{2,54} = 28.032$, $P < 0.001$). For planted seedlings, however, HGR did not differ significantly between tree fern species ($F_{1,27} = 0.13$, $P = 0.73$). Seedling survival was not affected by frond removal: 87% survived under control ferns and 84% under ferns with fronds removed ($\chi^2 = 0.03$, $df = 1$, $P = 0.85$).

Comparison of the growth rates of tree ferns and epiphytic seedlings

The HGR of *Cyathea* tree ferns was much faster than that of *Dicksonia* tree ferns, especially in high-light environments (Fig. 6). When growing in 2.5–7.0% PAR, the mean

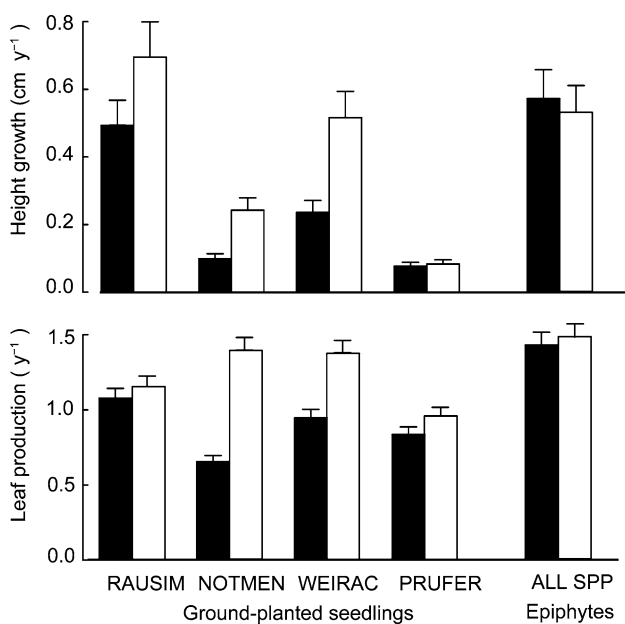


Fig. 5 **a** Effects of removing tree fern fronds (present shown by black bars, removed shown by white bars) on mean height growth rate, and **b** leaf production of seedlings planted on the forest floor [*Raukaua simplex* (RAUSIM), *Nothofagus menziesii* (NOTMEN), *W. racemosa* (WEIRAC) and *Prumnopitys ferruginea* (PRUFER)] and of epiphytic seedlings (all species together; ALL SPP). Frond removal led to an increase in percentage photosynthetically active radiation (%PAR) reaching the forest floor, from $1.09 \pm 0.03\%$ to $3.4 \pm 0.12\%$ ($t = 16.2$, $df = 816$, $P < 0.001$). Error bars are 1 SEM

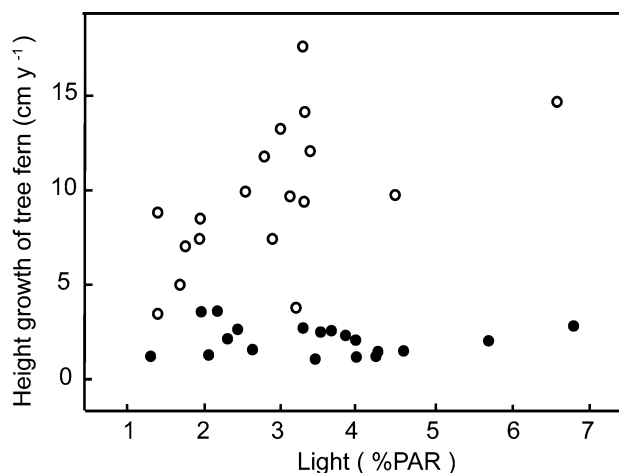


Fig. 6 Height growth rates (cm year⁻¹) of two tree fern species, *C. smithii* (filled circle) and *D. squarrosa* (open circle), as a function of %PAR immediately above their crowns. There was a significant light response for *Cyathea* growth ($= 4.7 + 1.7$ %PAR; $F_{1,16} = 7.4$, $P = 0.01$) but not for *Dicksonia* growth ($= 2.19 + 0.1$ %PAR; $F_{1,18} = 0.5$, $P = 0.50$)

height growth of *Cyathea* was 6 times greater than that of *Dicksonia* tree ferns (Table 3). The predicted mean height growth of 5-cm-tall seedlings (back-transformed from mean relative growth rates) was considerably less than that of *Cyathea* and *Dicksonia* (Table 3). Even when epiphytic seedlings had grown to a larger size (i.e. 30-cm height), mean growth rates were lower than those of the ferns (Table 3), although height growth at the upper 95% confidence interval exceeded that of *Dicksonia* (but not *Cyathea*) tree ferns.

Discussion

Importance of tree ferns as establishment sites

It has been generally assumed that regeneration in productive forests is dominated by competitive interactions and the possible role of positive interactions has received little attention. Only recently have studies started to consider the relevance of positive interactions during tree regeneration (Takahashi 1997). Here we show the facilitative role that tree fern trunks play in the establishment of seedlings in nutrient-rich forests. On the floor of temperate rain forests establishment sites are scarce, and standing tree fern trunks provide important opportunities for establishment (Wardle 1963; Veblen and Stewart 1980; Coomes et al. 2005; Fig. 1). Epiphytic regeneration on tree fern trunks has been described in many forests, in Australia (Ashton 2000), Jamaica (Newton and Healey 1989), and New Zealand (Pope 1926; Coomes et al. 2005), but this is the first study to examine epiphytic regeneration in terms of facilitation.

Table 3 Height growth^a [cm year⁻¹ with 95% confidence interval (CI)] of 5- and 30-cm-tall seedlings growing epiphytically on the trunks of *Cyathea* and *Dicksonia*, and on the forest floor beneath these tree ferns, in comparison with the height growth rate of tree ferns growing in contrasting PAR conditions

	<i>Cyathea</i>		<i>Dicksonia</i>	
	Mean	95% CI	Mean	95% CI
Seedling height growth (cm year ⁻¹)				
5-cm-tall seedlings on forest floor				
<i>Prumnopitys</i>	0.16	0.14–0.19	0.20	0.15–0.25
<i>N. menziesii</i>	0.18	0.08–0.28	0.38	0.28–0.48
<i>Raukaua</i>	0.23	0.16–0.30	0.19	0.12–0.26
<i>Weinmannia</i>	0.24	0.13–0.35	0.39	0.27–0.51
30-cm-tall seedlings on forest floor				
<i>Prumnopitys</i>	0.99	0.85–1.13	1.20	0.92–1.48
<i>N. menziesii</i>	1.10	0.50–1.69	2.27	1.68–2.86
<i>Raukaua</i>	1.39	0.96–1.82	1.14	0.71–1.57
<i>Weinmannia</i>	1.45	0.78–2.12	2.32	1.60–3.03
5-cm-tall seedlings growing on fern trunk				
<i>Coprosma</i>	0.19	0.13–0.24	0.34	0.27–0.42
<i>Griselinia</i>	0.22	0.15–0.29	0.30	0.14–0.45
<i>Weinmannia</i>	0.25	0.18–0.32	0.27	0.22–0.31
30-cm-tall seedlings growing on fern trunk				
<i>Coprosma</i>	1.52	1.10–1.93	1.59	1.30–1.89
<i>Griselinia</i>	1.32	0.93–1.72	1.79	0.85–2.73
<i>Weinmannia</i>	1.11	0.77–1.46	2.07	1.63–2.50
Tree fern height growth (cm year ⁻¹)				
1.0–2.5% PAR	6.7	5.06–8.35	2.4	1.54–3.26
2.5–7.0% PAR	11.1	9.04–13.16	1.86	1.54–2.18

^a Height growths were back-calculated from regression models

Recent papers have emphasized the importance of seed size in determining which species establish on elevated surfaces (Lusk and Kelly 2003), and most species that established epiphytically in our study were small-seeded (<6 mm in length) of anemochorous habit. The dominance of small-seeded species, such as *Weinmannia*, on standing tree ferns reflects the difficulty that larger seeded species, such as *Podocarpus* sp., have in dispersing to and establishing on vertical trunks. However, the relationship between SA and vertical distance from the top of tree ferns (*D*) was strongly ‘wedge-shaped’, with no seedlings found in many of the sites potentially available for recruitment (Fig. 3a, b). This indicates that even small seeds often fail to disperse onto the tree fern trunks, lodge among the fibres, or germinate successfully. The fact that the tiny-seeded *Weinmannia* comprised 85% of seedlings found on the shaded trunks of tree ferns runs contrary to the supposedly general relationship between seed size and shade tolerance (Kelly and Purvis 1993; Leishman 2001), and supports the view that there is no physiological reason why small-seeded species cannot

be shade tolerant, and that their rarity in forest understoreys relates to the fact that they require litter-free microsites or elevated surfaces (Metcalf and Grubb 1995; Christie and Armesto 2003). However, the fact that *N. menziesii*, the most abundant adult tree of anemochorous habit was almost absent from standing tree fern trunks (only two seedlings out of 114) but was the second most abundant species on fallen tree ferns, requires further investigation. Tree ferns have a single growing point at the top of their trunk and this may make them vulnerable to damage by epiphytes (Page and Brownsey 1986). In this study we found that *Dicksonia* trunks support more epiphytic seedlings than *Cyathea* trunks of comparable size, perhaps because trunks of *Cyathea* have a pendulous ‘skirt’ of dead fronds. Small trunks of *Cyathea* are completely covered by the skirt which restricts seed access to the tree fern trunk. Hence the skirt prevents seedlings from establishing too close to the growing tip of small *Cyathea*. As *Cyathea* tree ferns age, skirts shroud only the upper portion of the trunk, and seedlings therefore have the opportunity to establish on the trunk (Page and Brownsey 1986). Similarly, differences between tree fern species, in their suitability as sites for regeneration, may relate to differences in properties such as water retention, nutrient availability and allelochemistry (Mehlter et al. 2005). These factors require further investigation as they could negatively affect seedling growth and reduce the capacity of some tree species to recruit and establish on tree ferns.

Competition for light

On the forest floor of alluvial forests in New Zealand, tree ferns cast deep shade that can limit growth of ground-rooted seedlings. Light availability (measured as %PAR) on the forest floor and lower sections of tree ferns increased from 1 to 3.5 %PAR after frond removal, whereas in the upper sections it only increased from 3.1 to 4 %PAR. The three-fold increase in ground-level %PAR resulted in significant increases in height growth of planted seedlings, while no significant differences were found for epiphytic seedlings, which experienced a much smaller change in %PAR after frond removal. As light environments in forest understoreys are highly variable over space and time, short-term %PAR measurements may not accurately represent the light environments experienced during the life of an epiphytic seedling, rendering our experimental time frame too short for determining epiphytic seedlings responses to changes in %PAR associated with frond removal. Similarly, it is also possible that nutrient scarcity on tree fern trunks could limit seedling growth despite the observed increases in %PAR. Soils in these forests are considered relatively fertile (Coomes et al. 2005) and it is possible to assume that nutrient availability is lower on tree fern trunks than on the ground.

Therefore, we suggest that the lack of growth response of epiphytic seedlings, at higher light availability, may be due to nutrient limitation. In contrast to this pattern, Bellingham and Richardson (2006) found growth rates to be higher for epiphytic than for ground-rooted seedlings. However, their study was carried out in shallow soils that are likely to be less fertile than the alluvial soils of our study site. Thus, further work is required in order to elucidate if the facilitative role of tree ferns is site specific, as evidence suggests that tree ferns can provide sites where light and nutrient availability are higher than on the forest floor.

Escape from browsing

Selective browsing from introduced herbivores, such as deer, highlights the importance of tree fern trunks as sites for seedling regeneration. Deer were introduced into New Zealand in the 1850s and are now present in most natural ecosystems (Logan and Harris 1967). Deer are highly selective in their diet, and have virtually eliminated seedlings of their preferred species from within the browse layer of many New Zealand forests (Wardle 1991; Forsyth et al. 2005). We found that the upper parts of standing tree ferns are among the only places left for deer-preferred species to escape and regenerate in these alluvial forests, and might provide refugia for the long-term persistence of highly palatable species. However, the spread of introduced deer may also imperil these refugia because deer consume fronds of *Dicksonia*, and *Dicksonia* support more, and taller, seedlings than *Cyathea*. Hence, the effects of deer browsing on *Dicksonia* could not only lead to rapid tree fern population losses (Veblen and Stewart 1980; Bellingham and Allen 2003) but also to the loss of important regeneration sites where some woody species can establish successfully.

Facilitation in plant communities on fertile soils

When walking in these alluvial lowland temperate rain forests in New Zealand, one is immediately struck by the proliferation of epiphytic seedlings on tree fern trunks, and the near absence of seedlings on the forest floor. Our research has demonstrated that although seedling establishment is facilitated on tree fern trunks, their growth is slow and the chance of outgrowing a tree fern is slim (Table 3). Tree ferns may affect successional processes because they compete with some species but facilitate others, thus providing a filter for establishment. We found that seedling establishment is restricted to elevated surfaces and these comprise a tiny fraction (~1%) of the forest floor (Coomes et al. 2005). The relevance of epiphytic recruitment for *Weinmannia* was shown by the high proportion of individuals with signs of epiphytic regeneration (i.e. 60%). Other species that are abundant as mature trees, such as *Nothofagus*,

are uncommon as epiphytes on tree fern trunks and their success may be due to abundant regeneration on large fallen tree ferns (i.e. 46% of seedlings growing on fallen tree ferns). It is possible that some large-seeded species, such as *Nothofagus*, that do not reach higher surfaces of tree fern trunks are less affected by introduced deer as it has been reported that deer tend to avoid species with high foliar fibre such as *Nothofagus* (Forsyth et al. 2005).

The low probability of large-seeded species establishing on standing tree fern trunks restricts opportunities for conifer regeneration on the nutrient-rich soils. For example, a few giant trees of the large-seeded species such as *Dacrydium cupressinum* and *Prumnopitys ferruginea*, are very shade tolerant and could be expected to regenerate on the forest floor. They fail, however, because their seedlings cannot penetrate the dense layer of ground ferns (Coomes et al. 2005) and no epiphytic seedlings of these species were found on standing tree ferns. Thus, the facilitative effect of tree fern trunks is species specific.

Conclusion

Tree ferns may affect tree establishment processes in forests where they attain high abundance. Tree ferns have the potential to exert important effects on successional processes and are therefore likely to function as keystone species. In the temperate rain forest of New Zealand, the importance of tree fern trunks as sites for epiphytic regeneration results partly from intense browsing of ground vegetation by introduced herbivores, and it is unclear whether tree ferns had such an important role before these animals were introduced. Tree ferns are a common component of forests, growing in many wet and mild regions of the world (Large and Braggins 2004), and studies in these forests will shed light on the broader relevance of the facilitative and filtering effects that have been reported in this study.

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