Research

Oikos 117: 83–92, 2008
doi: 10.1111/j.2007.0030-1299.16136.x,

Subject Editor: Heikki Setälä, Accepted 30 July 2007

The potential for forest canopy litterfall interception by a dense fern understorey, and the consequences for litter decomposition

Fiona M. Dearden and David A. Wardle

F. M. Dearden, Dept of Animal and Plant Sciences, Univ. of Sheffield, Sheffield, UK, S10 2TN. – D. A. Wardle (david.wardle@svek.slu.se), Dept of Forest Ecology and Management, Swedish Univ. of Agricultural Sciences, SE-901 83 Umeå, Sweden, and Landcare Research, P. O. Box 40, Lincoln, New Zealand.

Most studies on litter decomposition have assumed that all falling plant litter reaches the ground where it then decomposes. In many forests a proportion of this litter may in fact be intercepted by understorey vegetation, but the ecological significance of this remains poorly understood. We performed two experiments in a temperate rainforest in southern New Zealand, in which there was a dense understorey of the crown fern *Blechnum discolor*. The fronds of this fern originate from a crown, and have a funnel-like arrangement that can trap falling litter and prevent it from reaching the ground. The first experiment measured the effects of ferns on the spatial distribution of litter accumulation over one year. The ferns intercepted a substantial proportion of the total litterfall, and the fern crowns (from which the fronds originate) retained 10% of the total incoming litterfall (despite occupying only 2% of the ground area). The retained litter had a substantially higher ratio of twig to foliar litter than did the incoming litterfall. Further, much of the litter not retained on the crowns of the ferns accumulated at the base of the fern trunks. The second experiment considered litter decomposition in fern crowns versus the ground under the ferns. The litter that had accumulated in the crowns was characterized by higher microbial basal respiration and active microbial biomass than was the litter that had accumulated on the ground. The use of litterbags revealed that litter decomposition rates were significantly higher on the fern crowns than on the ground at 30 cm and 60 cm from the fern trunks. These results show that litter interception ameliorates the decomposer environment and increases the rate of litter decomposition. In total, this study provides evidence for understorey ferns greatly influencing both the spatial distribution of litterfall and the decomposition of plant litter. Although the ecological role of understorey vegetation in forested ecosystems has received little attention to date, our results point to understorey species as an important driver of forest ecosystem processes.

In many forests, a proportion of the total canopy litterfall is likely to be intercepted by understorey vegetation before it reaches the forest floor. For example, in a Mexican tropical rainforest, Alvarez-Sanchez and Guevara (1999) found that litter input to the system was underestimated by up to 60% when interception of litterfall by an abundant understorey palm had not been accounted for. Nonetheless, most work on decomposition and nutrient cycling is underpinned by the assumption that all canopy litterfall reaches the ground, and that decomposition processes occur on or below the soil surface where they are strongly affected by local soil variables (Swift et al. 1979, Cadisch and Giller 1997, Berg and McClaugherty 2003). However, a small but growing number of studies have recognized the possibility of significant litterfall interception and decomposition in forest epiphytes (Richardson et al. 2000, Wardle et al. 2003, Nadkarni et al. 2004) and understorey palms (Rickson and Rickson 1986, Devasconcelos 1990, Alvarez-Sanchez and Guevara 1999). Despite this, little is known about the decomposition of litter that is intercepted by understorey vegetation and remains suspended in this vegetation without reaching the ground.

Many temperate and tropical forests have a significant understorey of ferns. The funnel-shaped growth habit of some fern species facilitates the interception of significant quantities of litter: the fronds radiate out and up from the fern crown (the portion of the fern from which the fronds originate), and overlap to form a funnel ('frond-funnel.'). In addition, some ferns with a frond-funnel, including tree ferns and some species of *Blechnum*, also have a trunk to support the crown and fronds. The trunk effectively isolates the crown and any litter trapped there, from the ground, and the frond-funnel may act to channel rainfall, throughfall and falling litter into the crown at the base of the funnel. The potential therefore exists for a large proportion of the incoming litterfall to be intercepted and retained by ferns within the frond-funnel so that it does not reach the ground.

In temperate rainforests throughout New Zealand, there are many areas in which a dense understorey is formed by

the endemic fern *Blechnum discolor* (Wardle 1963, Allan 1982, Bycroft et al. 1993). As individuals of this species mature, they develop a trunk that grows to 0.3 m or more (Allan 1982), and a crown of up to 15 cm diameter. A ring of sterile fronds is produced annually each Austral spring from this crown. The fronds are pinnate with closely spaced, tough and leathery pinnae and can grow to a length of 100 cm or more. As each frond matures, it remains more or less upright at the base, but the upper half of the frond arches outwards at between 30% and 60% from the horizontal, so that the fronds collectively form a funnel. As fronds can live several years, there are usually several concentric rings of fronds surrounding the crown, which collectively can serve as a very effective funnel (Fig. 1). Further, observations of *B. discolor* have revealed that considerable quantities of litter can accumulate and humus can develop on the crown (Fig. 1). In forests where ferns with this growth habit are abundant, the ferns may be intercepting and concentrating a potentially large portion of the total litterfall at the base of the funnel (i.e. on the fern's crown). This may have important, although currently unknown, consequences for decomposer processes, nutrient cycling and ultimately the functioning of the forest ecosystem.

Two inter-related experiments were performed in a temperate rainforest with dense *B. discolor* understorey in southern New Zealand, to answer the following questions: 1) does the dense fern understorey have the potential to intercept a significant proportion of the total litterfall derived from the forest canopy? 2) How does the decomposition rate of the intercepted litter occur in the crown of the fern differ from that of the litter that reaches the soil surface? The intention, in answering these questions in combination, is to better understand the ecosystem level consequences of litterfall interception by understorey vegetation.

Material and methods

Study site

In March 2003, two inter-related experiments were established on a single nearly level terrace in temperate rainforest in the Waitutu region of Fiordland National Park and Te Wahipounamu UNESCO World Heritage Area, in the southwest corner of South Island, New Zealand (46°2′S, 167°0′E). The terrace, which is intermediate in the Waitutu chronosequence (Coomes et al. 2005), has an elevation of approximately 80 m above sea level and emerged from the ocean approximately 80 000 years ago (Ward 1988). The soils are silt loams, with a pH of approximately 3.9, over a soft tertiary rock overlain with granite gravels. Soil total N concentrations are 307 g m^{-2}, total P concentrations are 11 g m^{-2}, and the ratios of soil C to N and C to P are 39 and 1031 respectively (Coomes et al. 2005). Waitutu receives an average annual precipitation of 1600–2400 mm and experiences an average temperature in January of 12°C and in June of 5°C (Ward 1988). The study was located in areas of forest where *B. discolor* was growing densely, such that fronds of neighbouring *B. discolor* individuals were overlapping.

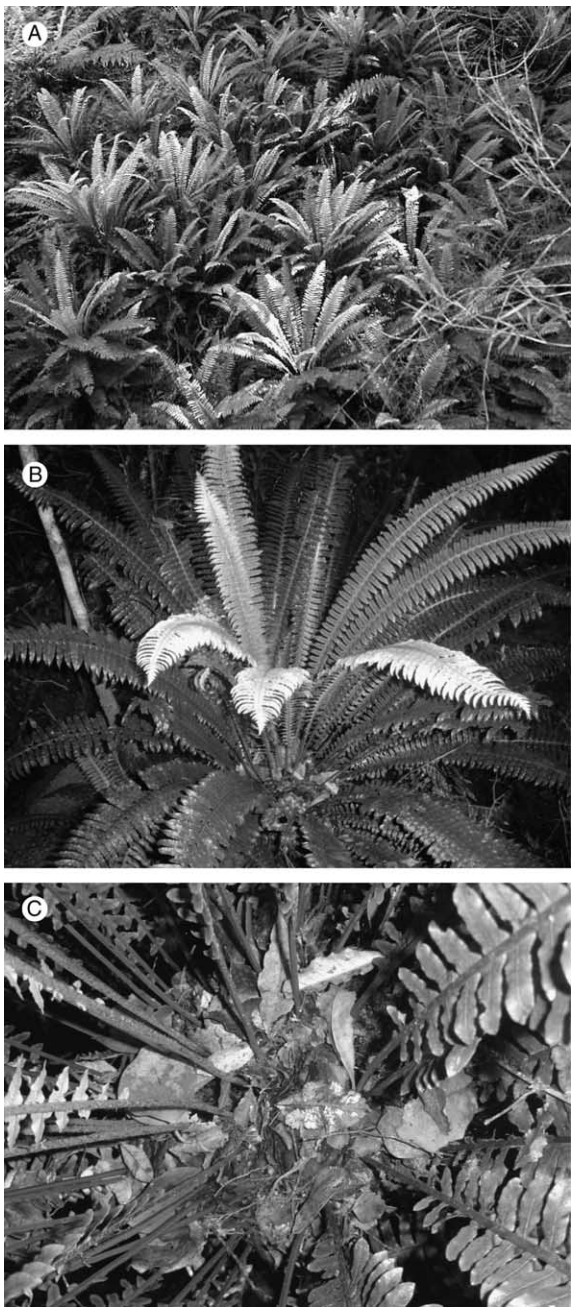

Fig. 1. *Blechnum discolor* in the forest understorey. (A) A dense stand of *B. discolor* covering the forest floor; (B) an individual of *B. discolor* with the characteristic funnel-shape; (C) accumulation of litter in the base of the *B. discolor* frond funnel over the fern's crown.

Ten replicate circular plots were established, each measuring 20 m in diameter; all experimental work was performed in these plots. The plots were dominated by plant species typical of temperate rainforest in New Zealand (Wardle 1963, Allan 1982). On all plots, the canopy was dominated by evergreen angiosperms. *Weinmannia racemosa* and *Nothofagus* spp. were co-dominants in all plots, *Nothofagus menziesii* was co-dominant with *W. racemosa* in nine of the ten plots, and *Nothofagus solandri* var. *cliffortioides* was co-dominant in the plot for which

N. menziesii was absent. In addition, large (>20 cm diameter at breast height) gymnosperms of the family Podocarpaceae were found on five of the plots. In the subcanopy, low numbers (between one and ten individuals) of tree ferns (largely *Dicksonia squarrosa*) were present in eight out of ten plots. Further characteristics of the forest are given in Table 1.

Morphometric measurements

Morphometric measurements were made during March 2003 of each of the *B. discolor* individuals present (261 ferns in total) in a subplot located within each of the ten main (20 m diameter) plots; each subplot was 3×5 m and was established in the centre of the main plot. This was done to allow the density of the *B. discolor* understorey to be quantified, and to enable the quantity of litter intercepted by the ferns to be considered in the context of the sizes of the individual ferns as well as the proportion of the ground surface that they covered. These measurements consisted of the height from the ground of the trunk and the frond funnel, the diameter of the fern crown, and the mean distance between neighbouring ferns. Measurements were also made of the area of the 'internal frond-funnel' (defined as the diameter at the frond tips for the innermost, most recently emerged, ring of fronds) and 'external frond-funnel' (defined as the diameter at the frond tips for the outer and oldest ring of fronds). The total numbers of ferns in each subplot were quantified. The total amount of litter accumulated in the crowns of 10 ferns (one per plot) was determined.

Litter interception experiment

The first experiment was established in the same subplot used for morphometric measurements during March 2003, to test the potential of the fern understorey to intercept falling litter. Within each plot, litter accumulation was measured over one year, in each of ten positions. Three of these positions involved three different fern crowns, with each fern manipulated in a different way. For the first fern, both fronds and accumulated litter were left intact (hereafter referred to as the 'intact fern'), and the crown was sprayed with a long-lasting glue, to cement the existing litter in position. This was done so that when litter was collected later, the newly accumulated litterfall could be readily distinguished from that which was present previously. A second fern had all litter removed from the crown, to determine whether litter already present affected future litter accumulation (hereafter referred to as the 'fern with litter removed'). A third fern had all fronds removed to the lowest pinnae (stipes were left attached to the crown from below the lowest pinnae), to see if the absence of the frond-funnel reduced accumulation of litter in the crown (hereafter referred to as the 'fern without fronds'). Glue was also applied to the litter in the crown of the fern without fronds. We created six additional positions by placing litter trays on the ground. Three of these positions comprised 30×30 cm litter trays (15 cm in depth, with nine 5 mm diameter holes in the bottom), placed in a row at 0–30 cm, 30–60 cm and 60–90 cm from the base of the trunk of the intact fern. The other three of these positions comprised 30×30 cm litter trays placed in a row (0–30 cm, 30–60 cm and 60–90 cm) from the base of the trunk of the fern without fronds. The final (tenth) position involved placement of a 30×30 cm litter tray above the fern understorey (on average 1.6 m above the ground), in order to quantify the incoming overstorey litterfall above the ferns (the baseline litter tray). Comparison of the litterfall per unit area between the baseline litter tray and the other nine positions provides a measure of the effects of the fern in influencing the spatial distribution of litterfall accumulation in the fern crowns and on the ground surface under the frond-funnels. The litter trays placed on the ground were used to measure how much litter was reaching the ground surface, and to test whether litterfall interception by the ferns changed with distance from the fern trunk. After one year, in March 2004, all litter that had accumulated in each position was collected. The litter was sorted into tree leaves, tree twigs, tree fern material, *B. discolor* and 'other' (reproductive, epiphytic and unidentified fragmentary material), and dried at 60°C for 48 h and weighed.

The amount of litter accumulated was calculated as grammes per unit area. To determine whether the frond-funnel was indeed funnelling litter to the fern's crown, the amount of litter accumulated on the crowns was calculated as grammes per unit area of the crown. Total litterfall for each of the ten positions was calculated as the sum of all overstorey litter types accumulated at that position. In order to calculate the overall effect of litter interception by the ferns on litter distribution, the total amount of litter that accumulated in and under each intact fern was estimated by totalling the amounts accumulated in the fern crown, and the amounts accumulated in three concentric rings on the forest floor around the trunk of the intact fern.

Table 1. Forest overstorey characteristics for the ten 20 m diameter plots.

Overstorey characteristic	All trees and shrubs	Total trees	Angiosperm trees	Gymnosperm trees	Tree ferns	Shrubs	Climbers
Mean total basal area (m^2 ha^{-1})	86.06 (8.82)	82.11 (8.82)	76.19 (8.24)	5.95 (2.74)	2.67 (0.891)	1.18 (0.605)	0.10 (0.083)
Mean dbh (cm)*	19.69 (1.82)	23.70 (2.07)	29.48 (3.49)	22.43 (10.6)	9.65 (1.77)	6.59 (1.21)	1.88 (1.04)
Median dbh (cm)	13.00	19.00	19.00	2.50	10.50	6.75	0.00
Mean stem density ha^{-1}	2021 (237)	840 (116)	799 (101)	41 (16.4)	204 (53.5)	118 (30.4)	19 (10.8)
Mean species richness (S)	6.70 (0.616)	3.20 (0.512)	2.50 (0.224)	0.70 (0.300)	1.20 (0.249)	2.20 (0.490)	0.30 (0.153)

*dbh is the diameter at breast height (1.35 m above the ground). Values in parentheses are SE of the mean.

These concentric rings were at the same distances from the fern trunks as were the three ground litter trays (0–30 cm (0.147 m^2 ring), 30–60 cm (0.312 m^2 ring) and 60–90 cm (0.578 m^2 ring) from the trunk), and the calculations were based on the amounts collected in the three ground litter trays under the intact fern. The amounts accumulated at each of the four positions were then converted to proportions of the total incoming litterfall (as determined using the baseline litter tray).

Litter decomposition experiment

A litterbag approach was used in the second experiment to determine whether litter would decompose at a similar rate in the fern crown as on the soil surface, and this was set up in March 2003. Freshly dead litter was collected from three species that occur in our plots: *Weinmannia racemosa, Nothofagus menziesii* and *Dicksonia squarrosa*. Litter was air-dried and a sub-sample of each species dried at 60°C for 48 h to correct for moisture content. For each of the three species, litterbags were prepared with a mesh size of 1 mm square, and each containing 2 g (dry weight) of litter. For *Weinmannia* and *Nothofagus*, each litterbag measured 12 × 3 cm; for the lower density *Dicksonia* litter, each litterbag measured 14 × 4 cm. Within each plot, three ferns were selected, so that there was a different fern for each of the three litter species. For each fern, two identical litterbags containing litter from one of the three litter species were buried in the litter already present on the fern's crown between the encircling fronds and the central area of new frond growth. Three further pairs of litterbags of that litter species were placed on the soil surface beneath this fern: one pair at the base of the trunk, a second pair 30 cm from the trunk and a third pair 60 cm from the trunk. For each pair of litterbags on the soil, the litterbags were placed 10 cm apart, i.e. approximately the same distance apart as the litterbags in the crown. The litterbags on the ground were covered with the litter already present on the forest floor, so that the litterbags were in contact with both the soil surface and the litter layer. The litterbags were harvested after one year (March 2004) and the contents cleaned, dried at 60°C, and then weighed to determine the mass loss. A standard automated colorimetric technique was used to analyse the N and P concentration of a sub-sample taken from each litterbag pair.

Litter decomposition is driven by heterotrophic microbes (Flanagan and van Cleve 1983, Singh et al. 1989), and microbial activity is strongly related to environmental organic matter (OM) content (Alvarez and Alvarez 2000). Therefore, in order to assess the habitat quality, activity, and biomass of the decomposer organisms, four samples of the litter layer were collected from each of the ten plots in March 2004. One of these samples came from litter that had accumulated in the crown of the same fern used for placement of *Weinmannia* litterbags. Three further samples came from the three ground positions previously described, but at least 5 cm from where the litterbags were placed. The litter in each sample was cut into 5 mm fragments and homogenized. The field-moist samples were then stored at 5°C until analysed. The litter samples were analysed for basal respiration (BR), and for substrate induced respiration (Anderson and Domsch 1978), which is a relative measure of active microbial biomass. Organic matter (OM) content of these samples was measured as loss on ignition in a muffle furnace heated at 550°C for 6 h. The BR and SIR were both measured as described by Wardle (1993). Briefly, each sample was either moistened with de-ionized water, or air-dried at room temperature, to achieve 70% moisture content. For each sample, a 2 g sub-sample was placed in a 130 ml airtight bottle and incubated at 20°C overnight. In the morning, each bottle was opened and gently shaken to refresh the air, then returned to the incubator. Evolution of CO_2 was measured (infra-red gas analyser) after 1 h and again after 4 h (Wardle 1993). Measurement of SIR (Anderson and Domsch 1978) was performed in the same way, but the samples were amended with 80 mg of glucose (i.e. 4% of the dry weight of the litter sample). The microbial metabolic quotient (the ratio of BR to SIR) was calculated, as a relative measure of absolute carbon-use efficiency (Anderson and Domsch 1985). The resource quality of the decomposer environment was calculated as the ratio of SIR to OM (Insam and Haselwandter 1989).

Data analyses

The data from the two experiments were analysed using analysis of variance (ANOVA), with plot as a blocking factor, in Genstat 8.1. Within each litter type, one-way ANOVAs were used to test for the effect of position on the amount of accumulated litterfall per unit area. For the decomposition experiment, a two-way ANOVA was used to test for the effects of litter species, position, and interactions between these two factors on litter mass loss. Data on BR, SIR, and variables derived from these measurements were analyzed by one-way ANOVAs testing for effects of position. Data were tested for normality (Kolmogorov-Smirnov test) and homoscedasticity (Levene's test, or Bartlett's test where data were normal) in Minitab 13.20, and transformed where appropriate. Where transformation did not produce an acceptable probability of homoscedasticity, the non-parametric Kruskal-Wallis test was performed.

Results

Fern understorey characteristics

In this study, the mean (±SE) *B. discolor* trunk height in the sub-plots was 0.43 m (±0.037), and the height of the ring of sterile fronds (frond-funnel) added nearly a metre (0.99 m ± 0.035) to the total fern height. The mean external and internal areas of the frond-funnels were 1.82 m^2 (±0.240) and 0.81 m^2 (±0.115) respectively. The trunks of ferns were spaced a mean distance of 0.92 m (±0.090) apart. Based on these sub-plots, there were 17 400 (±2180) *B. discolor* ferns ha^{-1}. The external edge of the frond-funnels overlapped considerably with their neighbours, so that the mean total area of all the external frond-funnels for the 15 m^2 sub-plots was 43.90 m^2 (±5.25). Consequently, the external frond-funnels covered 100% of the forest floor area, with considerable overlap between funnels. The mean total area of the internal

frond-funnels in the 15 m^2 sub-plots was 6.47 m^2 ($\pm$0.127) and covered 43% ($\pm$0.857) of the forest floor. The mean diameter of the fern crowns was 15.0 cm ($\pm$0.3), and the total area of all the crowns in the sub-plot was equivalent to 2.1% ($\pm$0.074) of the forest floor. Litter was found to have accumulated in all 261 ferns measured, and the amount of litter that had accumulated in the crowns was 58.35 g ($\pm$8.34) (based on a sample of ten). Seedlings were frequently found to have germinated in the fern crowns, but on only one occasion was a plant (*Coprosma* sp.) present that had developed beyond the seedling stage. On these plots, the ground under the ferns was largely devoid of vegetation, and no epiphytes were found growing on the trunks. This condition contrasts strongly with the dense bryophyte and low fern ground cover found elsewhere on the non-alluvial terraces in the Waitutu area.

Litter interception by ferns

The litter trap erected above the level of the fern understorey (the baseline tray) on each plot accumulated 25.42 g m^{-2} ($\pm$2.53) of litterfall over the year of the experiment. The effect of position on litter accumulation was highly significant for the total overstorey litterfall, and for the twig and foliage litter from trees (Table 2). There was no effect of position for the *B. discolor* litter and the 'other' litter (epiphytic, reproductive and fragmentary material) for which only very small amounts accumulated at any position. Only very small amounts of tree fern material occurred in any position (data not presented). The intact fern crown (for which neither trapped litter nor fronds were removed), and the fern with litter removed, both accumulated a significantly (and consistently) larger amount of the total litter, foliar litter and twig litter per unit area than did any litter tray (Table 2).

There was no significant difference in the amount of litter accumulated on the crowns between the intact ferns and ferns with litter removed. However, the crowns of the ferns without fronds (fronds removed) accumulated a significantly smaller amount of litter than was found at any other position for total litter, foliar litter and twig litter fractions. The amount of litterfall accumulated in the trays next to the fern trunks did not differ from the amount in the baseline litter tray. The amount of litter that accumulated in the litter trays on the ground was not affected by which fern the tray was under, but the amount of total litter and foliar litter declined with distance from the trunk for the intact fern. The effect of position on the twig litter fraction was different from the effect of position on the total and foliar litter fractions, which resulted in the ratio of twig to 'twig plus foliar' litter (i.e. 'twig proportion') being affected by position (Table 2). This ratio was highest in the crowns of the intact ferns and lowest in the baseline trays and those trays under the intact ferns. Further, this ratio was lower in the crowns of the ferns without litter and ferns without fronds than in the crowns of the intact ferns, and did not differ from the proportion in the trays under the ferns without fronds.

The mean amount of total litter that accumulated in and under each intact fern (an area of 1.06 m$\pm$0.016) over the study period was 251 g ($\pm$31.6). Of this, 10.83% ($\pm$1.90) accumulated on the crown of the intact fern, 18.60% ($\pm$2.40) accumulated on the forest floor between 0 and 30 cm from the trunk, 29.38% ($\pm$3.22) accumulated 30 to 60 cm from the trunk and 41.19% ($\pm$2.31) accumulated 60 to 90 cm from the trunk. The amount of litterfall input to the system in the year of the study (based on the baseline trays) was 2.54 Mg ha^{-1} ($\pm$0.253) and the total litter that accumulated in the crown of the intact ferns (adjusted for the areal coverage of crowns in the sub-plot of 2.1% ($\pm$0.074)) was 0.268 Mg ha^{-1} ($\pm$0.057). This equates to 9.99% ($\pm$1.62) of the total litter input.

The ground litter trays and some individual fern crowns contained small amounts of litter from *B. discolor*, whereas the baseline litter tray contained no *B. discolor* litter. The amount of *B. discolor* litter that reached the forest floor was 2.59 g m^{-2} ($\pm$0.955), based on the mean amount accumulated in the three trays placed below the intact ferns. The amount of *B. discolor* litter that accumulated varied significantly with position (Table 2). The overall litterfall input to the system over one year was 25.7 g m^{-2} ($\pm$2.49) (calculated from the mean amount of *B. discolor* litterfall in the ground litter trays plus the total litterfall in the baseline litter tray). Thus, *B. discolor* contributed 9.1% to the total litterfall in the system.

Effects of litterfall interception on the decomposer subsystem

The mean decomposition rate (% mass loss per annum $\pm$ SE) in the litterbags, across all species and positions, was 40.03% ($\pm$2.08). Within each species, the mean mass loss across all four positions (i.e. in the fern crown, and on the ground at 0 cm, 30 cm and 60 cm from the fern trunk) was 56.3% ($\pm$0.021) for *Weinmannia*, 51.5% ($\pm$0.021) for *Nothofagus* and 12.3% ($\pm$0.009) for *Dicksonia*. According to two-way ANOVA, decomposition rate varied significantly with both the litter species ($F = 380$; $p < 0.001$) and the position of decomposition ($F = 5.19$; $p = 0.002$) but the interaction between these was not significant ($F = 0.51$, $p = 0.801$). Across all species, litter placed in the crowns of ferns decomposed significantly faster than that placed at 30 cm and 60 cm from the trunk, and the same result was found for both *Nothofagus* and *Dicksonia* litter when considered separately, but not for *Weinmannia* litter (Table 3).

The post-harvest litter concentrations of N and P varied significantly among species (for N, $F = 64.63$, $p < 0.001$; and for P, $F = 8.01$, $p < 0.001$). Both N and P were higher for *Weinmannia* litter (N = 15.08 mg g^{-1} $\pm$0.381; P = 0.85 mg g^{-1} $\pm$0.049) than for either *Dicksonia* litter (N = 10.99 mg g^{-1} $\pm$0.337; P = 0.695 $\pm$0.037) or *Nothofagus* litter (N = 11.62 mg g^{-1} $\pm$0.335; P = 0.711 mg g^{-1} $\pm$0.044). However, the ratio of N to P did not vary among species ($F = 2.36$; $p = 0.100$). Nutrient concentrations were not affected by the position in which the litter decomposed (for N, $F = 1.57$; $p = 0.201$; for P, $F = 1.29$; $p = 0.281$; for the N to P ratio, $F = 0.74$; $p = 0.533$). There were no interactive effects of litter species and position on nutrient concentrations (for N, $F = 0.82$ and $p = 0.558$; for P, $F = 0.26$ and $p = 0.953$; for the ratio of N to P, $F = 0.31$ and $p = 0.930$).

Table 2. Distribution of one year's litter accumulation (mean ± SE in g m^{-2}) on the fern crown, on the forest floor at different distances from the fern, and above the fern understorey. F and p values in bold indicate statistical significance at p = 0.05.

Litterfall type	Baseline (above ferns)	On the fern crown			Distance from fern trunk on the ground below intact fern			Distance from fern trunk on the ground below the fern without fronds			ANOVA across all positions	
		intact fern	fern with litter removed	fern without fronds	0–30 cm	30–60 cm	60–90 cm	0–30 cm	30–60 cm	60–90 cm	F	p
Total*	25.42 (2.53) bc	130.63 (29.3) a	114.39 (24.6) a	8.72 (1.37) d	31.30 (4.40) b	22.55 (2.67) bc	17.89 (2.55) c	28.49 (3.99) b	23.59 (2.87) bc	21.07 (3.06) bc	**23.68**	< **0.001**
Tree foliage	16.71 (1.90) bc	40.11 (5.09) a	55.6 2 (11.4) a	2.67 (0.537) d	20.56 (3.52) b	14.47 (1.47) bc	11.46 (1.74) c	16.80 (2.27) bc	14.24 (1.93) bc	12.21 (1.58) c	**27.36**	< **0.001**
Tree twigs	6.84 (1.43) b	88.53 (27.3) a	55.09 (1.64) a	3.22 (0.889) d	8.46 (1.79) b	6.88 (1.89) b	5.30 (1.29) b	9.28 (2.07) b	7.46 (1.36) b	7.26 (1.56) b	**12.42**	< **0.001**
Twig proportion†	0.282 (0.052) c	0.581 (0.078) a	0.449 (0.065) b	0.451 (0.096) b	0.286 (0.058) c	0.290 (0.048) c	0.296 (0.059) c	0.335 (0.055) bc	0.339 (0.050) bc	0.334 (0.047) bc	**5.08**	< **0.001**
Other‡	1.87 (0.270)	1.99 (0.350)	3.48 (1.13)	2.57 (0.447)	2 29 (0.589)	1.19 (0.257)	1.14 (0.255)	2.33 (0.354)	1.70 (0.584)	1.51 (0.299)	1.93	0.060
B. discolor	0 (0)	0.156 (0.123)	0.210 (0.142)	2.66 (2.65)	0.179 (0.151)	0.277 (0.126)	0.321 (0.220)	0.249 (0.093)	0.046 (0.035)	0.341 (0.231)	1.19	0.310

* total litterfall was calculated from the foliar, twig, tree fern and 'other' fractions of the overstorey litter, and excluding *B. discolor* litter.
† twig proportion was calculated from tree twig litter/ (tree twig litter + tree foliar litter).
‡ 'other' litterfall includes reproductive, epiphytic and unidentified fragmentary litter from the overstoreys.
F and p values were derived from parametric one-way ANOVA.
Within each row, values followed by the same letter were not significantly different, and relate to ANOVA across all nine litter trap positions (Fisher's LSD, $p < 0.05$).

Table 3. Foliar litter decomposition rate (% mass loss over one year; standard errors in brackets) within the fern crown and on the ground for each of three species.

Litterbag species	In the crown	Distance on the ground from the fern trunk			F	p
		0 cm	30 cm	60 cm		
N. menziesii	58.42 (5.13) a	53.47 (5.10) ab	46.27(1.81) b	47.78 (3.16) b	**3.06**	**0.045**
W. racemosa	58.28 (4.29)	57.85 (3.96)	52.20 (3.61)	57.05 (4.96)	1.94	0.146
D. squarrosa	16.73 (2.66) a	11.90 (1.56) ab	10.98 (2.04) b	10.73 (0.962) b	**3.45**	**0.031**
All species	44.48 (13.9) a	41.07 (14.6) ab	36.48 (12.9) b	38.52 (14.2) b	**4.59**	**0.004**

F and p values are derived from ANOVA. Within each row, values followed by the same letter were not significantly different (Fisher's LSD, $p < 0.05$). Values in bold indicate statistical significance at $p = 0.05$.

The percent organic matter content of the litter layer varied significantly with sampling position (Kruskal-Wallis test, $H = 22.15$; $p < 0.001$) (Fig. 2). This was due to the consistently higher OM in the crown compared with the three positions on the ground, which did not differ from one other. Further, BR and SIR both varied significantly with position (for BR, $F = 3.74$, $p = 0.023$; for SIR, $F = 4.79$, $p = 0.008$), due to higher values in litter sourced from the crown than in litter collected from the three positions on the ground (Fig. 2). The ratios of BR to SIR and SIR to OM did not vary significantly with position ($F = 0.92$; $p = 0.445$, and $F = 1.63$; $p = 0.206$ respectively).

Discussion

A number of authors have observed that understorey and epiphytic vegetation in moist forests intercepts nutrients from rainfall and throughfall (Nadkarni 1994, Matzek and Vitousek 2003, Clark et al. 2005), but very few studies (Alvarez-Sanchez and Guevara 1999, Richardson et al. 2000) have recognized that vegetation may also intercept a significant proportion of falling litter. If this is the case then studies that ignore retention of fallen litter in the understorey vegetation might greatly underestimate total inputs of litter to the system (Alvarez-Sanchez and Guevara 1999). The present study has measured the amount of litter intercepted by a vegetation type not previously studied in this context, i.e. a dense fern understorey. We found evidence of significant funnelling of litter input by ferns, as a considerably larger amount of litter per unit area had accumulated after one year in the crowns of the intact ferns and ferns with litter removed than in any other position, including the litter trays placed above the fern canopy, and the ferns without fronds. Our results show that *B. discolor* crowns have the potential to retain 10% of the litter falling from the canopy (despite occupying only 2% of the ground surface), thus preventing it from reaching the ground. Removing the litter that was present in the crown at the start of the experiment (i.e. the ferns with litter removed) did not affect the amount of litter accumulated, except for the twig fraction. Twigs intercepted by the fronds were more likely to be retained than was foliage, and more so when the crown already contained litter. This is presumably because dead twig fragments, being larger, are less likely than dead leaves to fall through the gaps between fronds to the ground. Given that twig litter decomposes more slowly than does leaf litter, greater ratios of twig litter to foliar litter are likely to lead to net accumulation of undecomposed organic matter (Dearden et al. 2006). In this light, retention of twig litter in fern crowns may therefore encourage build up of litter quantity in the crowns.

Our results also show that *B. discolor* influences the spatial location of incoming litter, and therefore potentially the spatial distribution of nutrients released from the litter during decomposition. The amounts of the total and tree foliage litter fractions accumulated was the same above the understorey (i.e. in the baseline tray above the ferns) and on the ground at the base of the ferns. However, the amounts of the total and foliage litter fractions reaching the ground declined with increasing distance from the trunks for the intact ferns, and for the ferns with litter removed but which had intact frond-funnels. This decline was likely to be due at least partly to denser frond cover at the outer edges of the frond-funnel of the fern, which usually overlapped with the outer fronds of neighbouring ferns. However, some of the litter intercepted by the frond-funnel may not be retained in the crown, but instead filter through the bare portions of the frond raches (near their base) and land around the base of the trunk. This should increase the amount of litter accumulating near the trunk base relative to further from it. However, for all ferns, the accumulation of tree twig litter at the base of the trunk was no greater than the accumulation further from the trunk, and this is consistent with twig litter being preferentially retained within the crowns. Thus, in addition to intercepting 10% of the total litterfall and preventing it from reaching the ground, these ferns greatly affected the composition and local spatial pattern of litter reaching the forest floor. In total, the interception experiment answered the first question posed in this study, by showing that a dense fern understorey is able to intercept a large proportion of the incoming litterfall, and further that the amount of litter intercepted differs with litter type (i.e. twig vs foliar litter).

Litter collected from the crowns of the ferns was characterized by a larger and more active microbial biomass than was the litter collected from the ground. This difference suggests that the decomposition environment was more favourable within the crowns of the fern than on the ground, and this finding was reflected in the higher decomposition rates of litters placed in litterbags within the crowns. There was no significant difference in the microbial metabolic quotient (ratio of BR to SIR) (a measure of the ecological efficiency of the microbial community; Anderson and Domsch 1985) between the ground and the crowns, suggesting that despite differences in microbial activity,

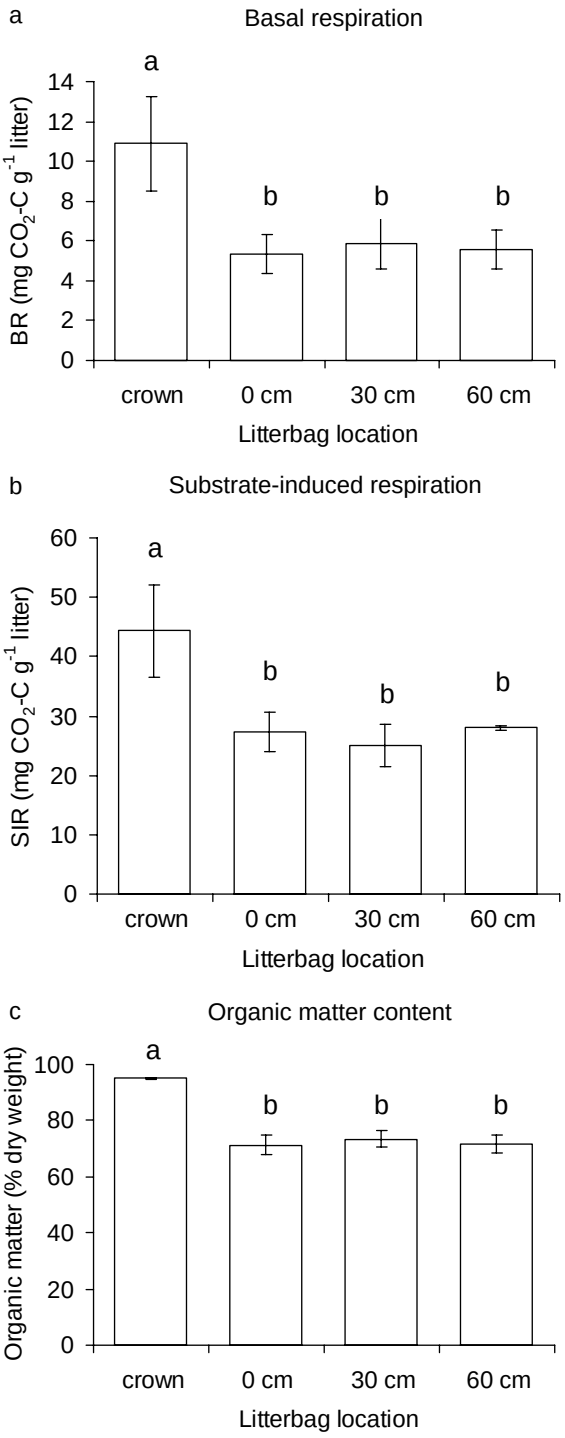

Fig. 2. Microbial activity (basal and substrate-induced respiration) and organic matter content for the natural litterfall accumulated in the crown of *B. discolor*, and on the ground below the ferns at 0 cm, 30 cm and 60 cm from the fern trunks. Within each panel, numbers topped with different letters are significantly different (Fisher's LSD, $p < 0.05$). Vertical bars are standard errors.

microbial resource use efficiency was unaffected (Anderson and Domsch 1985). Litter decomposition rates at the base of the trunk were intermediate between (and not significantly different from) decomposition rates in the crown or on the forest floor further from the trunk. This may have been due to environmental amelioration at the trunk base, and may be linked to the larger amounts of litter accumulating and decomposing at the trunk base relative to that on the forest floor further from the trunk. It is possible that the trunk base environment may also have been ameliorated through nutrients leaching down the trunk from the litter decomposing in the crown. Concentrations of N and P in the litterbags at the time of harvest were unaffected by positioning of the litterbags, but because net litter mass loss was greater in the crown than at 30 and 60 cm from the trunk, the net total amount of N and P retained in the litter placed in the crowns was significantly less than that in litter placed on the ground. This means that the fern crown environment reduces total retention of N and P in the litter. In total, the decomposition experiment has successfully answered the second question posed in this study, by showing that litter interception by ferns promotes litter decomposition rates, as well as the activity of microbes that carry out decomposition. This finding, in combination with our results pointing to accumulation of litterfall in the crowns of ferns, means that ferns can have an important ecological role by not only trapping litter but also influencing decomposition processes.

The possibility exists that *B. discolor* may directly access nutrients from the litter in the crown. Fine fern roots are commonly observed growing from the crown of *B. discolor* into the litter accumulated in the crown. Hunt et al. (2002) observed a similar growth habit in the Tasmanian tree fern *Dicksonia antarctica*, and suggested that *D. antarctica* may funnel rainwater to the aerial roots and thereby gain a competitive advantage over coexisting species. It is therefore possible that *B. discolor* also funnels resources to its crown. In addition to absorbing water, the ability of rainforest plants to absorb leachates and nutrient-rich throughfall through leaves and/or aerial roots has been recorded for both epiphytes (Nadkarni 1994, Matzek and Vitousek 2003, Clark et al. 2005) and palms (Rickson and Rickson 1986). Our findings indicate that *B. discolor* and similar ferns have the opportunity to utilize nutrients from decomposing litter and humus trapped in the crown, although this has not been tested to date and merits investigation. In addition, because litter accumulates at the base of the trunk of *B. discolor* relative to further from the trunk, ferns may also have preferential access to much of the litter that reaches the forest floor. This possible competitive advantage is combined with the ability of *B. discolor* to suppress establishment and growth of coexisting plant species by deep shading (Wardle 1963, de la Cretaz and Kelty 2002, Gillman and Ogden 2005).

In New Zealand, introduced browsing mammals such as European red deer preferentially browse the more palatable competitors of *B. discolor*, and the net result may be substantial promotion of *B. discolor* in locations where these mammals dominate (Wardle et al. 2001). Our results show that this domination by *B. discolor* may in turn influence the composition and spatial distribution of litter accumulation, and that this is in turn likely to alter decomposition patterns and nutrient fluxes at the forest stand level. It is becoming increasingly recognized that herbivorous mammals can influence nutrient cycling and decomposer processes at the ecosystem level through a variety of mechanisms (Bardgett and Wardle 2003). If (as

our evidence suggests) herbivores such as deer influence the spatial distribution and patterns of accumulation of litterfall through promoting plant species that intercept litter, then it points to an important though previously unreported mechanism by which herbivores can affect ecosystem processes.

There is increasing recognition that spatial redistribution of plant-derived resources can impact on both decomposer organisms (Sætre and Bååth 2000, Sulkava et al. 2001), and on the processes that they drive, such as decomposition and the supply of plant-available nutrients (Ettema and Wardle 2002). Our results emphasize that *B. discolor* can influence the spatial redistribution of several factors, such as resources, microbial activity, and release of plant-available nutrients from litter. This in turn is likely to determine the spatial distribution of tree seedlings, and potentially the density and spatial configuration of trees in the longer term, with likely reductions in total tree density. Further, patchiness of plant derived resources can in its own right affect decomposer activity (Sulkava et al. 2001), plant nutrient acquisition (Bonkowski et al. 2000) and plant growth (Wijesinghe and Hutchings 1997). Although the nature of these effects is generally poorly understood, it is possible that the effects of *B. discolor* on resource patchiness may, in its own right, influence the nutrition and growth of establishing tree seedlings. The consequences of this for forest succession and composition in the long term merit further investigation.

Litter interception may occur in forests where other fern species with funnelling fronds form dense understoreys. Dense understoreys of tree ferns with funnelling morphology have been described in both New Zealand (Coomes et al. 2005) and Australia (Drake and Mueller-Dombois 1993, Mueck et al. 1996), and tree ferns also occur in temperate and tropical rainforests in Africa, Asia and the Americas. Consequently, litter interception by fern understoreys may be widespread, and could play an important role in influencing nutrient cycling rates and the spatial distribution of litter-derived nutrients. In addition, our study highlights the likelihood that a proportion of forest litterfall may not reach the forest floor but instead remain suspended aboveground in vegetation where it will decompose independently of the soil environment. Although the ecological role of forest understorey vegetation remains poorly understood, there is increasing recognition that this vegetation can serve as an important driver of forest community and ecosystem processes (Nilsson and Wardle 2005, Hart and Chen 2006). Developing an understanding of how understorey vegetation may alter the spatial patterning of litterfall, and the consequences of this for decomposition and nutrient release processes, should help to advance our understanding of the functioning of structurally complex forest ecosystems.

Acknowledgements – The authors would like to thank Larry Burrows and Michael Gundale for advice and comments, Robert Keen for technical assistance, and Kelly Menchenton, Graeme Ure and Bruce Wardle for assistance in the field. This is a Waitutu Ecosystem Project publication, and the operational costs were covered by retained earnings from Landcare Research (New Zealand), and by the Foundation for Research, Science and Technology (FRST) contract CO9X0206.

References

Allan, H. H. 1982. Flora of New Zealand: Vol. 1. Indigenous Tracheophyta. – Manaaki Whenua Press.

Alvarez, R. and Alvarez, C. R. 2000. Soil organic matter pools and their associations with carbon mineralization kinetics. – Soil Sci. Soc. Am. J. 64: 184–189.

Alvarez-Sanchez, J. and Guevara, S. 1999. Litter interception on Astrocaryum mexicanum Liebm. (Palmae) in a tropical rain forest. – Biotropica 31: 89–92.

Anderson, J. P. E. and Domsch, K. H. 1978. A physiological method for the quantification of microbial biomass in soils. – Soil Biol. Biochem. 10: 215–221.

Anderson, J. P. E. and Domsch, K. H. 1985. A physiologically active method for the quantitative measurement of microbial biomass in soil. – Soil Biol. Biochem. 10: 215–221.

Bardgett, R. D. and Wardle, D. A. 2003. Herbivore mediated linkages between aboveground and belowground communities. – Ecology. 84: 2258–2268.

Berg, B. and McClaugherty, C. 2003. Plant litter: decomposition, humus formation, carbon sequestration– Springer..

Bonkowski, M. et al. 2000. Substrate heterogeneity and microfauna in soil organic 'hotspots' as determinants of nitrogen capture and growth of ryegrass. – Appl. Soil Ecol. 14: 37–53.

Bycroft, C. M. et al. 1993. Community structure (niche limitation and guild proportionality) in relation to the effect of spatial scale, in a Nothofagus forest sampled with a circular transect. – N. Z. J. Ecol. 17: 95–101.

Cadisch, G. and Giller K. E. (eds) 1997. Driven by nature: plant litter quality and decomposition. – Commonwealth Agricultural Bureau.

Clark, K. L. et al. 2005. Retention of inorganic nitrogen by epiphytic bryophytes in a tropical montane forest. – Biotropica 37: 328–336.

Coomes, D. A. et al. 2005. The hare, the tortoise and the crocodile: the ecology of angiosperm dominance, conifer persistence and fern filtering. – J. Ecol. 93: 918–935.

Dearden, F. M. et al. 2006. Changes in the ratio of twig to foliage in litterfall and consequences for decomposition across a long-term fire-induced chronosequence. – Oikos 115: 453–462.

de la Cretaz, A. L. and Kelty, M. J. 2002. Development of tree regeneration in fern-dominated forest understories after reduction of deer browsing. – Restor. Ecol. 10: 416–426.

Devasconcelos, H. L. 1990. Effects of litter collection by understorey palms on the associated macroinvertebrate fauna in Central Amazonia. – Pedobiologia 34: 157–160.

Drake, D. R. and Mueller-Dombois, D. 1993. Population development of rain-forest trees on a chronosequence of Hawaiian lava flows. – Ecology 74: 1012–1019.

Ettema, C. H. and Wardle, D. A. 2002. Spatial soil ecology. – Trends Ecol. Evol. 17: 177–183.

Flanagan, P. W. and van Cleve, K. 1983. Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. – Can. J. For. Res. 13: 795–817.

Gillman, L. N. and Ogden, J. 2005. Microsite heterogeneity in litterfall risk to seedlings. – Austral Ecol. 30: 497–504.

Hart, S. A. and Chen, H. Y. H. 2006. Understory vegetation dynamics of North American boreal forests. – Crit. Rev. Plant Sci. 25: 381–397.

Hunt, M. et al. 2002. Ecophysiology of the soft tree fern, *Dicksonia antarctica* Labill. – Austral. Ecol. 27: 360–368.

Insam, H. and Haselwandter, K. 1989. Are the soil microbial biomass and basal respiration governed by the climatic regime? – Soil Biol. Biochem. 22: 525–532.
Matzek, V. and Vitousek, P. 2003. Nitrogen fixation in bryophytes, lichens, and decaying wood along a soil-age gradient in Hawaiian montane rain forest. – Biotropica 35: 12–19.
Mueck, S. G. et al. 1996. How old are wet forest understories? – Aust. J. Ecol. 21: 345–348.
Nadkarni, N. M. 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. – Am. Zool. 34: 70–78.
Nadkarni, N. M. et al. 2004. Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica. – For. Ecol. Manage. 198: 223–236.
Nilsson, M.-C. and Wardle, D. A. 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. – Front. Ecol. Environ. 3: 421–428.
Richardson, B. A. et al. 2000. Effects of nutrient availability and other elevational changes on bromeliad populations and their invertebrate communities in a humid tropical forest in Puerto Rico. – J. Trop. Ecol. 16: 167–188.
Rickson, F. R and Rickson, M. M. 1986. Nutrient acquisition facilitated by litter collection and ant colonies on two Malaysian palms. – Biotropica 18: 337–343.
Sætre, P. and Bååth, E. 2000. Spatial variation and patterns of soil microbial community structure in a mixed spruce-birch stand. – Soil Biol. Biochem. 32: 909–917.
Singh, J. S. et al. 1989. Microbial biomass acts as a source of plant nutrients in dry tropical forest and savanna. – Nature 338: 449–500.
Sulkava, P. et al. 2001. Influence of soil fauna and habitat patchiness on plant (*Betula pendula*) growth and carbon dynamics in a microcosm experiment. – Oecologia 129: 133–138.
Swift, M. J. et al. 1979. Decomposition in terrestrial ecosystems. – Blackwell.
Ward, C. M. 1988. Marine terraces of the Waitutu district and their relation to the late Cenozoic tectonics of the southern Fiordland region, New Zealand. – J. R. Soc. N. Z. 18: 1–28.
Wardle, D. A. 1993. Changes in the microbial biomass and metabolic quotient during leaf litter succession in some New Zealand forest scrubland ecosystems. – Funct. Ecol. 7: 346–355.
Wardle, D. A. et al. 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. – Ecol. Monogr. 71: 587–614.
Wardle, D. A. et al. 2003. Island biology and ecosystem functioning in epiphytic soil communities. – Science 301: 1717–1720.
Wardle, P. 1963. The regeneration gap of New Zealand gymnosperms. – N. J. Bot. 1: 301–315.
Wijesinghe, D. K. and Hutchings, M. J. 1997. The effects of spatial scale of environmental heterogeneity on the growth of a clonal plant: an experimental study with *Glechoma hederacea*. – J. Ecol. 85: 17–28.