Pohlman, Catherine Louise (2006) ***Internal fragmentation in the rainforest: edge effects of highways, powerlines and watercourses on tropical rainforest understorey microclimate, vegetation structure and composition, physical disturbance and seedling regeneration.*** **PhD thesis,**
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Chapter Five: Vegetation Structure and Composition

5.1 Introduction

Numerous changes in vegetation occur at the edges of forest fragments. Immediately after edge creation, elevated wind speed and exposure to altered microclimate increase tree damage and mortality rates and therefore the frequency of canopy gaps near the edge (Laurance *et al.* 2002; Harper *et al.* 2005). Elevated tree mortality rates may persist over time (Williams-Linera 1990a; Laurance *et al.* 2002) although growth of vegetation on the very edge of the forest may lessen the severity of microclimatic conditions experienced in the adjacent understorey (Laurance *et al.* 2002; Harper *et al.* 2005). These initial and continuing alterations near the forest edge can be responsible for a range of changes in structure and composition of the floristic community (Harper *et al.* 2005).

Structural changes observed near edges of forest fragments include an increased abundance of lianas, increased density and growth of trees and saplings, an increase in the amount of coarse woody debris and a decrease in above-ground biomass (Williams-Linera 1990a; Harper and Macdonald 2002; Laurance *et al.* 2002; McDonald and Urban 2004). Species composition of the tree community can also be altered over time with an increase in abundance of early-successional tree species, a decrease in abundance of late-successional tree species and an increase in turnover rate near the forest edge (Laurance *et al.* 2002; McDonald and Urban 2004). The understorey community also responds to the altered edge microclimate. In tropical forest edges, the recruitment rate of tree seedlings, the abundance of shade-tolerant tree seedlings (Benitez-Malvido 1998; Benitez-Malvido and Martinez-Ramos 2003b) and species diversity of ferns decrease (Paciencia and Prado 2005). Both increases and decreases in the abundances of shrubs and herbaceous species have been found near fragment edges in temperate and boreal forests (Harper and Macdonald 2002; Kollmen and Buschor 2003; Nelson and Halpern 2005) while abundance of weed species may also increase (Fox *et al.* 1997).

In addition to edge effects caused by alterations in microclimatic conditions, changes in the faunal community may initiate changes in the trophic structure of forest fragments (Terborgh *et al.* 2006) or alter interactions between species (Murcia 1995). Changes in herbivory (Meiners *et al*. 2000; but see Benitez-Malvido 2001), seed predation (Jules and Rathcke 1999; Kollman and Buschor 2003) and pollination (Jules and Rathcke 1999) have all been observed in forest fragments. Mutualisms between plants and animals may also be disrupted in forest fragments. For example, seedling germination of the tree *Cupania vernalis* was lowered near edges of tropical forest fragments in Brazil because fewer seeds were 'cleaned' by ants (which remove the aril from seeds allowing them to germinate) (Guimaraes and Cogni 2002) and, in tropical forest fragments in Africa, fewer species with animal-dispersed seeds were recruited in small forest fragments than in continuous forest (Cordeiro and Howe 2001). In rainforest in north-eastern Australia, distributions of a number of small mammal species are affected by roads and powerlines; native *Rattus* spp. (*R. leucopus* and *R. fuscipes*) decrease in abundance whereas *Melomys cervinipes* increase near edges of powerlines and roads (Goosem and Marsh, 1997; Goosem 2000), whilst the White-tailed Rat, *Uromys caudimaculatus,* is less affected by proximity to roads and powerlines (Goosem and Marsh 1997) and the rainforest specialists, *Antechinus stuartii* and *Hypsiprimnodon moschatus*, tend to prefer the forest interior (Goosem 2004). *H. moschatus* is an important seed disperser (particularly of large, fleshy fruits), *U. caudimaculatus* may be both a seed predator and a scatter-hoarder whilst *M. cervinipes* is a seed predator (Lott *et al.* 1995; Harrington *et al.* 1997; Theimer 2001; Dennis 2003) and the other rodents may be both seed and seedling predators. Thus changes in faunal communities in forest near roads and powerlines have the potential to influence composition of the floristic community at the forest edge.

Forest near the edges of linear canopy openings has received less attention but reported edge effects include invasions by weed species along road and railway edges, lower species richness and abundance of native understorey species and alterations in the composition of the soil seed bank (Watkins *et al.* 2003; Devlaeminck *et al.* 2005; Hansen and Clevenger 2005). In this chapter, I will explore whether the structure and composition of the vegetation is changed near the edges of powerlines, highways and creeks.

5.1.1 Research Questions

This chapter addresses the following questions:

1) Is there evidence of a change in vegetation structure near the edges of linear canopy openings consistent with structural changes observed near the edges of forest fragments (eg increased liana abundance, increased abundance of small trees and saplings)? Does this differ among powerline, highway and creek edges?
2) Does above-ground biomass decrease at the edges of linear canopy openings (*cf.* Laurance *et al.* 1997)? Are there differences between edge types?
3) Is species diversity greater near the edges of linear canopy openings? Does this vary among powerline, highway and creek edges?
4) Is the plant community composition altered near the edges of linear canopy openings?
    a. Does functional group composition or proportion of species from different successional stages vary with distance from the forest edge and among edge types?
    b. Does the proportion of species with diaspores of differing size or dispersal strategy vary with distance from the forest edge and among the different edge types? For example, a reduction in the proportion of species with large, vertebrate-dispersed fruits might occur if the dispersers of these fruit avoid the forest edge.
5) Is there any evidence of a shift in successional status between adults and juveniles near the forest edge? For example, a shift towards earlier-successional species might occur if altered microclimatic conditions or disturbance regimes at the forest edge favoured the seedlings of early-successional species or inhibited the seedlings of late-successional species; alternatively, there might be a shift towards later-successional species if the plant community were "recovering" from the initial edge disturbance through successional processes (eg Matlack 1994).
6) Are any changes in plant community composition correlated with alterations in microclimate (especially altered light availability)?

5.2 Materials and Methods

5.2.1 Research Design

The aim of this section of the project was to assess the nature of the edge effects of linear canopy openings on the structure and species composition of rainforest vegetation. To this end, surveys of vegetation structure and floristic composition were conducted at the study sites described in Chapter Three (three edge types * two sites per edge type * two transects per site = 12 transects in total). At each transect, two 25 m lines were placed parallel to the forest edge at distances of 0.5 m, 4 m, 12 m, 25 m, 50 m and 100 m (and at –10 m within powerline clearings) from the forest edge (Figure 5.1); these are the same lines that were used for the measurement of variation in the understorey light environment (red:far red ratio, Chapter Four, Section 4.2.3). This allowed comparisons to be made between the understorey light environment and vegetation structure and floristic composition.

Stems ≥ 5 cm dbh (diameter at breast height; ~ 1.3 m) were measured within 50 cm of either side of these 25 m lines, producing two 25 m * 1 m plots for each distance along each transect. Stems 2 – 5 cm dbh were measured within 25 cm either side of these lines, producing two subplots of 25 m * 0.5 m for each distance along each transect (Figure 5.1). These elongated plots and subplots were used to obtain a more representative survey of the vegetation variation at each distance than square-shaped plots would have provided. All stems (trees, saplings, shrubs and lianas) within these size classes that were encountered within the appropriate plot (or subplot) were recorded, marked with brightly-coloured flagging tape and given an individual identification number. The dbh of each individual was measured with nylon diameter tape. For multi-stemmed individuals, the diameter of each stem was recorded (stems were differentiated from branches if they separated from the main stem below breast height). Lianas were included in the survey if they passed through the plot and were not part of a larger stem recorded elsewhere. I did not require that lianas be rooted within the plots (or subplots) as I merely wished to measure variation in the overall stem density of lianas with distance from the forest edge.

Seedlings, which were arbitrarily defined as all stems < 2 cm dbh, were recorded within three 1m * 1m quadrats per plot (Plate 5.1). These quadrats were placed at the beginning (~2.5 m), middle (~12.5 m) and end (~22.5 m) of each plot (Figure 5.1) to provide a spatially-separated sample of the seedling community within each plot. All seedlings, lianas and other stems < 2 cm dbh that were rooted within the quadrat were included in the survey (and marked with brightly-coloured flagging tape with an individual identification number; Plate 5.1). The height of each seedling was measured to the nearest 0.5 cm with a metal, hand-held measuring tape and the diameter at the base of each seedling was measured with Vernier callipers (resolution 0.02 mm).

Vegetation surveys were conducted between August 2003 and July 2005. There were no significant natural disturbances to the study area within this period. All marked individuals were identified to species or morphospecies level by a local expert (Mr Rigel Jensen) within two weeks of the initial marking of each transect. Epiphytes were not included in the vegetation survey.

Plate 5.1. An example of a 1 m * 1 m seedling quadrat. All seedlings within each quadrat were measured and marked with orange flagging tape and given an individual identification number and were subsequently identified to species level by a local expert (Mr Rigel Jensen). Photo by author.

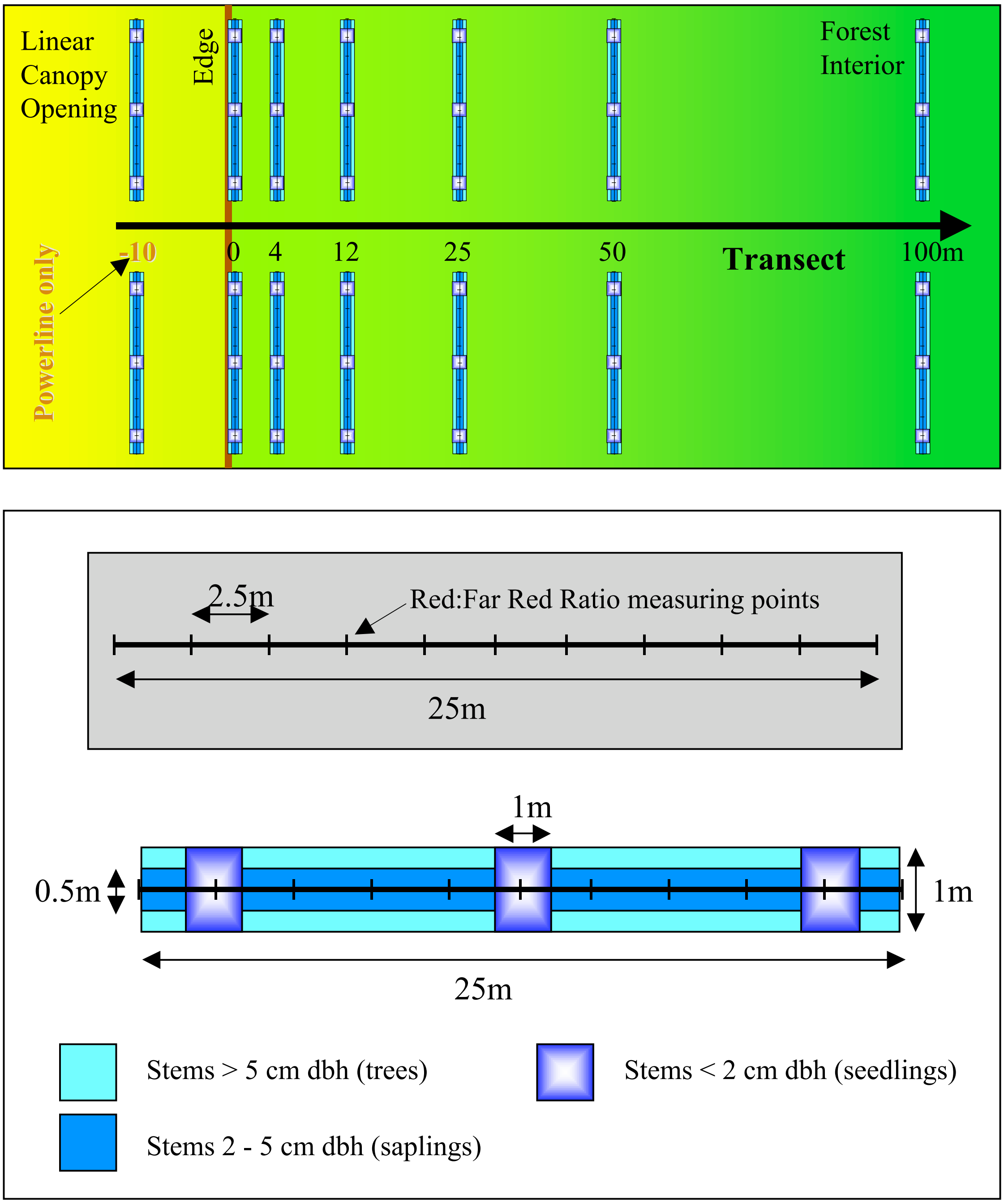


Figure 5.1. The vegetation survey design. Stems ≥ 5 cm dbh (diameter at breast height) were recorded within 25 m * 1 m plots (light blue); stems 2 - 5 cm dbh were recorded within 25 m * 0.5 m subplots (mid-blue); and stems < 2 cm dbh were recorded within 1 m * 1 m quadrats (shaded dark blue). These plots were placed in the same locations as the red:far red ratio measurements (Chapter Four) to allow comparisons to be made between vegetation structure, floristic composition and variation in the understorey light environment (red:far red ratio). Plots were placed at -10 m within powerline clearings only.

5.2.2 Analysis

All statistical analyses were performed using SPSS 11.0 for Macintosh.

5.2.2.1 Vegetation Structure and Species Diversity

The total numbers of stems (n) in each size class (≥ 5 cm dbh, 2 – 5 cm dbh, < 2 cm dbh) as well as the total number of species encountered (k) and the Shannon index of diversity (H') (Zar 1999) were analysed for each size class using ANOVAs with fixed factors of edge type and distance. The dependent variable was either n, k or H' for all stems within each size class combined across the two 25m^2 plots at each distance along each transect. N and k were $ln(1 + x)$ transformed prior to analysis to approximate normality.

Trees (non-liana stems ≥ 5 cm dbh) were divided into four size classes: < 10 cm diameter, 10 – 29.9 cm diameter, 30 – 49.9 cm diameter and ≥ 50 cm diameter. The number of trees within each diameter class was analysed using a backwards-conditional loglinear regression with factors edge type, distance and diameter class. As this analysis requires a frequency of ≥ 5 for each combination of factors, data for each distance for each edge type were pooled across all transects (so that frequencies represented counts per 200 m^2) and the two largest diameter classes (30 – 49.9 cm dbh and ≥ 50 cm dbh) were combined (into trees ≥ 30 cm dbh). The purpose of this analysis was to determine whether there were a greater proportion of smaller trees and a lower proportion of larger trees near the forest edge, which might arise from either greater survival and growth of younger trees or from increased mortality of larger trees at the forest edge (*cf.* Laurance *et al.* 2002).

Basal areas for trees, lianas and all stems ≥ 5 cm dbh were calculated from diameters measured for each stem ≥ 5 cm dbh. Data from the two 25 m^2 plots per distance per transect were pooled so that basal areas were calculated on the basis of cm^2 per 50 m^2. These data were analysed using ANOVA with fixed factors of edge type (powerline, highway and creek) and distance from the forest edge.

Above-ground biomass for trees ≥ 5 cm dbh was calculated for each distance along each transect using the "wet forest" equation (without tree heights) from Chave *et al.* (2005):

$$AGB_{est} = \rho * \exp(-1.239 + 1.9801 ln(D) + 0.207(ln(D))^2 - 0.0281(ln(D))^3)$$

Where AGB_{est} = estimate of above-ground biomass, D = basal diameter and ρ = wood specific gravity (wood density/1000). Data on the wood density (or wood specific gravity) of individual tree species were obtained from Osunkoya (1996), Cause *et al.* (1989), Hyland (1989) and from expert advice (Dr Steve Goosem, *pers. comm*., citing Floyd 1989 and Watson 1951). Where the wood density of an individual species could not be obtained, a family average (obtained from data in Cause *et al.* 1989 and Smith *et al.* 1991) was used as a surrogate (Appendix 1). In the case of one species (*Phaleria clerodendron*, Thymelaeaceae), no wood density data were available for either the species or the family so the mean wood density of the entire dataset (Appendix 1) was used. Data on wood density or biomass calculations could not be obtained for either lianas or treeferns (*Cyathea cooperi*) in north-eastern Queensland; these species had to be omitted from the analysis. However, as the basal area of lianas made up only a small proportion of the overall basal area (Figure 5.4) and the biomass of lianas is generally lower than that of trees (Laurance *et al.* 1997), this omission should not greatly alter the results. These data were analysed using ANOVA with fixed factors of edge type (powerline, highway and creek) and distance and dependent variable *ln*(above-ground tree biomass per 50 m^2).

5.2.2.2 Functional Group Composition

Each species encountered in the vegetation survey was classified according to growth habit (grass, herb, shrub, liana, fern, canopy tree or understorey tree), successional status (weed, early-successional, mid-successional or late-successional) and fruiting characteristics (dispersal mode and fruit size) (Appendix 2). Data on growth habit, successional status and fruiting characteristics of each species were obtained from the literature (firstly Cooper and Cooper 1994; Hyland *et al*. 2003: subsequently from Jones and Clemesha 1980; Williams 1984, 1987; Andrews 1990; Briggs and Leigh 1995; Osunkoya 1996; Lazarides *et al*. 1997; Tucker and Murphy 1997; van Raders 1999; Jackes 2001; Parsons and Cuthbertson 2001; Tucker 2001; White *et al.* 2004) and from expert advice (Dr Steve Goosem *pers. comm*.).

Abundances of weeds, grasses (including exotic grasses), ferns (climbing ferns and terrestrial ferns), early-, mid- and late-successional herbs and early-, mid- and late-successional shrubs were analysed using Spearman's Rank Correlation to test for variation with distance from the forest edge as these data could not be transformed to approximate normality. Abundances of all climbing plants (large woody lianas, slender lianas, climbing herbs and climbing ferns) as well as abundances of large woody lianas, slender lianas and climbing herbs were analysed using ANOVAs with fixed factors of edge type (powerline, highway and creek) and distance for each size class (≥ 5 cm dbh, 2 – 5 cm dbh and < 2 cm dbh).

Abundances of understorey and canopy trees were analysed for each size class (≥ 5 cm dbh, 2 – 5 cm dbh and < 2 cm dbh) using ANOVAs with fixed factors of edge type (powerline, highway and creek) and distance. Proportions of understorey tree individuals from early-, mid- and late-successional species and proportions of canopy tree individuals from early-, mid- and late-successional species were analysed using ANOVA (where data had an approximately normal distribution) with fixed factors of edge type (powerline, highway and creek), distance and size class (≥ 5 cm dbh, 2 – 5 cm dbh and < 2 cm dbh), or with Kruskal-Wallis Tests, where data could not be transformed to approximate normality.

Abundances of individuals from species with small (< 1.0 cm width), intermediate (1.0 – 2.0 cm width) and large (> 2.0 cm width), abiotically- and biotically-dispersed diaspores were analysed for each size class (≥ 5 cm dbh, 2 – 5 cm dbh and < 2 cm dbh) using ANOVAs with fixed factors of edge type (powerline, highway or creek) and distance. The aim of this specific analysis was to explore whether larger or biotically-dispersed fruits might be dispersal-limited near the forest edge, which might occur if the dispersers of larger fruit (eg the Southern Cassowary, *Casuarius casuarius*, the Musky Rat-kangaroo, *Hypsiprimnodon moschatus*, the Long-nosed Bandicoot, *Parameles nasuta*, and various native rats, *Rattus* spp.) are less abundant near the forest edge (*cf.* Murcia 1995) or if smaller, wind-dispersed seeds accumulate at the forest edge.

For all of these analyses, the two 25 m^2 plots per distance per transect were pooled such that abundances of stems in the largest size class (≥ 5 cm dbh) were measured on the basis of stems per 50 m^2, stems in the intermediate size class (2 – 5 cm dbh) were measured on the basis of stems per 25 m^2 and stems in the smallest size class (< 2 cm dbh) were measured on the basis of stems per 6 m^2.

5.2.2.3 Seedling Size Distribution

To further explore some of the patterns revealed in these analyses, I examined size distributions of seedlings of shrubs, understorey trees and canopy trees. The number of seedlings that fell within four height classes (< 20 cm, 20 – 50 cm, 50 – 100 cm and > 100 cm) was analysed using backward conditional loglinear analyses with variables edge type, distance and size class. These analyses were performed separately for shrubs, understorey trees and canopy trees. Data were pooled across all transects for each edge type. Data for the two largest size classes (50 – 100 cm and > 100 cm) were pooled for canopy tree seedlings (> 50 cm tall). For shrubs, data were further pooled into three distance categories (0 m & 4 m, 12 m & 25 m, 50 m & 100 m). A small proportion of small seedlings might be a sign of recruitment limitation; conversely, a large proportion of small seedlings might be an indication that the seedling pool is dominated by recently germinated individuals.

As physical disturbance to seedlings may reduce the height of older seedlings (Peters *et al.* 2004), size distributions of understorey tree and canopy tree seedlings were also examined according to basal diameter measurements. Four basal diameter size classes (< 3 mm, 3 – 4.98 mm, 5 – 10 mm, > 10 mm) were used for these analyses. Shrubs were not analysed in this way, because at least two shrub species (*Ixora baileyana* and *Atractocarpus hirtus*) appeared to reproduce vegetatively with broken fragments of larger stems taking root and giving rise to numerous small seedlings with large basal diameters (*pers. obs.*).

5.2.2.4 Seedling Species Composition and the Understorey Light Environment

To explore the relationship between light availability and the composition of the seedling community, the abundance of stems < 2 cm dbh within each of the functional groups described in the previous section (with the exception of the fruit size and dispersal mode groups) measured within each individual 1m * 1m seedling quadrat was correlated against the red:far red value measured for that quadrat (Chapter 4). As much of these data were non-normally distributed, Spearman Rank Correlations were used to analyse the relationships between the abundances of different functional groups, distance from the forest edge and the red:far red ratio.

5.3 Results

13 210 individuals (1092 stems $\geq$ 5 cm dbh, 957 stems 2 – 5 cm dbh and 11 161 stems < 2 cm dbh) were identified in the vegetation survey, representing 340 species, 215 genera and 88 families.

5.3.1 Vegetation Structure and Species Diversity

The total number of stems (n), is greater near the forest edge for all size classes (Table 5.1; Figure 5.2 a, b, c) although the number of stems 2 – 5 cm dbh is less along creek transects than powerline or highway transects (Table 5.1; Figure 5.2b) and the number of stems < 2 cm dbh is greater near creek edges than near powerline or highway edges (Table 5.1; Figure 5.2c). The number of species (k) is not significantly affected by either distance from the forest edge or edge type for stems $\geq$ 5 cm dbh or stems < 2 cm dbh (Table 5.1; Figure 5.2 d, f) but is greater near the forest edge (and less along creek transects than powerline or highway transects) for stems 2 – 5 cm dbh (Table 5.1; Figure 5.2e). Consequently, the Shannon diversity index (H') is not significantly affected by either distance from the forest edge or edge type for stems $\geq$ 5 cm dbh (Table 5.1; Figure 5.2g) but is greater near the forest edge (and less along creek transects than powerline or highway transects) for stems 2 – 5 cm dbh (Table 5.1; Figure 5.2h) and there is a marginally significant reduction in H' along creek transects relative to powerline or highway transects for stems < 2 cm dbh (Table 5.1; Figure 5.2i).

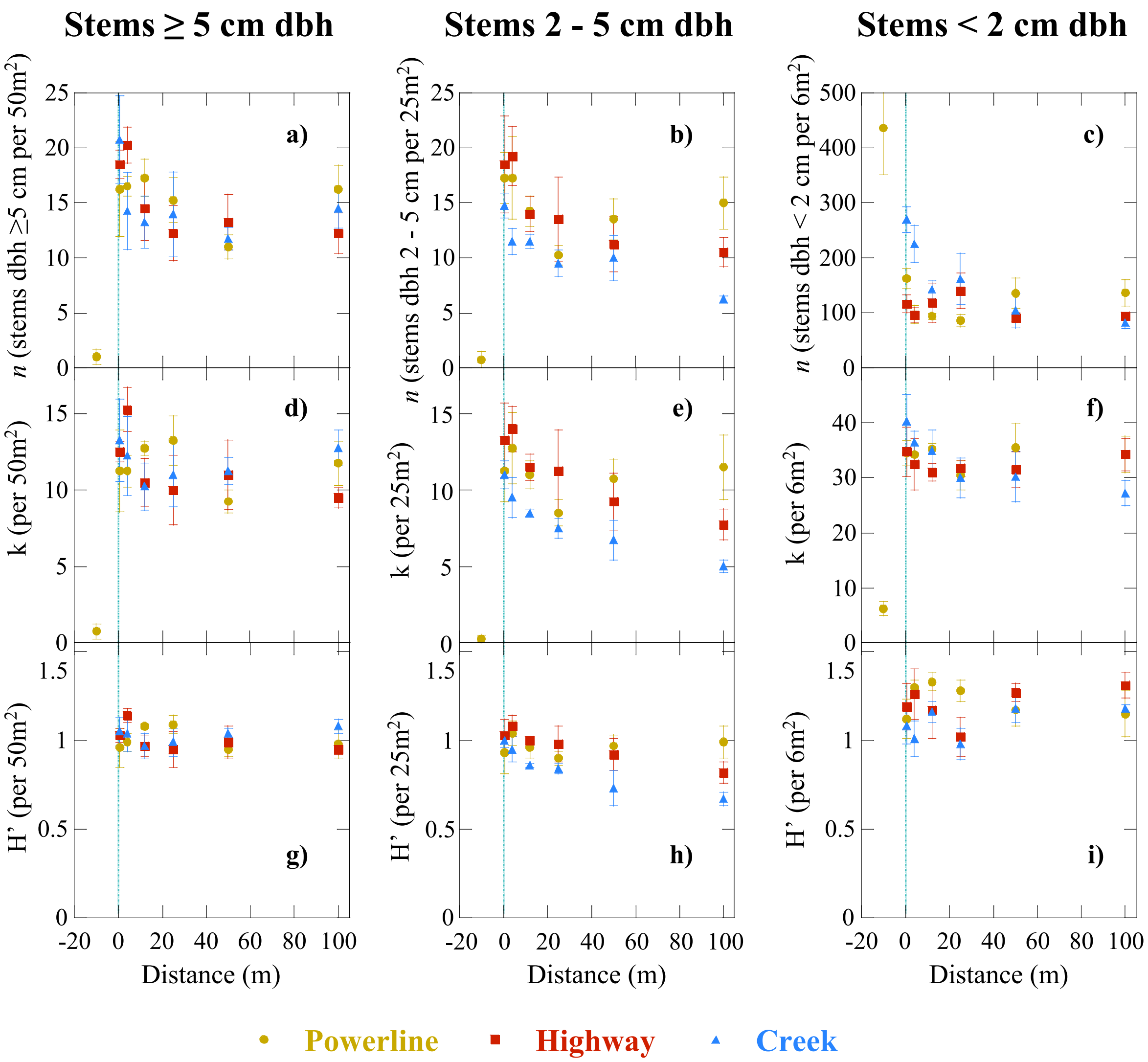


Figure 5.2. Density of stems (**a, b, c**), number of species (**d, e, f**) and Shannon diversity indices (**g, h, i**) for stems ≥ 5 cm dbh (**a, d, g**), stems 2 - 5 cm dbh (**b, e, h**) and stems < 2 cm dbh (**c, f, i**). Values represent means and error bars represent 1 standard error. Dashed vertical lines indicate the position of the forest edge.

Table 5.1. Variation in the numbers of individuals (n), species (k) and the Shannon Diversity Index (H’) with distance. Data were analysed using ANOVA. Significant effects are highlighted in bold and marginally significant effects are highlighted in italics.

Size Class	**Effect**	**Parameter**	***F***	**df**	***p*-value**
> 5 cm dbh	Edge Type	n	0.108	2	0.898
		k	0.061	2	0.940
		H’	0.278	2	0.758
	Distance	n	2.573	5	**0.037**
		k	0.818	5	0.542
		H’	0.326	5	0.895
	Edge Type * Distance	n	0.806	10	0.624
		k	0.998	10	0.457
		H’	1.054	10	0.413
2 – 5 cm dbh	Edge Type	n	6.286	2	**0.004**
		k	7.727	2	**0.001**
		H’	6.489	2	**0.003**
	Distance	n	4.229	5	**0.003**
		k	3.413	5	**0.009**
		H’	3.112	5	**0.015**
	Edge Type * Distance	n	0.692	10	0.728
		k	0.817	10	0.614
		H’	1.052	10	0.415
< 2 cm dbh	Edge Type	$ln(1 + n)$	4.309	2	**0.018**
		k	0.283	2	0.754
		H’	2.939	2	*0.061*
	Distance	$ln(1 + n)$	3.173	5	**0.014**
		k	1.167	5	0.337
		H’	0.909	5	0.482
	Edge Type * Distance	$ln(1 + n)$	2.748	10	**0.008**
		k	0.781	10	0.647
		H’	1.010	10	0.447

The loglinear analysis revealed a greater proportion of small (5 – 10 cm dbh) and intermediate (10 – 30 cm dbh) stems and a correspondingly lower proportion of large ($\geq$ 30 cm dbh) stems near the forest edge than in the forest interior (with the exception of the very edge – 0 m – itself) (distance * dbh class, $\chi^2 = 25.109$, df = 10, $p = 0.0051$; Figure 5.3a) and a smaller proportion of small stems and a greater proportion of large (> 30 cm dbh) stems along creek transects than along anthropogenic transects (edge type * dbh class, $\chi^2 = 11.115$, df = 4, $p = 0.0253$; Figure 5.3b; *post hoc* tests of proportions, one-way ANOVAs for edge type effects in total percent small, intermediate and large trees along each individual transect, percent small {5 – 10 cm dbh}, $F = 4.426$, $p = 0.046$, Bonferroni *post hoc* test, creek < powerline, $p = 0.067$; percent intermediate trees {10 – 30 cm dbh}, $F = 1.566$, $p = 0.261$; percent large trees {> 30 cm dbh}, $F = 4.985$, $p = 0.035$, Bonferroni *post hoc* test, powerline < creek, $p = 0.035$).

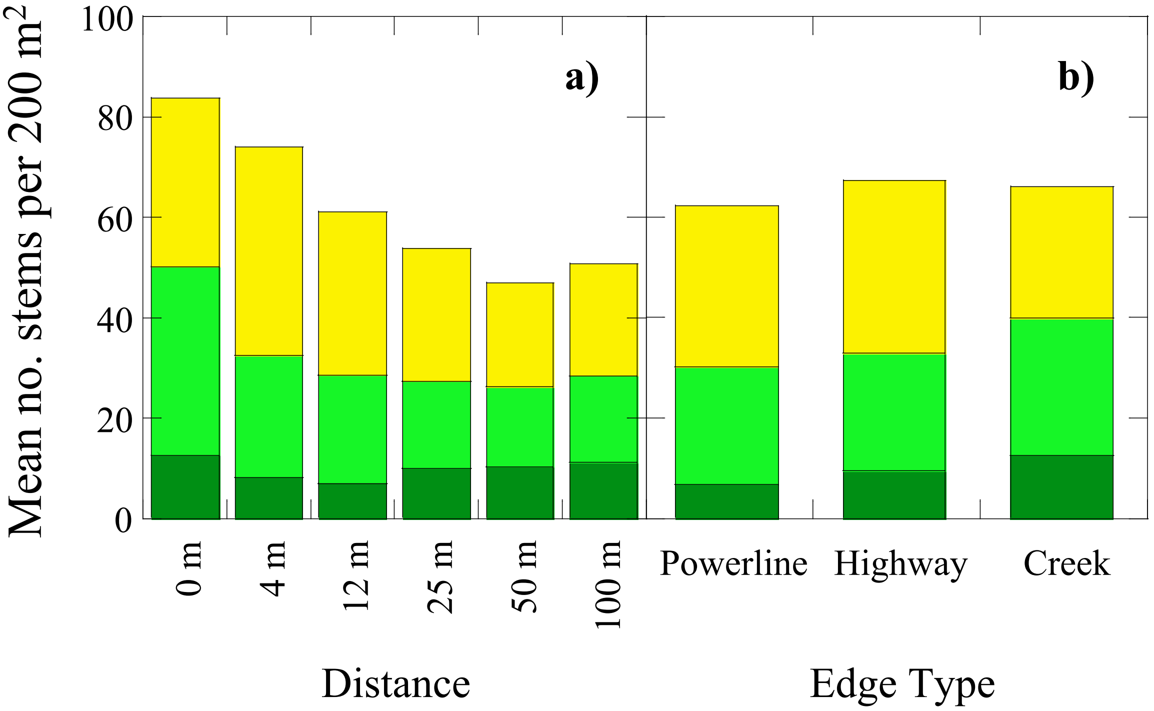


Figure 5.3. Distribution of diameter classes of stems $\geq$ 5 cm dbh, **a**) with distance from the forest edge and **b**) among edge types.

The basal area of stems ≥ 5 cm dbh was not affected by proximity to the forest edge [*ln*(total basal area), $F = 0.868$, df = 5, $p = 0.509$, Figure 5.4a; *ln*(tree basal area), $F = 0.853$, df = 5, $p = 519$, Figure 5.4b; *ln*(1+ liana basal area), $F = 0.849$, df = 5, $p = 0.522$, Figure 5.4c], although tree basal area and total basal area were slightly less along powerline transects than along creek or highway transects [*ln*(total basal area), $F = 3.660$, df = 2, $p = 0.032$, Bonferroni *post hoc* tests, powerline < highway, $p = 0.072$, powerline < creek, $p = 0.065$; *ln*(tree basal area), $F = 3.679$, df = 2, $p = 0.032$, Bonferroni *post hoc* tests, powerline < highway, $p = 0.072$, powerline < creek, $p = 0.063$]. The above-ground biomass of tree stems ≥ 5 cm dbh was less along powerline transects than along highway or creek transects (edge type, $F = 5.371$, df = 2, $p = 0.007$; Figure 5.5) but did not vary with distance from the edge (distance, $F = 1.003$, df = 5, $p = 0.425$; edge type * distance, $F = 1.183$, df = 10, $p = 0.324$).

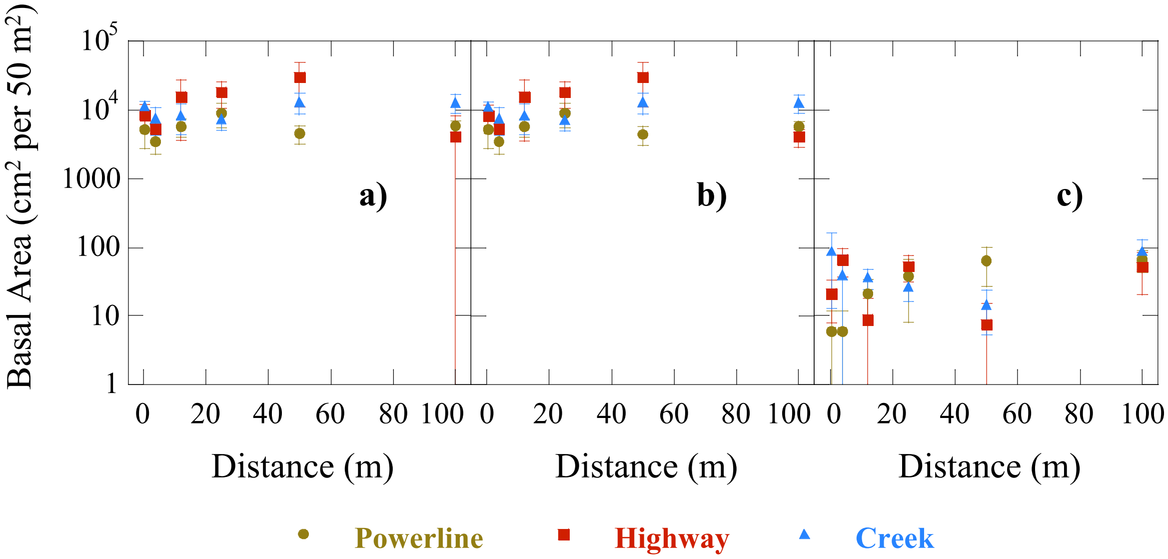


Figure 5.4. Basal area (cm^2 per 50m^2) of **a**) all stems ≥ 5 cm dbh, **b**) all trees ≥ 5 cm dbh and **c**) all lianas ≥ 5 cm dbh. Note the log scale on the y-axis.

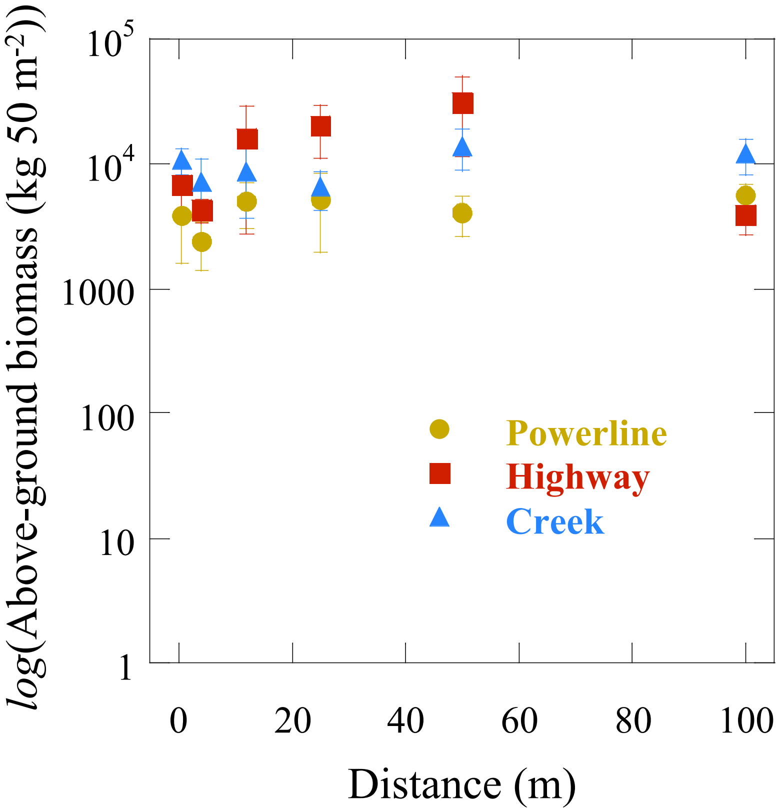


Figure 5.5. Above-ground biomass of trees ≥ 5 cm dbh (kg 50 m^{-2}). Note the log scale on the y-axis.

5.3.2 Functional Group Composition

5.3.2.1 Successional Status and Growth Habit.

Floral community composition was altered near the edges of powerlines, highways and creeks. Weeds were confined to within 12m of highway and creek edges and to the very edge (0.5 m) of powerlines (Table 5.2, Figure 5.6). Grasses were mostly included in the weeds data (eg *Urochloa maxima*, *Melinus minutiflora*) but native grasses extended to 25m from creek edges (at low densities, Table 5.2, Figure 5.7a). The abundance of ferns increased with proximity to creek edges (Table 5.2, Figure 5.7b); this result was driven largely by the abundance of terrestrial ferns although the climbing fern *Dicranopteris linearis* (Gleicheniaceae) was only observed along creek edges. The total abundance of herbs increased with proximity to the forest edge with this result being driven by increases in the abundance of early-successional herbs near powerline and creek edges (Table 5.2, Figure 5.8 a, b, c). There was a marginally significant increase in the abundance of late-successional herbs with distance from creek edges (Table 5.2), which was driven entirely by a very slight increase in the abundance of walking stick palms (*Linospadix microcarya* and *L. minor*, family Arecaceae) with distance from creek edges.

The abundance of small shrubs (dbh < 2 cm) decreased near the forest edge, particularly near powerline and creek edges, with this result being driven largely by the decrease in late-successional shrubs near the forest edge (Table 5.2, Figure 5.8 d, e, f). In contrast, the abundance of early-successional shrubs increased near the edges of powerlines and highways but decreased near creek edges (Table 5.2) but the overall numbers of early-successional shrubs were too low to alter the overall decline in small shrub abundance near the edge. No significant patterns were detected in the abundance of intermediate-sized shrubs (dbh 2 – 5 cm) possibly because overall numbers were low.

Table 5.2. Variation in the abundances of weeds, grass, ferns, herbs and shrubs with distance from the forest edge and among edge types. Data were analysed with Spearman Rank Correlations. Significant correlations are highlighted (* $\alpha < 0.05$, ** $\alpha < 0.01$, *** $\alpha < 0.001$; marginally significant, † $\alpha < 0.1$).

Size Class	**Parameter**	**Correlation Coefficient**			
		Powerline	**Highway**	**Creek**	**Overall**
< 2 cm dbh	Weeds	-0.305	-0.571**	-0.472 *	-0.448***
	Grass	-0.441*	-0.464*	-0.641***	-0.497***
	Ferns	-0.198	-0.091	-0.657***	-0.284*
	terrestrial ferns	-0.198	-0.195	-0.657***	-0.297*
	climbing ferns	NA	-0.058	-0.206	-0.100
	Herbs	-0.435*	-0.326	-0.385†	-0.353**
	early-successional	-0.490*	-0.113	-0.467*	-0.348**
	mid-successional	-0.054	-0.269	0.002	-0.102
	late-successional	-0.061	0.120	0.397†	0.187
	Shrubs	0.466*	0.271	0.457*	0.420***
	early-successional	-0.451*	-0.441*	0.458*	-0.131
	mid-successional	0.061	-0.065	-0.353†	-0.124
	late-successional	0.491*	0.319	0.480*	0.452***
2 – 5 cm dbh	Shrubs	0.155	-0.174	0.088	0.007
	early-successional	-0.177	-0.305	NA	-0.185
	mid-successional	NA	NA	NA	NA
	late-successional	0.282	-0.043	0.088	0.102

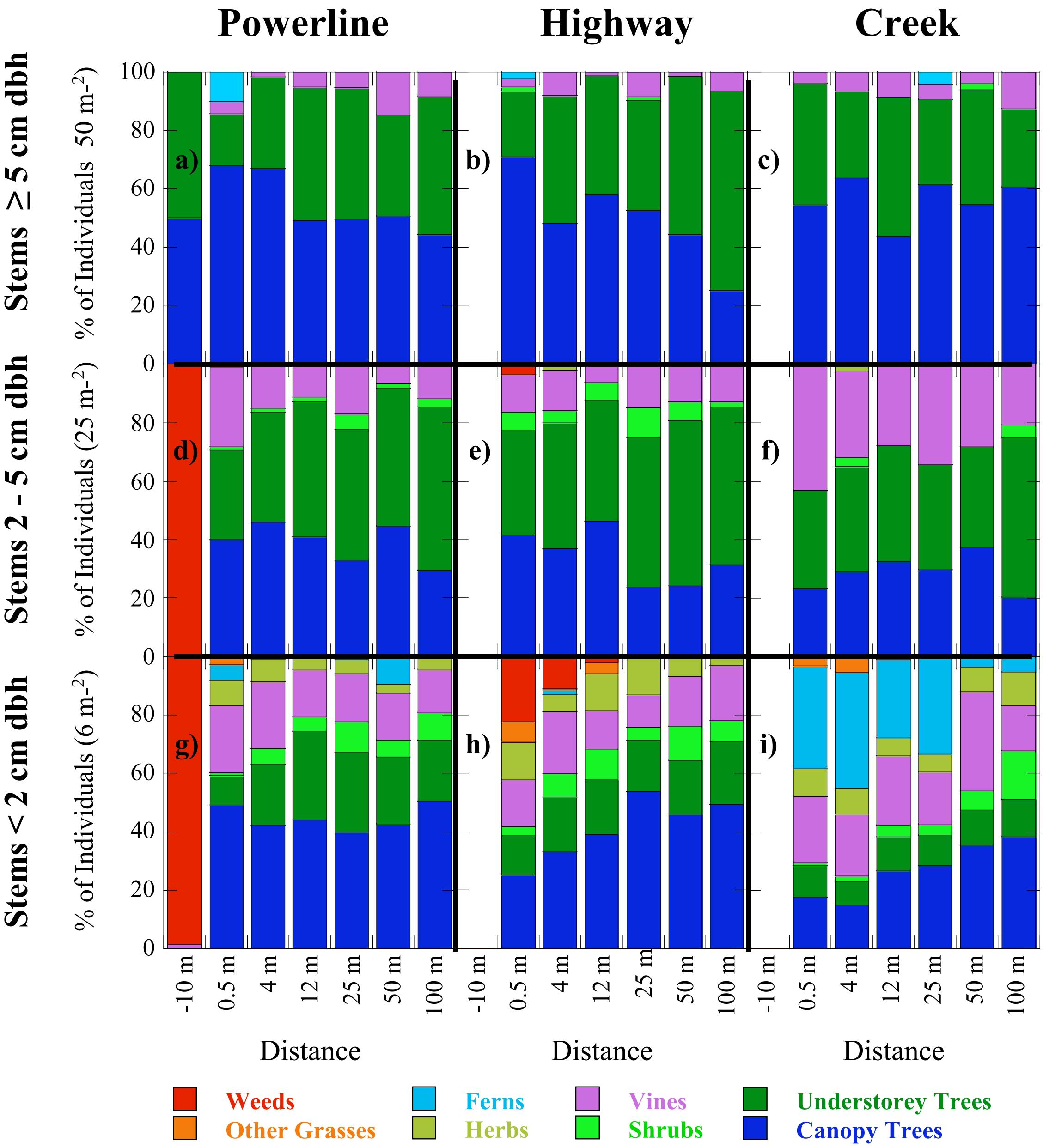


Figure 5.6. Growth habit composition of stems with dbh ≥ 5 cm (**a, b, c**), 2 - 5 cm (**d, e, f**) and < 2 cm (**g, h, i**). Ferns in the largest size class (dbh ≥ 5 cm) are the treefern *Cyathea cooperi* (Cyatheaceae), which was only observed on forest edges, in light gaps within the forest or in regrowth within the powerline corridor.

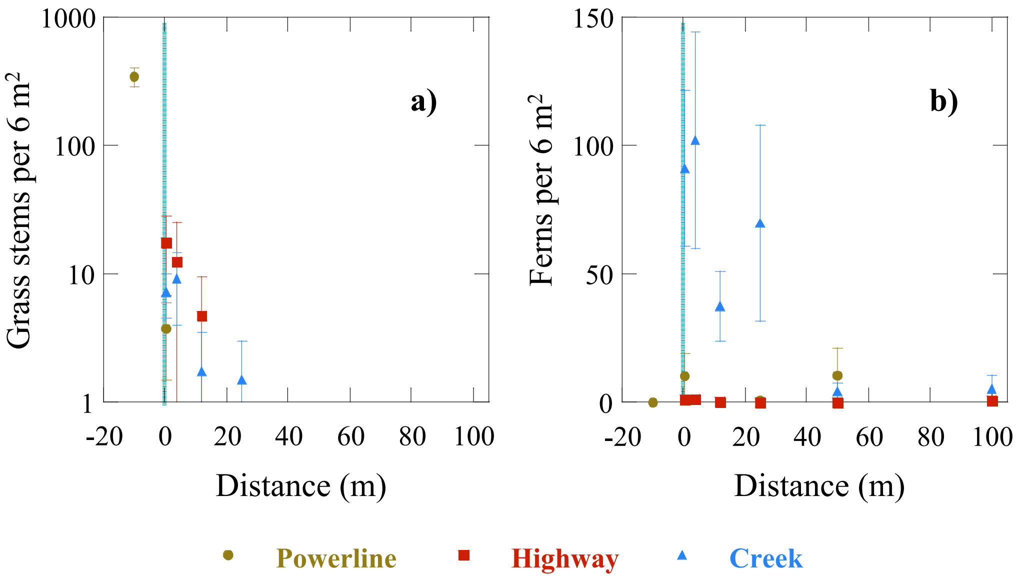
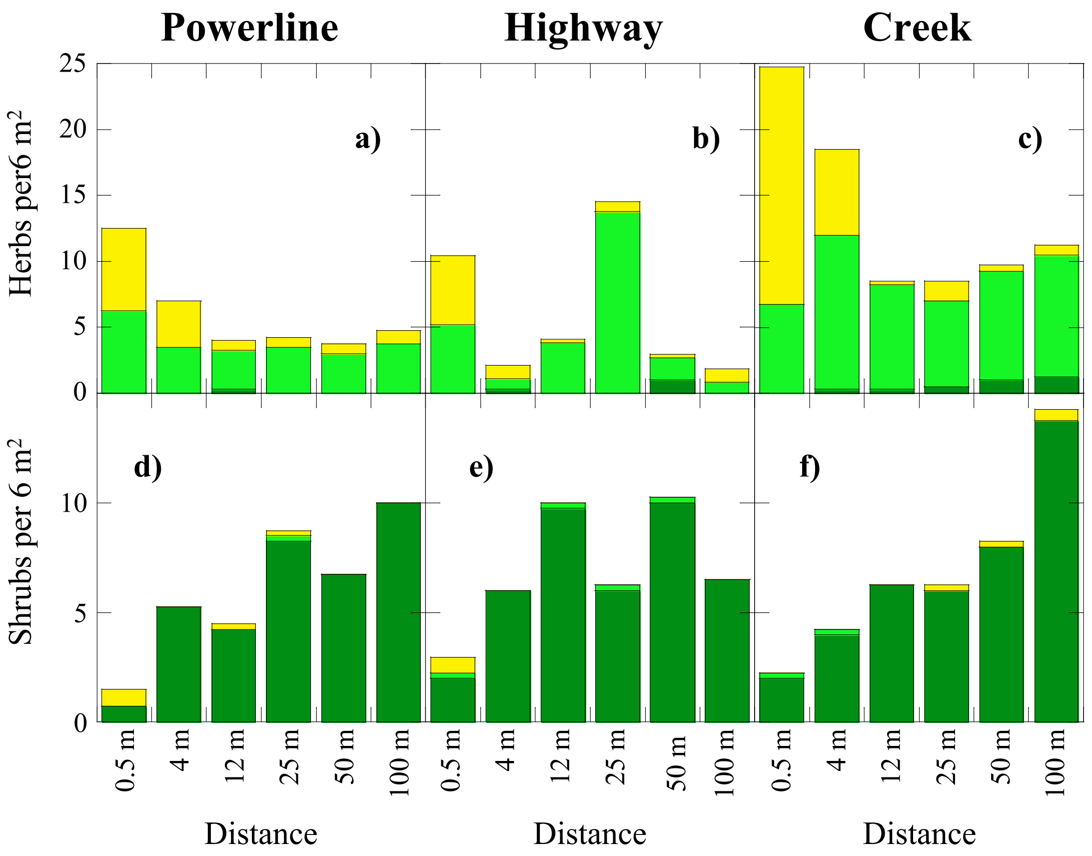


Figure 5.7. Abundance of **a**) grass and **b**) ferns, in the dbh < 2 cm size class. Climbing ferns and terrestrial ferns are combined in panel **b**. Values are means and error bars represent 1 s.e. Dashed vertical lines mark the position of the forest edge.



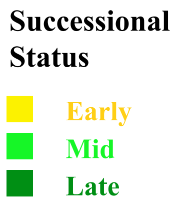


Figure 5.8. The abundance of herbs (**a, b, c**) and shrubs (**d, e, f**) in the dbh < 2 cm size class divided into early, intermediate and late successional categories.

Small (dbh < 2 cm) and intermediate-sized (dbh 2 – 5 cm) vines were more abundant near the forest edge (Table 5.3) although liana abundance was greatest along creek transects (Table 5.3). These patterns in overall vine abundance are mirrored by the individual patterns observed in large woody lianas and slender vines (Figure 5.9) although these patterns did not always achieve statistical significance (Table 5.3). The abundance of climbing herbs was not influenced by proximity to the forest edge (Table 5.3, Figure 5.9f); nor was the abundance of the largest woody lianas (≥ 5 cm dbh, Table 5.3, Figure 5.9a).

The overall abundance of individuals from understorey tree species was not altered by proximity to the forest edge for either tree- (≥ 5 cm dbh), sapling- (2 – 5 cm dbh) or seedling-sized (< 2 cm dbh) individuals (Table 5.4, Figure 5.10 a, c, e) although the abundance of sapling-sized individuals was lowest along creek transects (Table 5.4, Figure 5.10c; Bonferroni *post hoc* tests, creek < powerline, $p = 0.018$, creek < highway, $p = 0.012$). In contrast, the overall abundances of tree- and sapling-sized individuals from canopy tree species were elevated near the forest edge (Table 5.4, Figure 5.10 b, d) although the abundance of sapling-sized individuals was lowest along creek edges (Table 5.4, Figure 5.10d; Bonferroni *post hoc* tests, creek < powerline, $p = 0.001$, creek < highway, $p = 0.007$) and the abundance of seedling-sized individuals was not affected by either distance from the forest edge or edge type (Table 5.4, Figure 5.10f).

Table 5.3. Liana abundance. Data were analysed with ANOVA. Significant effects are highlighted in bold and marginally significant effects are highlighted in italics.

Size Class	**Effect**	**Parameter**	***F***	**df**	***p*-value**
> 5 cm dbh	Edge Type	*ln* (1 + large woody vines)	0.302	2	0.740
	Distance	*ln* (1 + large woody vines)	0.738	5	0.599
	Edge Type * Distance	*ln* (1 + large woody vines)	0.831	10	0.601
2 – 5 cm dbh	Edge Type	*ln* (1 + all vines)	4.363	2	**0.017**
		ln (1 + large woody vines)	1.497	2	0.233
		ln (1 + slender vines)	13.563	2	**< 0.001**
	Distance	*ln* (1 + all vines)	3.595	5	**0.004**
		ln (1 + large woody vines)	1.551	5	0.190
		ln (1 + slender vines)	1.581	5	0.181
	Edge Type * Distance	*ln* (1 + all vines)	0.579	10	0.824
		ln (1 + large woody vines)	0.683	10	0.735
		ln (1 + slender vines)	0.599	10	0.807
< 2 cm dbh	Edge Type	*ln* (1 + all vines)	7.148	2	**0.002**
		ln (1 + large woody vines)	8.385	2	**0.001**
		ln (1 + slender vines)	3.217	2	**0.048**
		ln (1 + climbing herbs)	4.917	2	**0.011**
	Distance	*ln* (1 + all vines)	8.374	5	**< 0.001**
		ln (1 + large woody vines)	1.857	5	0.117
		ln (1 + slender vines)	9.131	5	**< 0.001**
		ln (1 + climbing herbs)	0.308	5	0.906
	Edge Type * Distance	*ln* (1 + all vines)	1.166	10	0.332
		ln (1 + large woody vines)	1.069	10	0.402
		ln (1 + slender vines)	0.662	10	0.754
		ln (1 + climbing herbs)	1.175	10	0.328

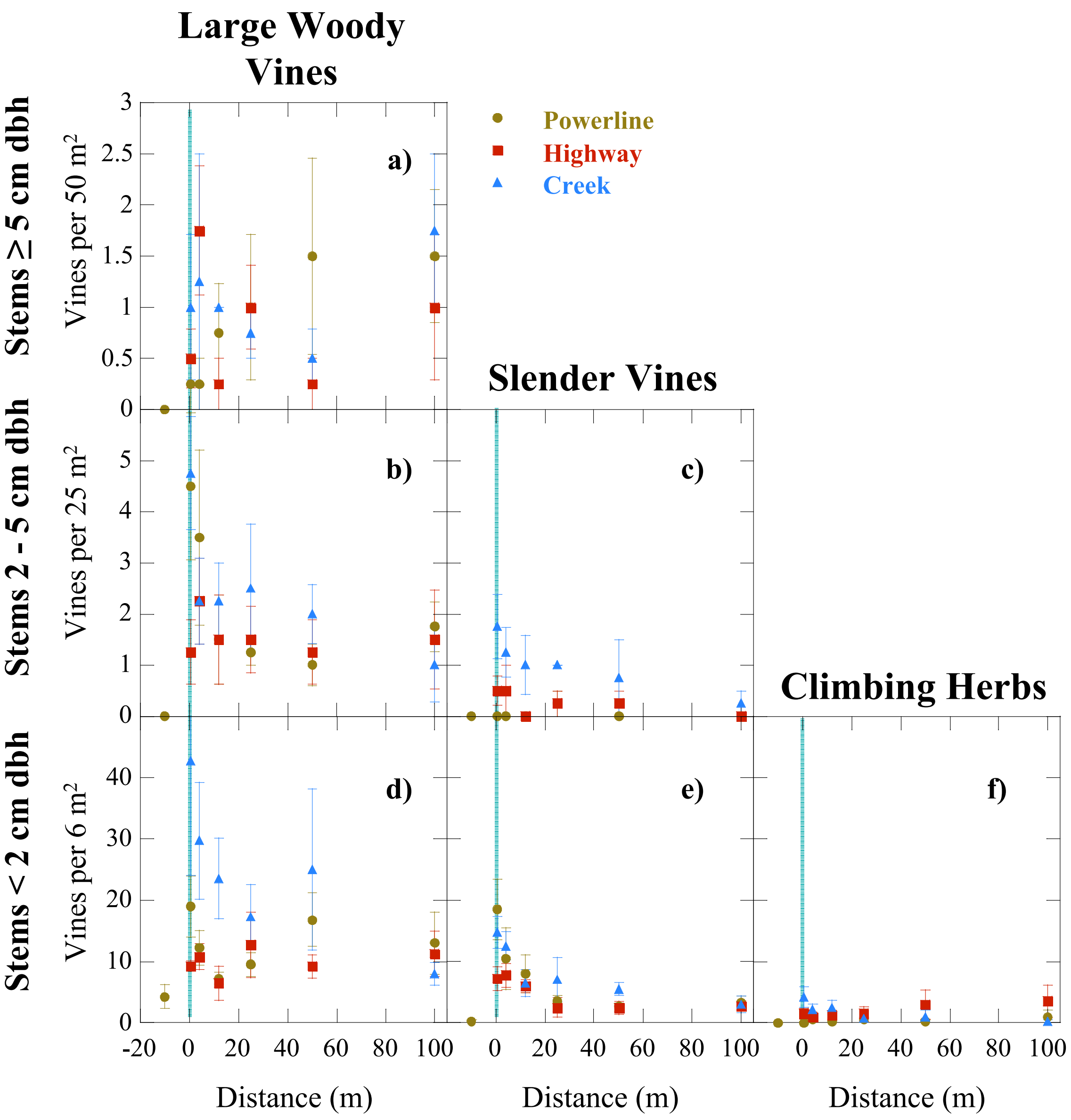


Figure 5.9. Liana abundance. The abundance of large woody vines (**a**, stems > 5 cm dbh; **b**, stems 2 - 5 cm dbh; **d**, stems < 2 cm dbh), slender woody vines (**c**, stems 2 - 5 cm dbh; **e**, stems < 2 cm dbh) and climbing herbs (**f**, stems < 2 cm dbh). Dashed vertical lines indicate the position of the forest edge.

Table 5.4. Variation in total numbers of understorey and canopy trees. These data were analysed using ANOVA. Significant effects are highlighted in bold and marginally-significant results are highlighted in italics.

Size Class	**Effect**	**Parameter**	***F***	**df**	***p*-value**
Trees	Edge Type	Understorey trees	0.712	2	0.495
		Canopy trees	0.367	2	0.695
	Distance	Understorey trees	0.490	5	0.782
		Canopy trees	5.310	5	**< 0.001**
	Edge Type * Distance	Understorey trees	1.831	10	*0.077*
		Canopy trees	0.827	10	0.605
Saplings	Edge Type	Understorey trees	5.726	2	**0.006**
		Canopy trees	8.166	2	**0.001**
	Distance	Understorey trees	0.241	5	0.942
		Canopy trees	4.352	5	**0.002**
	Edge Type * Distance	Understorey trees	0.491	10	0.888
		Canopy trees	0.886	10	0.552
Seedlings	Edge Type	*ln* (1 + Understorey trees)	3.768	2	0.950
		ln (1 + Canopy trees)	2.257	2	0.114
	Distance	*ln* (1 + Understorey trees)	0.226	5	0.950
		ln (1 + Canopy trees)	0.402	5	0.845
	Edge Type * Distance	*ln* (1 + Understorey trees)	1.562	10	0.143
		ln (1 + Canopy trees)	0.661	10	0.755

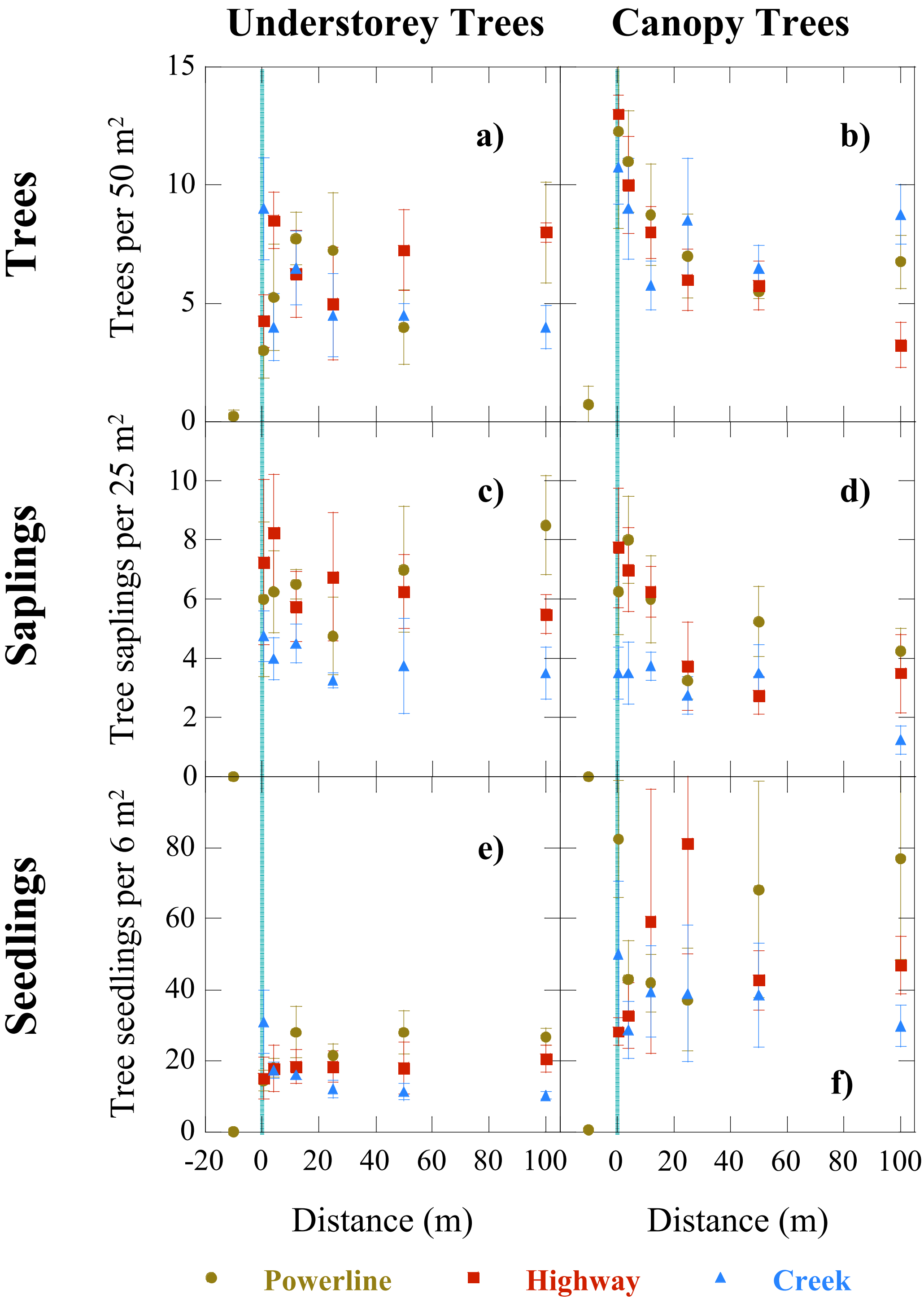


Figure 5.10. The abundance of understorey and canopy trees in tree (≥ 5 cm dbh), sapling (2 - 5 cm dbh) and seedling (< 2 cm dbh) size classes. Dashed vertical lines indicate the position of the forest edge.

The successional composition of understorey trees was altered near the forest edge. The proportion of early-successional understorey trees was greatest near creek edges although this effect was strongest in the two smallest size classes (2 – 5 cm dbh and < 2 cm dbh) (Table 5.5, Figure 5.11 c, f, i; Appendix 3) and greater near the forest edge than the forest interior overall (Table 5.5). Along highway edges, however, there were no early-successional tree-sized individuals (Figure 5.11b) but the proportion of early-successional saplings and seedlings increased towards the forest edge (Figure 5.11 e, h). The proportion of late-successional understorey trees was less near creek edges and powerline edges than near highway edges (Table 5.5, Figure 5.11; Appendix 3). The proportion of late-successional understorey trees also varied with size class, decreasing from trees to the smaller size classes along creek transects and increasing from trees to the smaller size classes along powerline transects (Table 5.5, Figure 5.11).

The successional composition of canopy trees varied with distance from the forest edge and among edge types (Table 5.6, Figure 5.12). The proportion of early-successional canopy trees was greater near the forest edge than in the forest interior although this increase was most pronounced in the largest size class and was least pronounced amongst seedlings along highway and powerline transects (Table 5.6, Figure 5.12) and, in general, declined with decreasing size class (Figure 5.12). There were no systematic differences among edge types (Appendix 3). The proportion of mid-successional canopy trees was greatest along powerline transects (Bonferroni *post hoc* tests, creek > powerline, $p = 0.058$), greater near the forest edge than in the forest interior and greatest in the seedling size class (Bonferroni *post hoc* tests, $p = 0.002$) (Table 5.6, Figure 5.12). The proportion of late-successional canopy trees was less near the forest edge than in the forest interior, lower among seedlings than saplings (Bonferroni *post hoc* tests, seedlings < saplings, $p = 0.011$, seedlings < trees, $p = 0.347$), and less near powerline edges (Bonferroni *post hoc* tests, creek > powerline, $p = 0.005$, highway > powerline, $p = 0.006$) than highway or creek edges (Table 5.6, Figure 5.12).

Table 5.5. Successional Composition of Understorey Trees. These data were analysed with Kruskal-Wallis analyses. Significant effects are highlighted in bold and marginally-significant results are highlighted in italics.

Effect	**Parameter**	χ^2	**df**	***p*-value**
Edge Type	% early-successional	23.817	2	**< 0.001**
	% mid-successional	2.303	2	0.316
	% late-successional	17.964	2	**< 0.001**
Distance	% early-successional	20.508	5	**0.001**
	% mid-successional	5.603	5	0.347
	% late-successional	8.338	5	0.139
Size Class	% early-successional	10.868	2	**0.004**
	% mid-successional	4.847	2	*0.089*
	% late-successional	0.766	2	0.682
Edge Type * Distance	% early-successional	54.360	17	**< 0.001**
	% mid-successional	16.831	17	0.466
	% late-successional	40.198	17	**0.001**
Edge Type * Size Class	% early-successional	36.699	8	**< 0.001**
	% mid-successional	9.107	8	0.333
	% late-successional	22.010	8	**0.005**
Distance * Size Class	% early-successional	39.909	17	**0.001**
	% mid-successional	18.309	17	0.370
	% late-successional	15.005	17	0.595
Edge Type * Distance * Size Class	% early-successional	91.121	53	**0.001**
	% mid-successional	44.293	53	0.797
	% late-successional	62.538	53	0.174

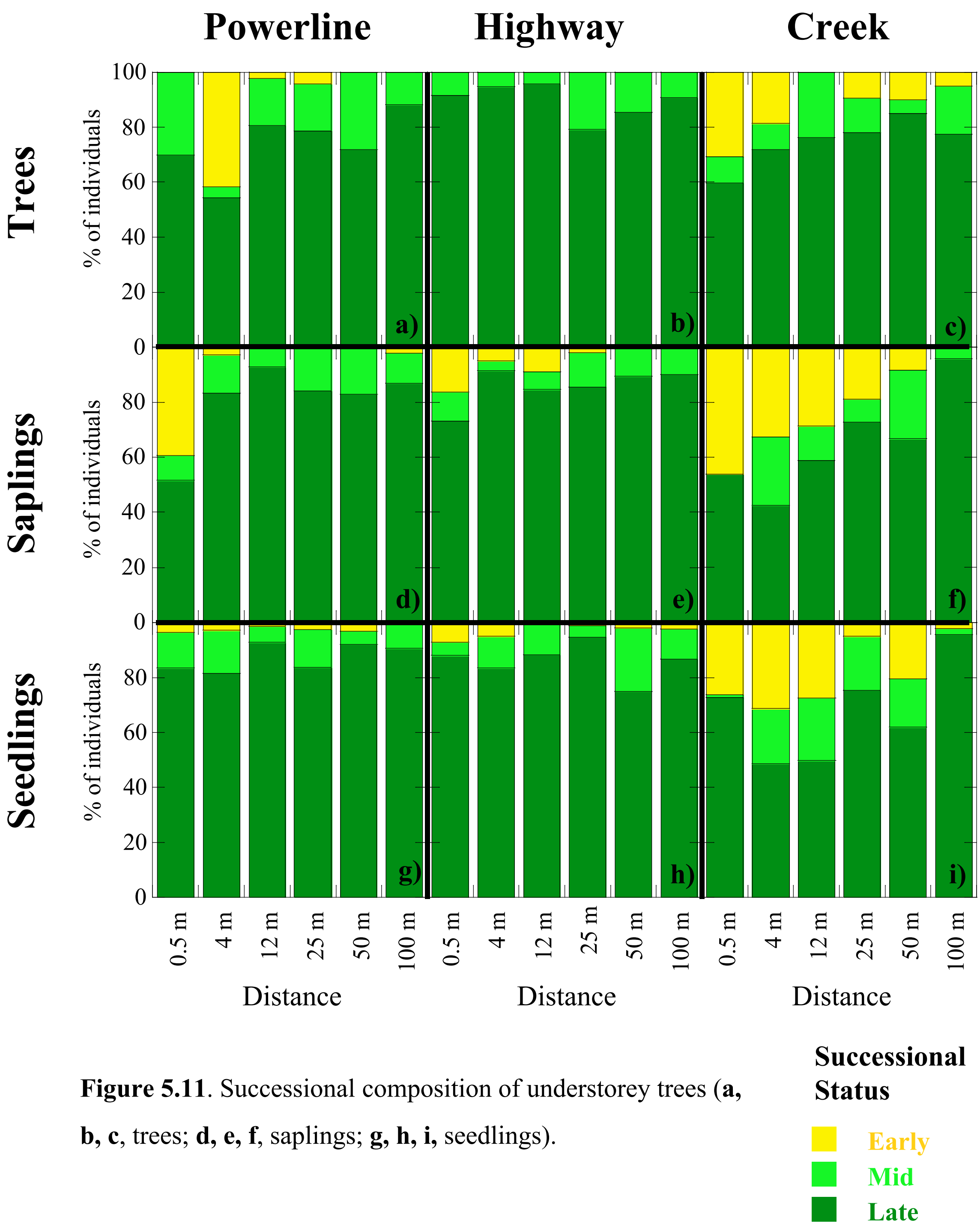


Figure 5.11. Successional composition of understorey trees (**a, b, c**, trees; **d, e, f**, saplings; **g, h, i,** seedlings).

Table 5.6. Successional Composition of Canopy Trees. Data for % mid-successional and % late-successional canopy trees were analysed with ANOVA and data for % early-successional canopy trees were analysed using Kruskal-Wallis analyses. Significant effects are highlighted in bold and marginally-significant results are highlighted in italics.

Effect	**Parameter**	***F*** **(or χ^2)**	**df**	***p*-value**
Edge Type	% early-successional	4.628 (χ^2)	2	*0.099*
	% mid-successional	3.334	2	**0.038**
	% late-successional	7.209	2	**0.001**
Distance	% early-successional	39.393 (χ^2)	5	**< 0.001**
	% mid-successional	4.078	5	**0.002**
	% late-successional	15.564	5	**< 0.001**
Size Class	% early-successional	8.996 (χ^2)	2	**0.011**
	% mid-successional	8.216	2	**< 0.001**
	% late-successional	5.015	2	**0.008**
Edge Type * Distance	% early-successional	55.676 (χ^2)	17	**< 0.001**
	% mid-successional	1.684	10	*0.089*
	% late-successional	1.847	10	*0.057*
Edge Type * Size Class	% early-successional	14.686 (χ^2)	8	*0.066*
	% mid-successional	0.603	4	0.661
	% late-successional	0.895	4	0.468
Distance * Size Class	% early-successional	55.963 (χ^2)	17	**< 0.001**
	% mid-successional	0.627	10	0.789
	% late-successional	0.765	10	0.662
Edge Type * Distance * Size Class	% early-successional	84.909 (χ^2)	53	**0.004**
	% mid-successional	0.653	20	0.867
	% late-successional	0.623	20	0.891

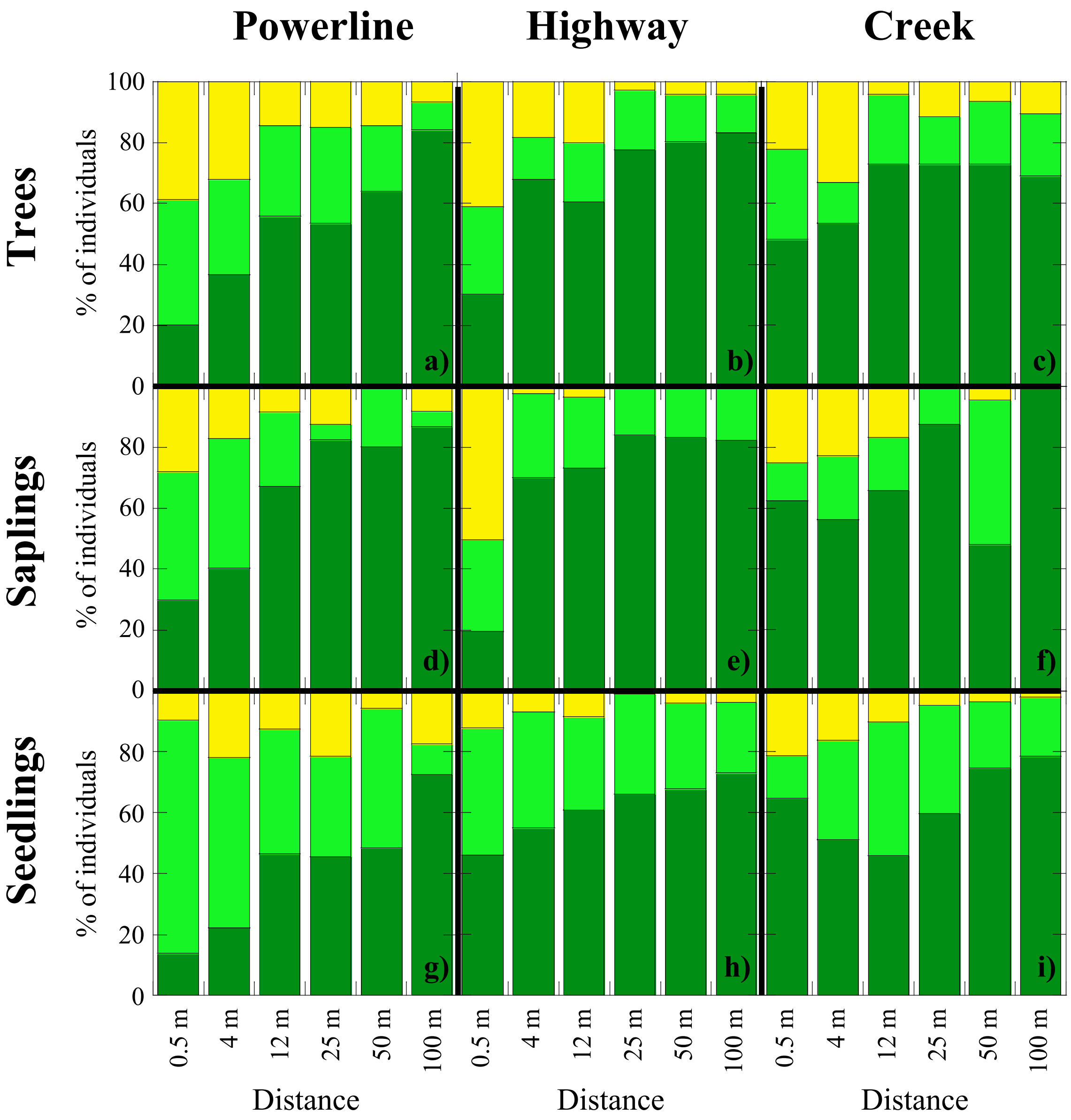


Figure 5.12. Successional composition of canopy trees (**a, b, c**, trees; **d, e, f**, saplings; **g, h, i,** seedlings).

5.3.2.2 Diaspore Size and Dispersal Mode.

The abundance of individual trees and lianas ≥ 5 cm dbh from small-fruited (< 1.0 cm width) species which are dispersed by animals increased towards the forest edge (Table 5.7, Figure 5.13, a, b, c) as did the abundance of small-fruited, abiotically-dispersed species although this increase was only marginally significant (Table 5.7, Figure 5.13 a, b, c). The abundance of large-fruited, abiotically-dispersed species was lower along creek transects than along powerline (Bonferroni *post hoc* test, $p = 0.038$) or highway transects (Bonferroni *post hoc* test, $p = 0.092$; Table 5.7, Figure 5.13 a, b, c). The abundance of intermediate-fruited, biotically-dispersed species was marginally less along creek transects than along powerline transects (Bonferroni *post hoc* test, $p = 0.081$; Table 5.7, Figure 5.13 a, b, c).

Among saplings and lianas with stems 2 – 5 cm dbh, the abundance of individuals from small-fruited, biotically-dispersed species and large-fruited (> 2.0 cm width) biotically-dispersed species also increased towards the edge of the forest (Table 5.7, Figure 5.13 d, e, f). Similarly, the abundance of biotically-dispersed species with intermediate-size fruit was less along creek transects than along powerline transects (Table 5.7; Figure 5.13 d, e, f; Bonferroni *post hoc* test, $p = 0.002$). The abundance of saplings and lianas 2 – 5 cm dbh from biotically-dispersed, large-fruited species was also least along creek transects and greatest along powerline transects (Table 5.7; Figure 5.13 d, e, f; Bonferroni *post hoc* tests, creek < powerline, $p < 0.001$, creek < highway, $p = 0.095$, highway < powerline, $p = 0.073$) and greater near the forest edge than in the forest interior (Table 5.7, Figure 5.13 d, e, f).

Among seedling-sized stems < 2 cm dbh, the abundance of individuals from intermediate-fruited (1.0 – 2.0 cm width) biotically-dispersed species was greater along powerline transects than along highway or creek transects (Table 5.7, Figure 5.13 g, h, i; Bonferroni *post hoc* tests, creek < powerline, $p = 0.003$, highway < powerline, $p = 0.060$) and there was a significant interaction between distance and edge type (Table 5.7) such that abundance was reduced near highway edges relative to the forest interior (Figure 5.13h; one-way ANOVA within highway transects, effect of distance, $F = 3.907$, $p = 0.014$) but was not affected by proximity to the edges of either powerlines (one-way ANOVA, $F = 1.067$, $p = 0.411$) or creeks (one-way ANOVA, $F = 1.532$, $p = 0.230$). The abundance of individuals from small-fruited, abiotically-dispersed species increased towards the forest edge and was greater along creek transects than along powerline or highway transects (Table 5.7, Figure 5.13 g, h, i; Bonferroni *post hoc* tests of edge type differences, $p < 0.001$). Ferns, which increase at creek edges (Figure 5.7b), fall within this dispersal category and may have been responsible for these results; however, when ferns were removed from the analysis, the effects of edge type and distance were maintained although weakened (*ln* (1 + {small abiotic – ferns}), edge type $F = 2.899$, df = 2, $p = 0.064$ [creek > powerline, Bonferroni *post hoc* tests, $p = 0.044$]; distance, $F = 4.286$, $p = 0.002$; edge type * distance, $F = 0.184$, $p = 0.997$). The abundance of species with small, biotically-dispersed fruits increased with proximity to the forest edge (Table 5.7, Figure 5.13 g, h, i) but was not affected by edge type (Table 5.7). In contrast, although the abundance of large-fruited, biotically-dispersed species was lower along creek transects than along powerline transects (Table 5.7; Figure 5.13 g, h, i; Bonferroni *post hoc* test, $p = 0.002$), it was not affected by proximity to the forest edge (Table 5.7).

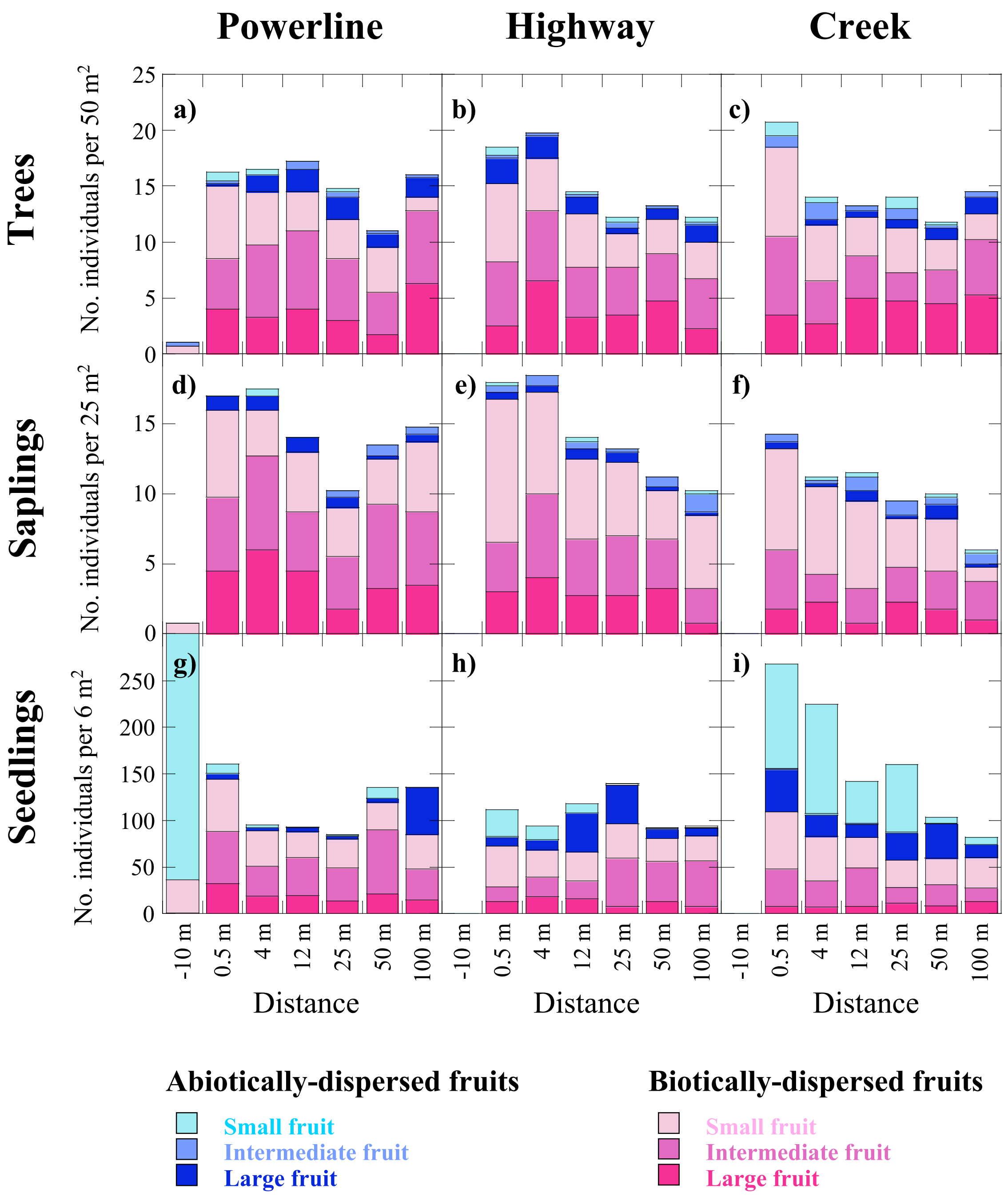


Figure 5.13. The abundances of individuals (**a, b, c**, dbh ≥ 5 cm; **d, e, f**, dbh 2 - 5 cm; **g, h, i**, dbh < 2 cm) with small (width < 1.0 cm), intermediate (width 1.0 - 2.0 cm) and large (width > 2.0 cm) diaspores, divided into species with biotic and abiotic dispersal of diaspores.

Table 5.7. Abundances of individuals with differing diaspore sizes and dispersal modes. Diaspore size classes are small (width < 1.0 cm), intermediate (width 1.0 – 2.0 cm) and large (width > 2.0 cm) and dispersal modes are divided into abiotic and biotic. Data were analysed with ANOVA. Significant results are highlighted in bold and marginally significant results are highlighted in italics.

Size Class	**Effect**	**Parameter**	***F***	**df**	***p*-value**
> 5 cm dbh	Edge Type	Abiotic, small fruits	0.521	2	0.597
		Abiotic, intermediate fruits	2.267	2	0.113
		Abiotic, large fruits	3.900	2	**0.026**
		Biotic, small fruits	0.794	2	0.457
		Biotic, intermediate fruits	2.666	2	*0.079*
		Biotic, large fruits	1.092	2	0.343
	Distance	Abiotic, small fruits	2.156	5	*0.073*
		Abiotic, intermediate fruits	0.350	5	0.880
		Abiotic, large fruits	1.373	5	0.249
		Biotic, small fruits	3.211	5	**0.013**
		Biotic, intermediate fruits	1.266	5	0.292
		Biotic, large fruits	0.820	5	0.541
	Edge Type * Distance	Abiotic, small fruits	0.445	10	0.917
		Abiotic, intermediate fruits	0.711	10	0.710
		Abiotic, large fruits	1.211	10	0.305
		Biotic, small fruits	0.458	10	0.910
		Biotic, intermediate fruits	0.974	10	0.477
		Biotic, large fruits	1.823	10	*0.078*
2 – 5 cm dbh	Edge Type	Abiotic, small fruits	0.464	2	0.631
		Abiotic, intermediate fruits	1.512	2	0.230
		Abiotic, large fruits	0.391	2	0.678
		Biotic, small fruits	2.374	2	0.103
		Biotic, intermediate fruits	6.694	2	**0.003**
		Biotic, large fruits	10.227	2	**<0.001**
	Distance	Abiotic, small fruits	0.555	5	0.734
		Abiotic, intermediate fruits	0.711	5	0.618
		Abiotic, large fruits	0.495	5	0.779

Size Class	**Effect**	**Parameter**	***F***	**df**	***p*-value**
	Distance (*cont.*)	Biotic, small fruits	2.751	5	**0.028**
		Biotic, intermediate fruits	0.386	5	0.856
		Biotic, large fruits	3.180	5	**0.014**
	Edge Type * Distance	Abiotic, small fruits	0.655	10	0.760
		Abiotic, intermediate fruits	0.515	10	0.872
		Abiotic, large fruits	0.514	10	0.873
		Biotic, small fruits	1.237	10	0.289
		Biotic, intermediate fruits	0.802	10	0.627
		Biotic, large fruits	1.607	10	0.130
< 2 cm dbh	Edge Type	Abiotic, small fruits	29.506	2	**< 0.001**
		Abiotic, intermediate fruits	1.210	2	0.306
		Abiotic, large fruits	2.986	2	*0.059*
		Biotic, small fruits	0.583	2	0.562
		Biotic, intermediate fruits	6.194	2	**0.004**
		Biotic, large fruits	6.771	2	**0.002**
	Distance	Abiotic, small fruits	5.244	5	**0.001**
		Abiotic, intermediate fruits	0.994	5	0.430
		Abiotic, large fruits	0.379	5	0.861
		Biotic, small fruits	3.424	5	**0.009**
		Biotic, intermediate fruits	0.615	5	0.689
		Biotic, large fruits	0.317	5	0.901
	Edge Type * Distance	Abiotic, small fruits	1.624	10	0.125
		Abiotic, intermediate fruits	1.203	10	0.310
		Abiotic, large fruits	0.420	10	0.931
		Biotic, small fruits	0.386	10	0.948
		Biotic, intermediate fruits	3.165	10	**0.003**
		Biotic, large fruits	0.905	10	0.535

5.3.2.3 *Seedling Size Distribution*

Loglinear analyses revealed that there was a smaller proportion of small shrubs near the forest edge than in the forest interior (distance * size class, $\chi^2 = 34.841$, df = 6, $p < 0.0001$; Figure 5.14) and more small shrubs and fewer larger shrubs along creek transects than along powerline or highway transects (edge type * size class, $\chi^2 = 22.538$, df = 6, $p = 0.0010$; Figure 5.14). For understorey tree seedlings, the proportion of small seedlings (< 20 cm tall and/or < 3 mm diameter) increased towards creek edges and decreased towards powerline edges and declined very slightly towards highway edges (height: edge type * distance * size class $\chi^2 = 47.233$, df = 30, $p = 0.0236$; basal diameter: edge type * distance * size class $\chi^2 = 66.488$, df = 30, $p = 0.0001$; Figure 5.15). For canopy tree seedlings, the proportion of small seedlings marginally increased at the edge of creek transects, towards the interior and on the very edge of powerline transects and at intermediate distances along highway transects (height: edge type * distance * size class $\chi^2 = 114.263$, df = 20, $p < 0.0001$; basal diameter: edge type * distance * size class $\chi^2 = 121.109$, df =30, $p < 0.0001$; Figure 5.16). The proportion of larger canopy tree seedlings also increased towards the powerline edge (Figure 5.16 a and d).

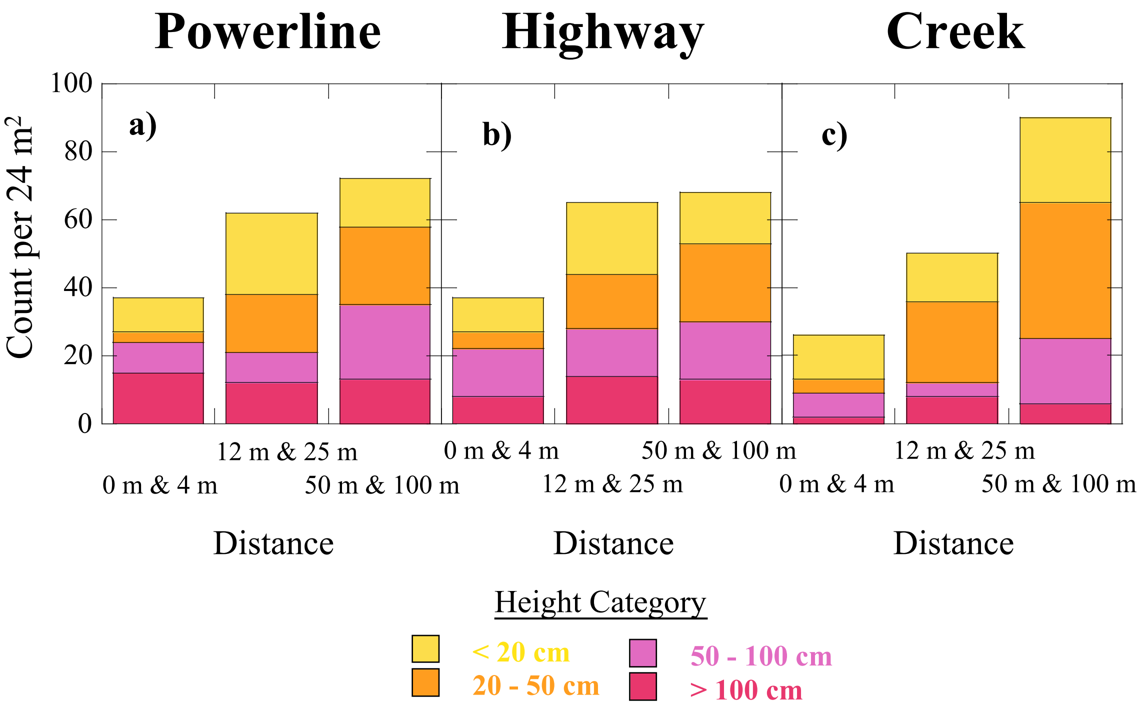


Figure 5.14. Size distribution of shrubs < 2 dbh for **a**) powerlines, **b**) highways and **c**) creeks. Numbers are total counts pooled across all four transects per edge type.

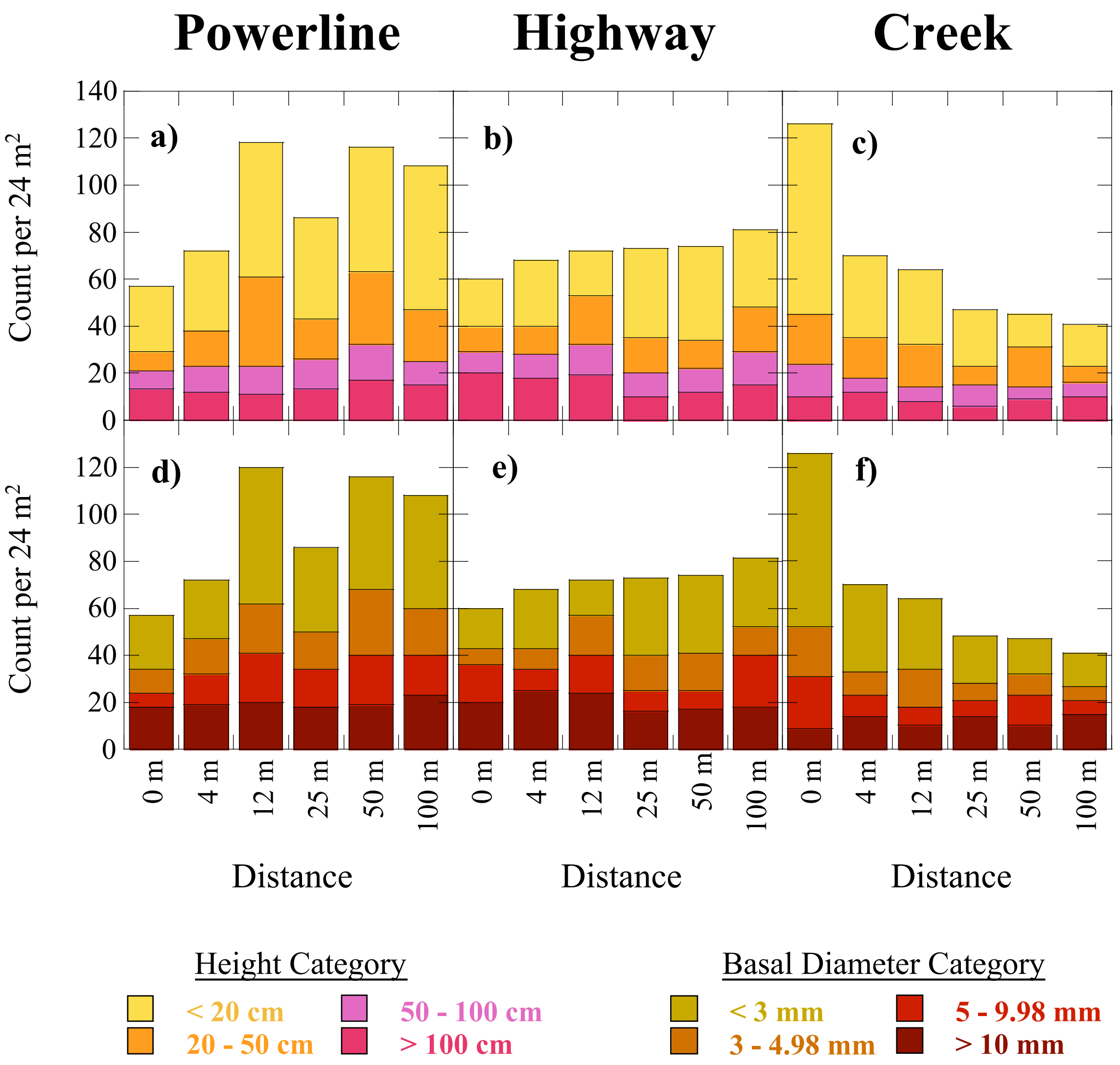


Figure 5.15. Size distribution of understorey tree seedlings < 2 dbh for powerlines (**a** and **d**), highways (**b** and **e**) and creeks (**c** and **f**). Numbers are total counts pooled across all four transects per edge type. Data has been divided into height categories and basal diameter categories.

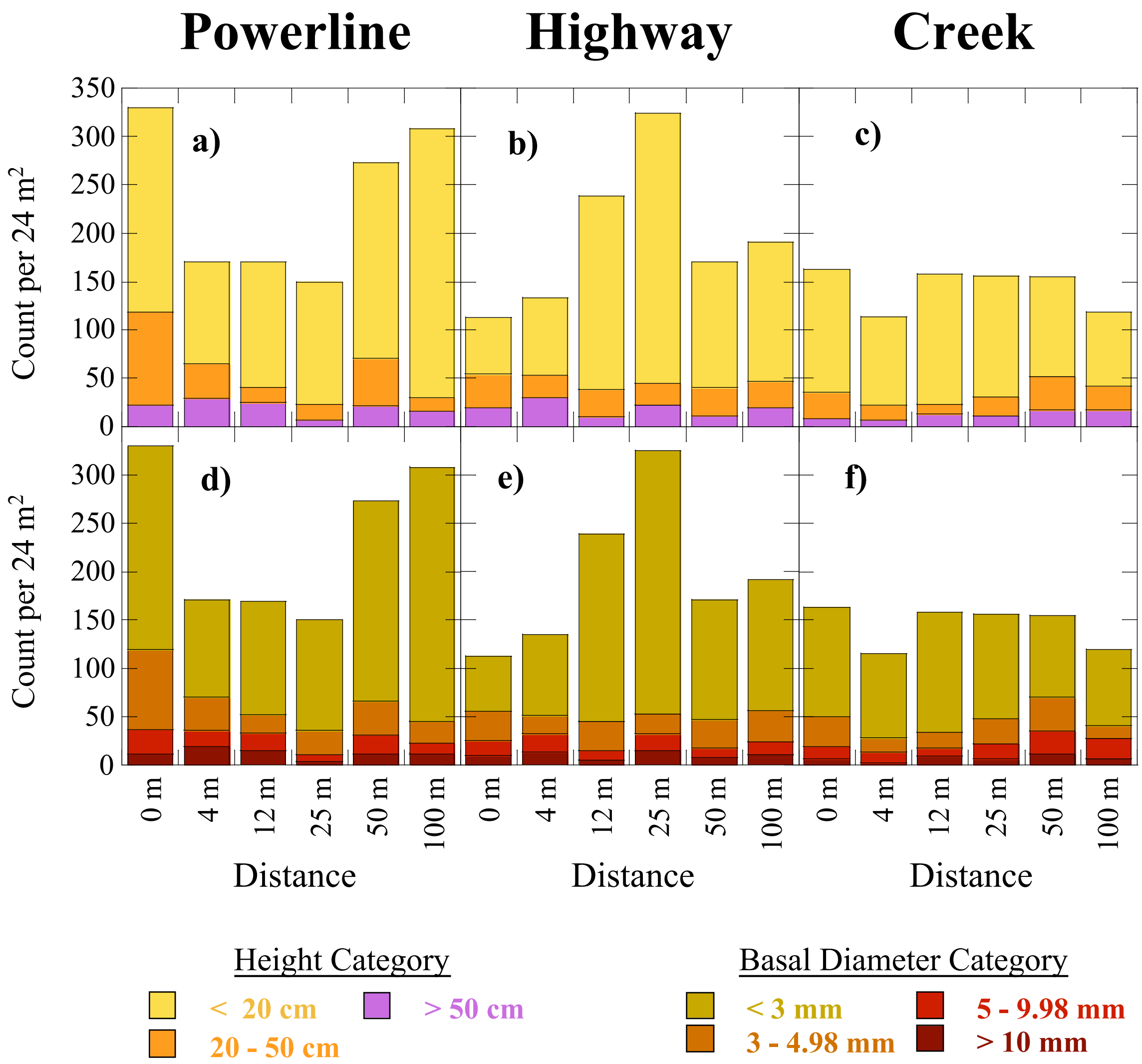


Figure 5.16. Size distribution of canopy tree seedlings < 2 dbh for powerlines (**a** and **d**), highways (**b** and **e**) and creeks (**c** and **f**). Numbers are total counts pooled across all four transects per edge type. Data has been divided into height categories and basal diameter categories.

5.3.3 Seedling Species Composition and the Understorey Light Environment

The abundances of a number of plant functional groups were correlated with the understorey light environment as measured with the red:far red ratio. In most (but not all) cases, where a significant correlation with red:far red ratio was detected, a correlation with distance was also detected (Table 5.8). The correlations between distance from the forest edge and abundance of small stems (< 2 cm dbh) in individual 1 m^2 quadrats were consistent with the distance effects detected on a per-transect basis for the abundances or proportions of different functional groups (Section 5.3.2.1), with few exceptions; these being early-successional canopy trees, late-successional understorey trees and late-successional canopy trees. However, the previous analyses of these particular groups were of the proportions, rather than the absolute abundance, of understorey trees and canopy trees represented by different successional categories, at different distances from the forest edge. Discrepancies between analyses based on proportions and abundances might have been caused by changes in the absolute numbers of canopy tree seedlings and understorey tree seedlings with distance from the edge, however, no such distance effects were detected (Table 5.4). The per-transect abundance of understorey tree seedlings appeared to decrease near powerline and highway edges and increase near creek edges (Figure 5.9e), which may have masked any significant effects in the previous analysis. The total abundances of understorey tree seedlings and canopy tree seedlings were also negatively correlated with red:far red ratio (Spearman's rank correlation; understorey tree seedlings –0.238, $p < 0.001$; canopy tree seedlings –0.152, $p = 0.001$).

The abundances of weeds, grasses, woody lianas, terrestrial ferns, early-successional herbs and early-successional understorey trees were positively correlated with the red:far red ratio and negatively correlated with distance from the forest edge whilst the abundances of late-successional shrubs and late-successional understorey trees were negatively correlated with the red:far red ratio and positively correlated with distance from the edge. The abundances of climbing herbs, climbing ferns, mid-successional herbs, late-successional herbs, early-successional shrubs, mid-successional shrubs, mid-successional understorey trees and all successional groups of canopy trees were either uncorrelated with the red:far red ratio or displayed correlations on one edge type only (Table 5.8). Functional groups that were positively correlated with red:far red ratio tended to increase towards the forest edge whilst functional groups which displayed negative correlations with the red:far red ratio tended to decrease towards the forest edge (Table 5.8). Not all functional groups that displayed edge gradients, however, were correlated with the red:far red ratio. For example, late successional canopy tree seedlings were positively correlated with distance from the edge but were not correlated with red:far red ratio.

Table 5.8. Spearman Rank Correlations between the abundance of seedlings in different vegetation functional groups and the red:far red ratio and distance from the forest edge. These results are for seedling abundances within individual seedling quadrats (1m * 1m). Quadrats within powerline clearings (distance –10 m) were not included in these analyses. Significant correlations are indicated (* $\alpha < 0.05$, ** $\alpha < 0.01$, *** $\alpha < 0.001$; marginally significant, † $\alpha < 0.1$).

Functional Group	**Red:Far Red Ratio Correlation**	**Distance Correlation**
Weeds		
Overall	0.178***	-0.233***
Powerline	-0.122	-0.122
Highway	0.303***	-0.351***
Creek	0.197*	-0.174*
All grasses		
Overall	0.224***	-0.237***
Powerline	0.173*	-0.174*
Highway	0.227**	-0.204*
Creek	0.205*	-0.321***
Native Grasses only		
Overall	0.202***	-0.235***
Powerline	0.173*	-0.174*
Highway	0.155†	-0.198*
Creek	0.205*	-0.321***
Large woody vines		
Overall	0.156***	-0.116*
Powerline	0.083	-0.057
Highway	0.161†	-0.025
Creek	0.049	-0.280***

Functional Group	**Red:Far Red Ratio Correlation**	**Distance Correlation**
Slender vines		
Overall	0.297***	-0.297***
Powerline	0.143†	-0.330***
Highway	0.272***	-0.236**
Creek	0.110	-0.334***
Climbing herbs		
Overall	0.089	-0.040
Powerline	0.009	0.102
Highway	0.039	0.132
Creek	0.170*	-0.307***
Climbing ferns		
Overall	0.083	-0.100*
Powerline	NA	NA
Highway	-0.058	-0.016
Creek	0.168*	-0.200*
Terrestrial ferns		
Overall	0.258***	-0.250***
Powerline	0.224**	-0.189*
Highway	0.038	-0.120
Creek	0.150†	-0.445***
Early-successional herbs		
Overall	0.224***	-0.249***
Powerline	0.199*	-0.286***
Highway	0.165*	-0.067
Creek	0.334***	-0.360***
Mid-successional herbs		
Overall	0.060	-0.025
Powerline	0.033	0.033
Highway	0.015	-0.152†
Creek	0.079	0.038

Functional Group	**Red:Far Red Ratio Correlation**	**Distance Correlation**
Late-successional herbs		
Overall	-0.063	0.086
Powerline	0.028	-0.024
Highway	-0.032	0.026
Creek	-0.255**	0.178*
Early-successional shrubs		
Overall	0.035	-0.066
Powerline	0.015	-0.167*
Highway	0.111	-0.214**
Creek	-0.045	0.173*
Mid-successional shrubs		
Overall	-0.049	-0.023
Powerline	-0.128	0.024
Highway	0.052	-0.025
Creek	-0.138†	-0.073
Late-successional shrubs		
Overall	-0.114*	0.269***
Powerline	-0.054	0.344***
Highway	-0.180*	0.205*
Creek	0.013	0.264***
Early-successional understorey trees		
Overall	0.200**	-0.187***
Powerline	0.045	-0.008
Highway	0.088	-0.074
Creek	0.246**	-0.380***
Mid-successional understorey trees		
Overall	-0.006	0.003
Powerline	-0.031	0.005
Highway	0.003	0.081
Creek	-0.067	-0.077

Functional Group	**Red:Far Red Ratio Correlation**	**Distance Correlation**
Late-successional understorey trees		
Overall	-0.208***	0.100*
Powerline	-0.173*	0.278***
Highway	-0.248**	0.157†
Creek	0.073	-0.133
Early-successional canopy trees		
Overall	-0.004	-0.149**
Powerline	-0.082	0.011
Highway	0.074	-0.094
Creek	0.128	-0.396***
Mid-successional canopy trees		
Overall	-0.032	-0.076
Powerline	0.050	-0.258**
Highway	0.040	0.148†
Creek	-0.045	-0.116
Late-successional canopy trees		
Overall	-0.072	0.220***
Powerline	-0.052	0.230**
Highway	-0.069	0.329***
Creek	-0.063	0.086

5.4 Discussion

5.4.1. Vegetation Structure and Species Diversity

5.4.1.1. Is Vegetation Structure Altered Near the Forest Edge?

Vegetation structure has been altered near the edges of linear canopy openings; both liana and tree densities and total stem density were greater near the forest edge than in the forest interior. These changes were dependent on the type of linear canopy opening. For example, total stem density was greater near the forest edge than in the forest interior but creek transects had fewer stems in the 'sapling' size range (2 – 5 cm dbh) and more stems in the 'seedling' size class (< 2 cm dbh) than powerline or highway transects. The abundance of lianas < 5 cm diameter was also elevated near the forest edge and was greater along creek transects than powerline or highway transects. There was a larger proportion of small (< 10 cm dbh) and intermediate-sized (10 – 30 cm dbh) trees near the forest edge than in the forest interior and a greater proportion of intermediate-sized and large (> 30 cm dbh) trees along creek transects than along powerline and highway transects as well as a greater proportion of large trees along highway transects than powerline transects.

The increased abundance of small and intermediate trees and stems 2 – 5 cm dbh is consistent with other edge studies in tropical and temperate forests where increased recruitment due to elevated canopy disturbance and light availability (Laurance *et al.* 1998b) resulted in a greater abundance of saplings and small trees near the forest edge (Williams-Linera 1990a; Harper and Macdonald 2002). The lower proportion of large trees at the edge suggests that there might be an increase in the mortality of larger trees similar to that observed in forest fragment studies (Laurance *et al.* 2000; Harper *et al.* 2005) but other data in this study do not support that conclusion (Chapter 6). Similar shifts toward smaller tree diameters have been observed near road edges in subalpine coniferous forest in Japan (Nagaike 2003) and tropical rainforest in Africa (Malcolm and Ray 2000) although sapling density increased near the road edge in Japan but decreased near road edges in Africa (Malcolm and Ray 2000; Nagaike 2003) and, in both cases, these structural changes were attributed to greater disturbance of the forest canopy near the road edge.

The increased abundance of slender vines < 5 cm diameter at the edges of linear canopy openings is consistent with similar increases observed at the edges of tropical forest fragments (eg Williams-Linera 1990a; Laurance 1997a; Laurance *et al.* 1997, 2001a). The lack of an edge effect in the abundance of lianas ≥ 5 cm diameter, in combination with the increased abundance of smaller vines (and consequent lower proportion of larger vines relative to smaller vines near the forest edge) is also consistent with the lower proportion of large lianas near Amazonian fragment edges (Laurance *et al.* 2001a) and suggests that a similar positive relationship between liana abundance and edge-related disturbance may be operating near linear canopy openings. It is also possible that there has been insufficient time for the growth of an elevated abundance of large lianas at the forest edge. However, the edge patterns detected by Laurance *et al.* (2001a) had developed in forest fragments isolated for less than 20 years, which is comparable with the age of the current powerline and highway edges in this study (~15 years). Vines are thought to be favoured by disturbance as disturbed areas of forest offer a profusion of smaller trees and saplings which vines require for climbing support (Putz 1984). Additionally, the deeper root systems and highly efficient vascular systems of lianas may allow them to take greater advantage of the elevated light levels in disturbed forest whilst being less affected by reduced moisture availability than the seedlings of trees and shrubs (Schnitzer 2005). The increased abundance of lianas near the edges of linear canopy openings may thus be a consequence of increased disturbance near the forest edge.

The lower abundance of smaller trees and stems 2 – 5 cm dbh and the higher abundances of stems < 2 cm dbh and of lianas < 5 cm diameter along creek transects, as compared to powerline and highway transects, is intriguing. It is possible that smaller trees and saplings may be more vulnerable to periodic flooding (Hupp and Osterkamp 1996; Nakamura *et al.* 1997; Robertson and Augspurger 1999; Turner *et al.* 2004; Sabo *et al.* 2005) that larger trees with more advanced root systems may be able to withstand. The existence of edge gradients in tree and sapling density similar to (though lesser than) those found near powerlines and highways indicates that there has been sufficient time since the last moderate-to-severe flooding event for these gradients to become re-established although not for the edge to become “sealed” to the same extent as anthropogenic edges (see also Chapter 4). The higher light availability near creek edges (Chapter 4) may thus be a consequence of a diminished midstorey, which seems also likely to be responsible for the increased abundance of lianas and stems < 2 cm dbh along creek edges (as compared with anthropogenic edges).

5.4.1.2. Is Above-Ground Biomass Lower Near the Forest Edge?

Total basal area was not affected by proximity to the forest edge; the generally smaller size negated the greater number of trees at the edge. Similarly, the above-ground biomass of trees ≥ 5 cm dbh was not lower near the forest edge although biomass was lower along powerline transects than highway or creek transects possibly due to the lower proportion of large trees along powerline transects as compared to creek transects. Although wood density may be as much as 25% lower in small trees than in large trees (Dr Steve Goosem, *pers. comm.*) and there was a predominance of smaller trees near the forest edge, a 25% reduction in biomass at the edge would not be sufficient to lower the above-ground biomass of trees ≥ 5 cm dbh below that found in the forest interior. Thus, in contrast to the results reported for forest fragments in the Amazon (Laurance *et al.* 1997), above-ground tree biomass was not reduced at the edges of linear canopy openings in my study area. In the Amazonian study, a large amount of biomass near forest edges was lost due to the disproportionately high mortality rate of large trees (≥ 60 cm dbh), which contain a large fraction of the total above-ground biomass (Laurance *et al.* 2000). In this study, although there was a reduced proportion of larger trees (≥ 30 cm dbh) near the edge, large trees did not appear to suffer a disproportionate mortality risk near the forest edge (Chapter 6).

5.4.1.3. Is Species Diversity Greater Near the Forest Edge?

The species diversity of stems 2 – 5 cm dbh was greater near the edges of linear canopy openings than in the forest interior and less along creek transects than powerline or highway transects. In contrast, the species diversity of stems ≥ 5cm dbh and < 2 cm dbh was unaffected by proximity to the forest edge. Although increased species diversity is frequently reported near forest edges (eg Fox *et al.* 1997; Gehlhausen *et al.* 2000; Guirado *et al*. 2006), this is often caused by the intrusion of exotic or generalist species from the surrounding matrix (Fox *et al.* 1997; Gascon *et al.* 2000; Guirado *et al*. 2006; Kupfer *et al.* 2006). Although there was some intrusion of exotic species into the forest in the seedling size class (< 2 cm dbh), there were very few exotic species in the sapling size class (2 – 5 cm dbh) thus the intrusion of exotic species cannot explain the increased sapling diversity near forest edges. Additionally, differences in species dominance did not explain differences in diversity as species evenness (J; Zar 1999) did not differ between the forest edge and the forest interior for any size class. Alternatively, increased species diversity may be a consequence of increased abundance

(Denslow 1995; Hubbell *et al.* 1999). However, if increased stem abundance alone were responsible for the increase in diversity of stems 2 – 5 cm dbh, it is curious that the elevated abundance of large (≥ 5 cm dbh) and small (< 2 cm dbh) stems did not also produce similar increases in species diversity near the forest edge. The lower diversity of stems 2 – 5 cm dbh along creek edges appears likely to be a result of lower stem density along creek transects. Studies of fragment edges have reported inconsistent edge changes in sapling species diversity, with diversity increasing in some studies and being unaffected in others (eg Malcolm and Ray 2000; Harper *et al.* 2005).

5.4.2. Functional Group Composition

5.4.2.1 Successional Status and Growth Habit.

The functional group composition of the rainforest understorey was altered near the edges of powerlines, highways and creeks. Abundance of herbs, grasses and weeds increased and shrub abundance decreased near the forest edge although the magnitude of these changes varied between edge types. Changes in herb and shrub abundance were only statistically significant on powerline and creek edges while alterations in weed and grass abundance were greatest on highway and creek edges. Weeds did not penetrate beyond the very edge (0.5 m) of the powerline although there were dense thickets of *Rubus alceifolius* (Rosaceae) along the forest edge and the powerline clearing itself was dominated by exotic grasses such as *Urochloa maxima* and *Melinus minutiflora* with occasional patches of *Lantana camara* (Verbenaceae). Near highways, weeds such as *R. alceifolius*, *L. camara* and *U. maxima* were found in large, well-lit gaps along the edge penetrating to within 12 m from the edge. In contrast, herbaceous weeds such as *Ageratum conyzoides* (Asteraceae) and *Sanchezia parvibracteata* (Acanthaceae) were found in very low abundances in well-lit microsites within 12 m of creek edges but exotic grasses were not found near creek edges. These differences in weed species abundance and edge penetration may relate to differences in types of edge disturbance and weed propagule pressure between highways, powerlines and creeks. Although powerlines and highways may both act as conduits for the movement of exotic species (Goosem 1997), regular highway maintenance may disturb the forest edge near highways more frequently than the forest edge is disturbed within powerline clearings (since the cessation of annual burning within the Palmerston powerline in the 1990s, the forest edge may have in fact encroached slightly into the clearing; Dr Miriam Goosem, *pers. comm.*). The high volume of traffic along the Palmerston highway may also be a source of propagules for exotic species (Goosem 2004). Similarly, weed propagules are likely to reach creek edges through dispersal via water (eg Jansson *et al.* 2005) whilst the higher light levels found near creek edges (possibly as a result of periodic flood disturbance) allow the germination and growth of these species (eg Fine 2002).

Abundance of ferns increased most strongly towards creek edges although this was largely driven by the increased abundance of the fern-ally, *Selaginella longipinna* (Selaginaceae). The increase in fern abundance near creek edges may be due to a combination of higher light availability and lower vapour pressure deficit (Chapter 4) as fern-allies often require moist environments for reproduction (Andrews 1990). The increase in vine abundance at the forest edge was largely attributable to increases in the abundance of woody lianas and slender vines rather than climbing herbs which consisted of mostly late-successional species from the genera *Freycinetia* (Pandanaceae), *Pothos* and *Rhaphidophora* (Araceae).

Changes in herb and shrub abundance appear to be mostly consistent with an increase in early-successional species and a decrease in late-successional species near forest edges (eg Laurance *et al.* 1998b; McDonald and Urban 2004) with weed species limited to the areas of highest light availability (Table 5.8). Native grasses, apparently preferring higher light environments (Table 5.8), appeared to occupy niche positions between the highest light environments where weeds dominated and the more shaded environment where other native species were predominant (*pers. obs.*) and were especially abundant along creek edges possibly due to the higher light levels near creek edges than near anthropogenic edges (Chapter 4).

Abundances of understorey trees, saplings and seedlings were not affected by proximity to the forest edge but species composition was altered with respect to distance from the edge, among edge types and between adults and juveniles. Proportions of individuals from early-and late-successional species were altered near the forest edge but the proportion of individuals from mid-successional species was unaffected. A greater proportion of early-successional individuals (and a correspondingly lower proportion of late-successional individuals) occurred along creek transects than along powerline or highway transects although the proportion of early-successional individuals tended to increase towards the forest edge for all three edge types. Very low proportions of early-successional individuals were found along highway transects; in fact, there were no early-successional understorey trees ≥ 5 cm dbh along highway transects and only a slight increase in the proportion of early-successional saplings and seedlings near the highway edge. Creek edges and powerline edges displayed opposing patterns of successional composition between trees, saplings and seedlings; the proportion of early-successional individuals declined near powerline edges and the proportion of late-successional individuals increased when adult and juvenile life-stages were compared. In contrast, proportions of early-successional individuals increased (and the proportion of late-successional individuals decreased) between adult and juvenile life-stages near creek edges. These data suggest that, for understorey trees, high light availability and periodic flood disturbance near creek edges are favouring the continued recruitment of early-successional species whilst increased foliage density and therefore lower light levels (Chapter 4) near powerline edges (presumably as a consequence of edge sealing; Harper *et al.* 2005) have led to declining recruitment of early-successional species following what may have been a pulse of increased recruitment near the time of edge creation. It is curious that this effect was stronger along powerline transects than highway transects as understorey light levels were similar near the edges of both types of anthropogenic feature. However, as there were no tree-sized early-successional understorey tree species near highway edges but the proportion of early-successional individuals was lower for seedlings than for saplings, it is likely that a similar effect of reduced early-successional recruitment following edge sealing has occurred.

The abundances of trees and saplings of canopy tree species were elevated and the species composition of seedlings, saplings and trees of canopy tree species was altered near the forest edge. The proportion of individuals from early-successional species increased and the proportion from late-successional species decreased towards the forest edge. However, in contrast to the understorey tree data, the strongest declines in the proportion of individuals from late-successional canopy tree species occurred on anthropogenic transects (with powerlines displaying greater declines than highways) rather than creek transects. Similarly, the proportion of individuals from mid-successional species increased with proximity to the edges of powerlines and highways but did not show clear patterns near creek edges. A general increase from adult to juvenile life-stages in the proportion of mid-successional individuals occurred, especially along powerline transects. Proportions of early-successional species increased towards the forest edge for all edge types and size classes except seedlings along powerline transects where no clear pattern was obvious. Proportions of early-successional individuals were, however, generally lower for seedlings than for saplings and trees. These data suggest that, for canopy trees near powerlines and highways, edge creation may have caused increased recruitment of early- and mid-successional species but that the recruitment of early-successional species may be declining over time whilst the recruitment of mid-successional species is increasing over time. It is surprising that these changes are stronger near anthropogenic edges, given that light availability is greatest along creek edges; however, as the abundances of canopy tree seedlings from early-, mid- and late-successional species were not correlated with light availability (Table 5.8), it may be that greater moisture stress near anthropogenic edges (Chapter 4) was the mechanism underlying the decrease in late successional seedlings and increase in mid-successional seedlings near anthropogenic edges.

The contrasting patterns of successional-group composition in understorey and canopy tree species near powerlines and highways are intriguing and suggest a possible course of events following anthropogenic edge creation. The increased proportion of early-successional species near the forest edge, and the declining proportions of early-successional understorey and canopy tree individuals in younger size classes near anthropogenic edges, suggest that there may have been an initial pulse of early-successional seedling recruitment soon after edge creation (*cf.* Harper *et al.* 2005) when these edges would have been structurally 'open' (*cf.* Kapos 1989), which declined as foliage density and the degree of edge sealing increased over time (Chapter 4; *cf.* Malcolm 1994; Didham and Lawton 1999). Decreased light availability would have reduced the germination and recruitment of light-demanding pioneer seedlings (Whitmore 1996) and the elevated tree and sapling density near the edge would have increased the mortality of early-successional seedlings and saplings via shading from over-topping trees and denser foliage (Condit *et al.* 1996; Thomas 1996; Wright *et al.* 2003). The higher proportion of early-successional canopy trees, as compared to early-successional understorey trees, may have resulted from an increased mortality of shaded understorey trees as they were overtaken by taller-growing individuals whilst early-successional canopy trees "escaped" this effect (Condit *et al.* 1996; Turner 2001; Wright *et al.* 2003).

Lower light availability near anthropogenic edges (as compared with creek edges) may be responsible for reduced germination and recruitment of early- and mid successional understorey tree species but it is curious that mid-successional canopy tree seedlings responded so strongly to proximity to the forest edge. The observed greater decline in relative abundance of late-successional canopy trees, as compared to late-successional understorey trees near anthropogenic edges, and the increase in mid-successional canopy trees near the forest edge, whilst mid-successional understorey trees were unaffected by proximity to the edge, are curious but consistent with the slower growth and greater potential for mortality by shading of shorter tree species (Condit *et al.* 1996; Thomas 1996; Turner 2001; Bohlman and O'Brien 2006), at least for individuals ≥ 5 cm dbh, which reach different relative positions within the forest canopy and subcanopy. Amongst seedlings and saplings, however, in non-pioneer tree species, there is a general trend towards slower maximum growth rates in shorter species than in taller species (Lieberman *et al.* 1985; Thomas 1996; Nascimento *et al.* 2005) and, as maximum growth rate is correlated with shade-tolerance (Kitajima 1994; Kobe 1999; Lusk and Del Pozo 2002), it follows that mid-successional understorey tree species may have lower growth rates and greater shade-tolerance than mid-successional canopy tree species. However, although this may explain why mid-successional understorey tree seedlings and saplings did not respond to edge proximity as strongly as mid-successional canopy seedlings and saplings, it does not explain the greater edge response of late-successional canopy tree seedlings and saplings as compared to late-successional understorey tree seedlings and saplings. Alternatively, as light availability (red:far red ratio) is correlated with the abundance of early- and late-successional understorey tree seedlings but not early- and late-successional canopy tree seedlings (Table 5.8), a different process may be driving changes in the species composition of canopy tree juveniles. For example, moisture stress is greater near anthropogenic edges than creek edges (Chapter 4; higher VPD and air temperature near anthropogenic edges than in the forest interior or near creek edges) although it is unclear whether moisture stress would differentially affect understorey and canopy tree juveniles (eg understorey trees were particularly susceptible to drought stress on Barro Colorado Island, Panama; Condit *et al.* 1996). Further studies of the light and moisture requirements of understorey and canopy seedlings would be required to determine whether or not this is the case.

5.4.2.2 Diaspore Size and Dispersal Mode.

Changes in the faunal community near the edges of linear canopy openings might translate into a lower abundance of large-fruited, biotically-dispersed plant species, if the dispersers of these fruits avoid the forest edge. However, the abundance of large-fruited, biotically-dispersed plants was not affected by distance from the edge for stems

≥ 5 cm dbh or stems < 2 cm dbh and was slightly greater near the edge for stems 2 – 5 cm dbh. The most notable alterations were the increase in the abundance of species with small, abiotically-dispersed diaspores in stems < 2 cm dbh near the edge and the general increase in small-fruited, biotically-dispersed species near the forest edge for all stem size classes, both of which tended to be strongest near creek edges. Abiotically-dispersed species with small diaspores include the fruits of some exotic herbaceous species, native and exotic grass seeds, some native herbaceous species (*Aneilema acuminatum* [Commelinaceae] and *Pseuderanthemum variable* [Acanthaceae]), some vine fruits (eg *Sageretia hamosa* and *Ventilago ecorollata* [Rhamnaceae], *Pararistolochia australopithecus* [Aristolochiaceae] and *Pandorea nervosa* [Bignoniaceae]) and some canopy tree species (free seeds of *Flindersia brayleyiana* [Rutaceae], *Cardwellia sublimis* [Proteaceae] and *Gessois biagiana* [Cunoniaceae]). Slightly elevated wind speeds near the forest edge, particularly near creek edges (Chapter 4, Figure 4.6), may assist in the dispersal of these diaspores as might flowing water (and occasional minor flooding) near creek edges (eg Jansson *et al.* 2005). The abundance of the species with abiotically-dispersed, small diaspores was highest near creek edges and lowest near powerline edges (even after fern species had been removed from the analysis). This suggests that greater maximum understorey wind speeds and dispersal via water may be important in the dispersal of these diaspores whilst higher weed species propagule pressure from traffic may also be influencing the abundance of these species near highway edges.

The increase in the abundance of small-fruited, biotically-dispersed species most likely reflects the shift towards more early- and mid-successional species near the forest edge as early-successional species tend to have smaller fruits than late-successional species (Osunkoya *et al.* 1994; Osunkoya 1996; Murray *et al.* 2005). However, it is also possible that the diaspores of these species are being further concentrated near the edge through bird dispersal if frugivorous birds spend disproportionate periods of time near forest edges. For example, in Neotropical rainforests, some frugivorous bird species can spend a greater proportion of time foraging in well-lit gap and edge environments (with potentially greater plant productivity and thus food resources) than in the forest interior (eg Restrepo *et al.* 1999; Armesto *et al.* 2001; Wunderle *et al.* 2005; but see Restrepo and Gomez 1998 and Laurance *et al.* 2003). These trends have not been specifically studied in Australian rainforests although two studies suggest that frugivorous birds capable of dispersing fruits up to ~28 mm wide are found in small fragments and near forest road edges (Warburton 1997; Mr Greg Dawe, *unpublished data*; Dr Andrew Dennis, *unpublished data*; Appendix 4). Additionally, although Southern Cassowaries (*Casuarius casuarius*; which disperse the largest rainforest fruits; Westcott *et al.* 2005) are not found in small forest fragments (Harrington *et al.* 1997), anecdotal evidence suggests that they do not avoid the edges of highways, powerlines or creeks (Dr Miriam Goosem, *pers. comm*., Mr Greg Dawe, *unpublished data*; and personal observations of cassowaries foraging near creek and powerline edges and scat sightings near highway edges) although the scatterhoarding Musky Rat-kangaroo (*Hypsiprimnodon moschatus*; which is known to scatterhoard the seeds of some large-fruited species; Dennis 2003) may tend to avoid forest near highway edges (Goosem 2004). Overall, these data do not support the hypothesis of reduced dispersal of larger-fruited species near the forest edge. Studies of the abundance of disperser species near the edges of linear canopy openings and comparisons of the rate of dispersal of fruits of different sizes near the edge and in the forest interior would be needed to further test this hypothesis.

5.4.3. Seedling Species Composition and the Understorey Light Environment

Light availability is one of the most important environmental factors influencing the distribution of species and composition of the plant community within tropical rainforests (eg Osunkoya *et al.* 1993; Whitmore 1996; Webb and Peart 2000; Capers *et al.* 2005). Consistent with this, functional groups which increased in abundance near the forest edge tended to also be positively correlated with red:far red ratio whilst functional groups which decreased in abundance near the edge tended to display negative correlations with red:far red ratio. Exceptions to these trends were early-, mid- and late-successional canopy tree seedlings which were correlated with distance from the edge but not with red:far red ratio.

These results suggest that elevated light availability near the forest edge (Chapter 4) is at least partly responsible for the altered abundances of weeds, grasses, herbs, shrubs, ferns, lianas and understorey trees although the mechanisms responsible for changes in the abundances of canopy tree seedlings are less clear. However, there was a greater proportion of small canopy tree seedlings (Figure 5.16) than small shrubs (Figure 5.15) or small understorey tree seedlings (Figure 5.14), and it is possible that clumps of recently-germinated canopy tree seedlings in the vicinity of parent trees may have obscured any patterns between abundance and light availability. Tree seedlings may germinate in a wide range of favourable and unfavourable microsites and suffer heavier mortality in unfavourable microsites, giving rise to clearer patterns of habitat associations in larger individuals than smaller individuals (Webb and Peart 2000). Alternatively, other mechanisms may have given rise to the edge patterns observed in canopy tree seedlings; eg, greater moisture stress near the edges of anthropogenic linear canopy openings may have led to higher seedling mortality rates in some species although a species' drought tolerance is not necessarily correlated with its successional status (Engelbrecht and Kursar 2003; Bunker and Carson 2005). Changes in rates of herbivory or pathogen infection may also have altered growth rates or survival rates of different species near the edge (Augspurger 1984; Osunkoya *et al.* 1993; Coley and Barone 1996; Benitez-Malvido and Lemus-Albor 2005). Further studies of these potential mechanisms would be required to determine whether any have contributed to the observed patterns of functional group abundance.

As seedling survival and growth of most species increases with increasing light level, at least within approximately 1 – 50% of full sunlight (Poorter 1999), species which decreased near the forest edge and displayed negative correlations with red:far red ratio are unlikely to directly suffer reductions in growth rate and survival with increasing light availability unless they include very shade-tolerant species that suffer declines in growth rate (and increased photoinhibition) at high light levels, relative to low to moderate light levels (Poorter 1999). It is possible that these negative correlations represent either secondary correlations with other abiotic parameters (eg increasing vapour pressure deficit; Chen *et al.* 1995) or an indirect effect of inter-specific competition on the abundance of late-successional species. For example, at low light levels (1 – 6 % of full sunlight), seedling species composition is influenced by differences in low-light survival rates, which are largely determined by inter-specific differences in light compensation points (Agyeman *et al.* 1999; Kobe 1999) while, at higher light levels, which are likely to be above the light compensation points of most species, differences in species' growth rates will influence species' competitive ranking such that faster growing species will tend to out-compete slower-growing, more shade tolerant species (Agyeman *et al.* 1999; Kobe 1999). Thus, reductions in the abundance of late-successional species at higher light levels may be an indirect result of increased competition with faster-growing, early-successional species. However, understorey light levels measured in this study were generally low (Chapter 4). Using the correlation between red:far red ratio and percent canopy transmittance developed by Capers and Chazdon (2004) for tropical wet forests in Costa Rica as an approximation, light levels measured in this study would have varied between 1% and ~4 %, relative to light intensity above the forest canopy, with occasional patches up to ~8%, especially along creek transects. At the lower light levels, many species may be at or near their light compensation points (Agyeman *et al.* 1999; Kobe 1999; Poorter 1999) and small increases in light level may have strong effects on seedling survival although the range of light levels may be too small to allow growth rate and competitive differences between early-, mid- and late-successional species to be fully expressed (Agyeman *et al.* 1999; Kobe 1999; Poorter 1999). Even the higher light levels experienced along creek edges may not be sufficient to allow the maximum growth rates of any tree species (Agyeman *et al.* 1999; Kobe 1999; Poorter 1999) although the approximate upper light level of 8% full sunlight would likely be greater than the light compensation point of many early-successional species (Davies 1998; Agyeman *et al.* 1999; Kobe 1999; Baker *et al.* 2003). This suggests that differences in survival rates, rather than growth rates, may be largely responsible for edge patterns in seedling species composition. Alternatively, if tree-fall rates are elevated near the forest edge (Chapter 6, Figure 6.2), elevated light levels within canopy gaps and recovering canopy gaps (Chapter 6, Figure 6.4; Chapter 4, Figure 4.9) will be more prevalent near the forest edge, and may provide more opportunities for 'growth release' (a period of faster seedling or sapling growth that begins with gap creation and ends after the canopy has recovered; Clark and Clark 2001; Brienen and Zuidema 2006) of seedlings and saplings near the forest edge than in the forest interior. Such a pattern might also act to obscure correlations between current light levels and seedling species composition (*cf.* Nicotra *et al.* 1999).

5.4.4. Synthesis.

Forest structure and plant species composition were altered near the edges of linear canopy openings, relative to the forest interior. Structural changes (increased stem density, increased liana abundance, higher proportion of smaller trees) are consistent with those observed near forest fragment edges (Williams-Linera 1990a; Laurance *et al.* 2001a; Harper and Macdonald 2002; Nagaike 2003). The lower proportion of small trees (< 10 cm dbh) and stems 2 – 5 cm dbh along creek transects, relative to anthropogenic transects, suggests that smaller individuals may be more vulnerable to periodic flood disturbance than larger individuals (Hupp and Osterkamp 1996; Nakamura *et al.* 1997; Robertson and Augspurger 1999; Turner *et al.* 2004; Sabo *et al.*

2005); this may have resulted in a less-developed subcanopy layer and, consequently, a greater light availability (Chapter 4) near creek edges, which may be partly responsible for the increased abundance of lianas < 5 cm dbh and stems < 2 cm dbh near creek edges relative to anthropogenic edges.

The abundance and proportion of different functional groups (defined according to successional status and growth habit) were altered near the forest edge although there was no evidence of a decline in large-fruited, biotically-dispersed species that might accompany edge-related alterations in the faunal community (eg Goosem 2004). Weeds were confined to patches with high light availability within 12 m of highway and creek edges and 0.5 m of the powerline edge. Native grasses appeared in a narrow band of relatively high light availability between the weed species and the rainforest understorey species (although this extended to within 25 m of creek edges). In general, the abundance of early-successional (and thus presumably light-demanding) species increased whilst the abundance of late-successional species decreased near the edges of linear canopy openings although the proportion of early-successional understorey and canopy tree seedlings declined with decreasing size class along anthropogenic transects. These patterns suggest that the understorey light environment near anthropogenic edges is no longer suitable for the recruitment of early-successional tree species possibly due to greater edge sealing whilst the understorey near creek edges remains favourable for the recruitment of a variety of species, both light-demanding and shade-tolerant. The increase in mid-successional canopy tree seedlings near anthropogenic edges, which is uncorrelated with light availability, suggests that the more-desiccating conditions experienced near anthropogenic edges (Chapter 4) may be exerting an influence on species composition. Further studies on the desiccation-tolerance of canopy tree seedlings would be required to determine whether this is, in fact, the case. These data are consistent with the ‘bottom-up’ influence of microclimate and edge structure on species composition at the forest edge (Murcia 1995; Didham and Lawton 1999; Harper *et al.* 2005). Further research needs to be conducted into possible ‘top-down effects’ of changes in the faunal community influencing the plant community (Terborgh *et al.* 2006).

5.5 Conclusions

I addressed six research questions in this section of the project:

1) Is rainforest vegetation structure altered near the edges of linear canopy openings and are there any structural differences among powerline, highway and creek edges?
2) Does above-ground biomass decrease at the edges of linear canopy openings (*cf.* Laurance *et al.* 1997)? Are there differences among edge types?
3) Is species diversity higher near the edges of linear canopy openings? Does this vary among powerline, highway and creek edges?
4) Is the plant community composition (defined, firstly, according to successional status and growth habit and, secondly, by diaspore size and dispersal mode) altered near the edges of linear canopy openings?
5) Is there any evidence of a shift in successional status between adults and juveniles near the forest edge?
6) Are any changes in the plant community composition correlated with alterations in microclimate (especially altered light availability)?

In regard to the first question, total stem density in all stem size classes, the abundance of lianas < 5 cm diameter and the proportion of small and intermediate (< 30 cm dbh) trees increased near the edges of linear canopy openings relative to the forest interior. Creek transects had a higher proportion of large and intermediate (≥ 10 cm dbh) trees, a lower abundance of stems 2 – 5 cm dbh and a higher abundance of lianas < 5 cm diameter than anthropogenic transects possibly due to the removal of smaller trees and saplings by periodic flood disturbance (Hupp and Osterkamp 1996; Nakamura *et al.* 1997; Robertson and Augspurger 1999; Turner *et al.* 2004; Sabo *et al.* 2005) and the subsequent growth of lianas in the higher light environment provided by the reduced subcanopy density (Chapter 4). The above-ground biomass of trees ≥ 5 cm dbh was not lower near the edges of linear canopy openings (question 2).

In response to the third question, the Shannon diversity index is higher near the forest edge for stems 2 – 5 cm dbh (‘sapling’ size class) but not for stems < 2 cm dbh (‘seedling’ size class) or stems ≥ 5 cm dbh (‘tree’ size class). These different patterns between seedling-, sapling- and tree-sized individuals do not appear to be consistently related to increased stem density (detected in all size classes) or weed intrusion (predominantly detected in the smallest size class) near the forest edge.

In regard to the fourth question, plant community composition is altered near the edges of linear canopy openings. The abundances of weeds, grasses and herbs are higher and the abundance of shrubs lower near the forest edge than in the forest interior and the abundance of ferns is elevated near creek edges. Amongst understorey trees, there are a greater proportion of early-successional species and a lower proportion of late-successional species near the forest edge than in the forest interior, and this pattern is strongest along creek transects. In contrast, amongst canopy trees, the proportion of early-successional species increased near the forest edge, the decline in late-successional species was less pronounced near creek edges than powerline and highway edges and the proportion of mid-successional species increased near the powerline edges. There was no evidence of a decline in the abundance of large-fruited, biotically-dispersed species near the edges of linear canopy openings (question 4b) suggesting that these species do not suffer greater dispersal limitation near the forest edge than in the forest interior.

With regard to the fifth question, there was evidence of a shift in successional composition between adults and juveniles of understorey and canopy trees. Amongst understorey trees, the proportion of early-successional species declined between adults and juveniles near anthropogenic edges suggesting that microclimatic conditions were no longer suitable for the recruitment of early-successional understorey tree species near anthropogenic edges probably as a result of increased edge sealing. Amongst canopy trees, the proportion of early-successional species decreased and the proportion of mid-successional species increased with decreasing size class near anthropogenic edges but not creek edges. These patterns were stronger near powerline edges than near highway edges. These edge patterns suggest that different processes are influencing the regeneration of tree species near natural and anthropogenic linear canopy openings; specifically, anthropogenic edges are becoming more ‘sealed’ over time while the potential influence of more desiccating edge conditions is maintained whilst creek edges retain sufficiently high light levels (and sufficiently low levels of moisture stress) to allow the continued recruitment of species from a variety of successional stages and growth habits.

In response to the sixth question, with the exception of the successional composition of canopy tree seedlings, shifts in the abundance and proportions of different plant functional groups (defined according to successional status and growth habit) near the edges of linear canopy openings are consistent with correlations with light availability (positive correlations with red:far red ratio amongst functional groups that increased near the forest edge and negative correlations with red:far red ratio amongst functional groups that decreased near the forest edge). It is possible that other abiotic edge gradients (eg greater moisture stress) may also be influencing the regeneration of canopy tree species.

I recommend the following lines of enquiry for further study:

1) The abundance of shrubs was lower near the edges of powerlines and creeks than in the forest interior. Further studies should be conducted to a) determine the underlying mechanisms behind this decline and b) measure the "linear barrier effect" of powerlines and creeks on shrub populations. Isolation of populations through a linear barrier effect might be measured through studies of the genetic structure of more abundant shrub species (eg *Atractocarpus hirtus*, *Ixora baileyana*) on either side of a linear canopy opening and through measurements of dispersal rates of diaspores between the forest interior and the forest edge, across the linear canopy opening and between sites within the forest interior.
2) The "linear barrier effect" (the isolation of populations on either side of a linear canopy opening; Goosem 1997) could be measured for more abundant plant species through studies of the genetic structure of populations on either side of linear canopy openings and through studies of the dispersal rates of diaspores across linear canopy openings and within the forest.
3) Long-term monitoring of the recruitment, mortality and growth rates of adults and juveniles of canopy trees, understorey trees, shrubs, herbs and lianas, at the forest edge and in the forest interior, would allow a true measure of the vital rates of populations of different plant species and provide a more reliable indication of the likely future course of forest dynamics near the edges of linear canopy openings as compared to the forest interior.
4) Further studies of the basic ecology and physiological requirements of almost all species encountered in this survey are required.
    a. There is very little information available on the ecology of lianas and other climbing plants within the Wet Tropics World Heritage Area of

north-eastern Australia. Considering the important role that lianas play in the dynamics of disturbed and undisturbed forest (Laurance *et al.* 2001a; Schnitzer 2005; Phillips *et al.* 2005) and the possible future increase in the importance of lianas under anthropogenic climate change (Phillips *et al.* 2002; Lewis *et al.* 2004; Wright *et al.* 2004), the lack of ecological studies on lianas in palaeotropical rainforest is alarming.

b. Even less information is available on the ecology of ferns and fern allies than of climbing plants within the Wet Tropics World Heritage Area.

c. Information on the successional status of tree, shrub, herb and grass species within the Wet Tropics is based largely on the observations of experts (eg Osunkoya 1996) rather than quantified measures of species' distributions or physiological tolerances. This deficit could be addressed through a combination of field and shade-house experiments; the responses of seedlings to light and moisture availability could be measured in controlled, shade-house experiments and the shade-tolerance of species could be measured by monitoring the survival of seedlings in shade in the field (*cf.* Clark and Clark 1989, shade tolerance measured as the negative slope of the log of survival over time in shade). These responses could also be correlated with various seedling traits (eg relative growth rate, specific leaf area, root:shoot ratio, photosynthetic light response curves, seed mass, cotyledon function, etc). The distributions of different plant species in the field, in relation to the edge and the forest interior, could then be compared with the experimentally measured shade-tolerance and moisture response, to test whether more light-demanding or more drought-tolerant species are favoured near the forest edge (McDonald and Urban 2004; Ries *et al.* 2004).

Chapter Six: Physical Disturbance

6.1 Introduction

The physical disturbance regime (frequency, scale and types of disturbance) determines many aspects of the structure, composition and diversity of a forest ecosystem. Disturbances to the forest canopy can cause damage to or mortality of adult trees and increase the availability of light in the forest understorey (Denslow 1980; Chazdon and Fetcher 1984). Gaps in the forest canopy may provide important opportunities for the growth of seedlings and suppressed saplings in the understorey (Martinez-Ramos *et al.* 1988; Uhl *et al.* 1988), reduce pathogen-related mortality in seedlings (Augspurger 1984; Osunkoya *et al.* 1992) and, especially in larger gaps caused by multiple tree-falls, provide opportunities for the germination and growth of light-demanding pioneer species (Brokaw 1985; Schnitzer and Carson 2001). In fact, periodic disturbance to the forest canopy, through cyclones, wind storms and flooding from rivers, is one of the mechanisms believed to maintain the diversity of plant species in rainforests, by preventing the exclusion of less-competitive species (Connell 1978).

In contrast, disturbance near the edges of forest fragments can have catastrophic effects on the diversity of the forest community (eg Laurance *et al.* 1998a; Gascon *et al.* 2000). The combination of increased moisture stress and greater exposure to wind disturbance at fragment edges can lead to elevated rates of tree mortality (especially tree-fall mortality) (Williams-Linera 1990a; Laurance *et al.* 1998a; Peltonen 1999; Harper and Macdonald 2002; D'Angelo *et al.* 2004), which can increase the turnover rate of trees near the edge, favouring faster-growing, earlier successional species, rather than the original forest interior species (Laurance 1997a; Laurance *et al.* 1998b) and dramatically altering the plant community at the forest edge (Laurance *et al.* 1997, 2002). Over time, especially in locations where the contrast between the forest fragment and the surrounding habitat is great or where the edge is repeatedly exposed to fire, the disturbed edge vegetation may become dominated by weedy or ruderal vegetation which prevents the regeneration of primary forest species, resulting in the fragment edge contracting inwards, with the potential for the total collapse of the fragment's forest ecosystem (Gascon *et al.* 2000). In this chapter, I will explore whether tree-fall disturbance may be elevated near the edges of natural and anthropogenic linear canopy openings, relative to the forest interior.

At a finer scale, physical disturbance due to falling canopy debris and leaf litter is a major cause of damage and mortality for seedlings and saplings (Aide 1987; Clark and Clark 1989, 1991; Guariguata 1998; Drake and Pratt 2001; Peters *et al.* 2004). Rates of physical damage vary both between forests (Mack 1998; Gillman *et al.* 2004; Gillman and Ogden 2005) and within forests (Clark and Clark 1989; Mack 1998; Scariot 2000; Drake and Pratt 2001; Gillman *et al.* 2004; Peters *et al.* 2004; Gillman and Ogden 2005), with these differences associated with variation in species composition of canopy and subcanopy tree species (Drake and Pratt 2001; Gillman *et al.* 2004; Peters *et al.* 2004; Gillman and Ogden 2005), changes in topography (Mack 1998), presence of protective vegetation (eg some lianas and shrubs) (Mack 1998; Gillman and Ogden 2005) and differences in the faunal community (which may also contribute to seedling physical damage through trampling, digging and burrowing) (Clark and Clark 1989; Mack 1998; Drake and Pratt 2001). This variation results in a range of "microsites" within a forest which differ in risk of physical damage to seedlings and saplings (Gillman *et al.* 2004; Gillman and Ogden 2005).

Seedlings and saplings of different species exhibit differing abilities to survive and recover from small-scale physical disturbance (Clark and Clark 1991; Guariguata 1998; Gillman *et al*. 2003; Pauw *et al.* 2004). For example, Pauw *et al.* (2004) found that rain forest tree saplings at La Selva Biological Station in Costa Rica were clustered into either a "tolerator" or an "escaper" strategy. Tolerators had a greater ability to survive and recover from physical damage, but this came at the cost of increased biomass allocation to roots and a slower growth rate, whereas escapers allocated greater biomass to the stem and relied on their faster growth rates to minimise the time spent in the most vulnerable size class. The tolerator strategy was thus associated with a higher root-to-shoot ratio and slower growth rates and Pauw *et al.* (2004) suggest that the tolerator strategy might also be associated with increased shade-tolerance and allocation to storage organs; this suggestion is echoed by a number of other authors (Clark and Clark 1991; Guariguata 1998; Peters *et al.* 2004). Regardless of whether a greater ability to recover from stem damage is associated with greater shade tolerance, however, it is likely that the variation in physical disturbance rates within forests will affect differentially the seedling and sapling mortality of different species. Therefore this may provide another axis for the regeneration niche of rain forest plant species and potentially affect the structure of the plant community (Clark and Clark 1992; Guariguata 1998; Gillman et al. 2003, 2004; Pauw *et al.* 2004; Peters *et al.* 2004;

Gillman and Ogden 2005). For example, Peters *et al.* (2004) found that the composition of the sapling community in the western Amazon was altered beneath the canopy of a common palm species (*Iriartea deltoidea*, which has large fronds that can cause significant damage to saplings).

The rate of litterfall is elevated near the edges of forest fragments in the Biological Dynamics of Forest Fragments Project in the central Brazilian Amazon (Vasconcelos and Luizao 2004), which may influence the seedling community at the forest edge (Benitez-Malvido 1998). The rate of seedling physical damage due to litterfall does not appear to have been assessed near the forest edge in this region, but is elevated in small forest fragments relative to continuous forest (Scariot 2000). This chapter also investigates the question of whether the rate of physical disturbance due to falling litter and canopy debris is elevated near the edges of natural and anthropogenic linear canopy openings. The overall aim of this chapter is to examine whether physical disturbance (both tree-fall disturbance and small-scale disturbance to seedlings) is elevated near the edges of linear canopy openings and whether this differs between the different types of linear canopy openings.

6.1.1 Research Questions

1) Is tree-fall disturbance elevated near the forest edge? Is this affected by edge type?
2) Is physical damage to seedlings elevated near the forest edge? Is the rate of damage different between different edge types?
3) Does physical disturbance correlate with light availability?

6.2 Materials and Methods

Three approaches were used to address the research questions: firstly, the number of fallen trees was surveyed, to examine whether tree-fall disturbance might be elevated near the forest edge; secondly, the rate of physical damage to seedlings caused by falling debris and leaf litter was measured using artificial seedlings (*cf.* Clark and Clark 1989) and; thirdly, in a follow-on to the artificial seedling experiment, the height:basal diameter ratio of tall (≥ 50 cm) seedlings was measured, to determine whether seedling stature might be more suppressed by physical disturbance near the forest edge (*cf.* Peters *et al.* 2004).

6.2.1 Tree falls

The number of fallen trees was surveyed using the belt transects described in Chapter 5 for the vegetation survey (Figure 6.1), to determine whether there was a greater number of fallen trees near the forest edge than in the forest interior. All fallen trees (or logs) with a diameter ≥ 5cm that were encountered along these transects were counted. Unfortunately, mortality due to tree-fall and wind-throw could not be measured over time, and the age of the fallen trees encountered in the survey could not be determined. However, an increase in the number of fallen trees near the forest edge would be consistent with an increase in the tree-fall mortality and disturbance rates, although not definitive. In the absence of long-term monitoring studies, “snap-shot” correlational studies can provide useful data. A further caveat arises from the difference in humidity between the forest interior and forest edge (Chapter 4, VPD), which could conceivably result in a faster rate of decay in the forest interior and a subsequent deficit of smaller fallen trees in the interior relative to the forest edge. This might possibly bias the results towards a lower number of tree-falls in the forest interior and a lower number of old small tree-falls overall. There is also the possibility that some of the small “tree-falls” recorded in the survey were in fact branch-falls from larger trees, rather than individual tree-falls. Attempts were made in the field to determine whether a “tree-fall” was in fact a branch-fall, but there remains the possibility that at least some of these determinations were incorrect.

To address these last two caveats, I recorded the diameter and the “decay class” of each fallen tree I encountered in the survey and I have divided the analysis according to these different categories. I used four arbitrary decay categories (0 – 25% decay, 25 – 50% decay, 50 – 75% decay, >75 % decay) based on my subjective assessment of the extent of decay of each tree-fall in the field. No other observer recorded these data, to minimise observer error.

6.2.1.1 Statistical Analysis

Overall tree-fall numbers (corrected for branch falls and where one tree fell across more than one belt transect, in which case it was counted on the belt transect closest to the base), were pooled between the two 25 m belt transects per distance per main transect (Figure 6.1) for analysis. The total number of tree-falls (per combined 50 m belt transect), the number of tree-falls in decay classes 1 – 3 (< 75 % decayed), the number of tree-falls with a diameter ≥ 10 cm and the number of tree-falls with a diameter ≥ 10 cm and in decay classes 1 – 3, were used as the dependent variables in separate analyses of covariance (ANCOVA), with fixed factor edge type (powerline, highway and creek) and covariate distance. Tree-fall numbers were $ln(1 + x)$ transformed to approximate normality. The purpose of these analyses was to determine whether there was a greater number of tree-falls at the forest edge than in the forest interior (and whether there was any effect of edge type), both for all tree-falls encountered and for those tree-falls less likely to be affected by potentially different rates of decomposition between the forest edge and interior (assumed to affect the smallest and most decayed tree-falls to a greater extent).

To explore the influence of the edge on the diameter class of fallen trees (and whether one size class might be more susceptible to edge-related disturbance, *cf.* Laurance 2000), I compared the diameter class distribution of fallen trees with that of living trees (dbh ≥ 5 cm) measured in the vegetation survey (Chapter 5). Living and fallen trees were divided into the following diameter classes; 5 – 9.9 cm, 10 – 29.9 cm, 30 – 49.9 cm and ≥ 50cm. To ensure sufficient data for analysis the most decayed fallen trees (decay class 4) were included. A hierarchical loglinear analysis was performed on these data, to determine whether the relative proportions of trees within each diameter class differed between living and fallen trees, between the edge and the forest interior and between edge types. To provide a minimum frequency of 5 in each "cell" (combination of categories) for loglinear analysis, distance from the forest edge was pooled into three categories (0 m & 4 m, 12 m & 25 m, and 50 m & 100 m) and the largest two size classes (30 – 49.9 cm and ≥ 50 cm) were combined into one category (≥ 30 cm).

To explore the possible consequences of an elevated level of tree-fall disturbance for the understorey light environment experienced by seedlings, I divided the red:far red ratio light measurements described in Chapter 4 into those associated and not associated with fallen trees. This was done by comparing the position of each fallen tree with positions of individual red:far red measurements and assigning each fallen tree to the closest red:far red measurement. Red:far red measurements were thus divided into the categories "tree-fall present" and "tree-fall absent" for a) all fallen trees, b) fallen trees of decay classes 1 – 3, c) fallen trees with a diameter ≥ 10 cm and d) fallen trees of decay classes 1 – 3 with a diameter ≥ 10 cm. An analysis of variance

(ANOVA) was then performed on these data, with dependent variable red:far red ratio and fixed factors distance, edge type (powerline, highway and creek) and tree-fall presence/absence.

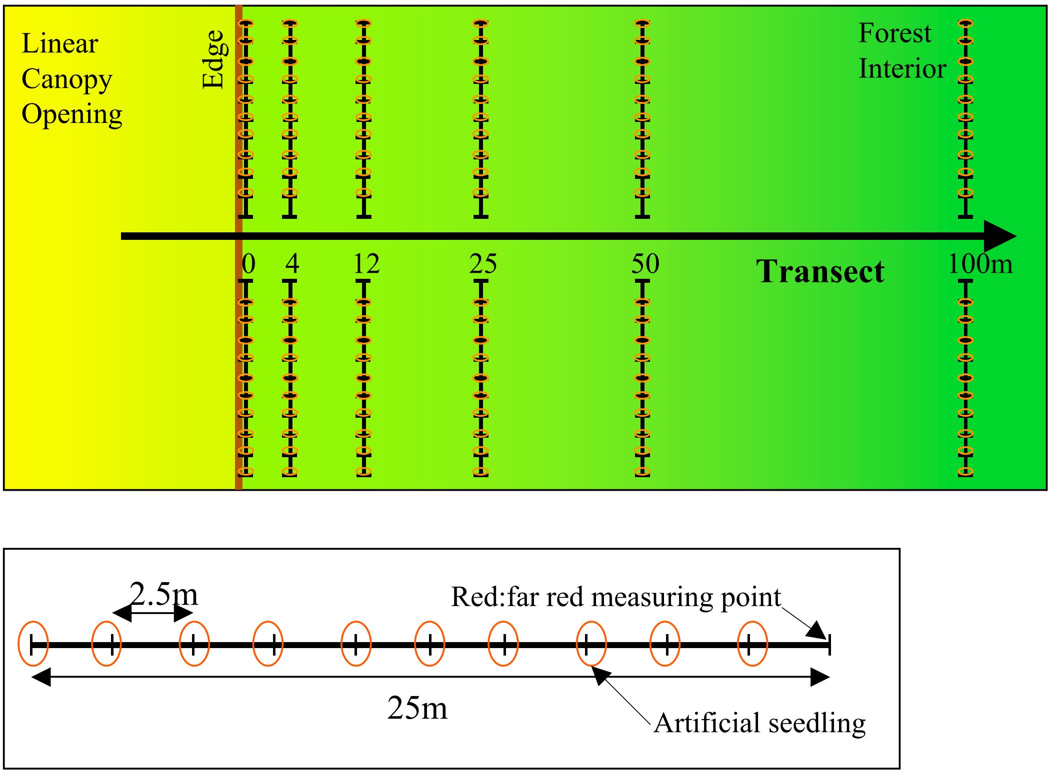


Figure 6.1. The field site survey design for the tree-fall survey and the artificial seedling experiment. All fallen trees encountered along each 25m line were measured (diameter and decay status). Artificial seedling locations are shown with orange circles.

6.2.2 Artificial Seedling Experiment

Artificial seedlings were used to assess whether physical disturbance to seedlings, due to falling deadwood and leaf litter, is greater at the forest edge than in the forest interior. Artificial seedlings were constructed following the design of Clark and Clark (1989), as modified by Scariot (2000). Each artificial seedling was constructed from two plastic drinking straws, and a 13 cm piece of stiff wire (1.25 mm diameter); the two drinking straws were stapled into a “t” shape (to provide an artificial “stem” and two artificial “leaves”) and the 13 cm piece of wire was inserted 3 cm into the bottom of the “stem”, to provide a 10cm long “root”; the “root” was attached securely to the “stem” with a small piece of very fine (0.7 or 0.9 mm diameter) wire. Green straws were used in

Scariot's (2000) study, to avoid attracting the attention of animals; in my study, green straws were unavailable, so black straws were used (Plate 6.1).

Ten of these artificial seedlings were placed along 22.5 m lines running parallel to the forest edge, with individual seedlings spaced 2.5 m apart. Two of these lines were placed at 0 m, 4 m, 12 m, 50 m and 100 m from the forest edge, along each of the transects described in Chapter 3 (n = 1440). These were the same lines used for the measurement of the red:far red ratio (see section 4.2.3) and, with the exception of the "0" mark along each line (the start of each of the 25 m lines used in both the red:far red ratio measurements and the vegetation surveys), the same individual measuring points (Figure 6.1).

Artificial seedlings were placed out in the field between 16th and 21st December, 2004 and monitored approximately once per month until 29th June 2005. At each census, the condition of each artificial seedling was recorded (undamaged, lying under debris, lying under litter, bent, "uprooted", chewed or missing) and damaged or missing seedlings were replaced. Unfortunately, due to unexpected difficulties accessing some sites (especially powerline site one), regular monthly censuses of all transects were not possible. Thus, no attempt has been made to analyse the disturbance data on a monthly basis; only the cumulative overall levels of damage at each site have been used in the analysis.

6.2.2.1 Statistical Analysis

The overall damage to artificial seedlings was obtained by determining which individual seedlings had been damaged at any time within the six-month monitoring period. Damage categories "chewed" and "missing" were not included in the analysis, as the focus of this study was physical damage rather than biotic damage and seedlings classified as "missing" could not be definitively assigned either a biotic or physical cause of damage. These data were analysed using a backwards conditional binomial logistic regression, with the dichotomous dependent variable being "damaged" (value = 1) or "undamaged" (value = 0) for each individual artificial seedling. Each edge type (powerline, highway and creek) was analysed separately, using the independent continuous variables – distance and red:far red ratio. This analysis calculates a model of the probability of the dependent variable being equal to 1, based on a set of specified predictor variables (independent variables) (Pallant 2005). Backward conditional regression eliminates variables that do not significantly contribute to the model, leaving only the significant variables remaining in the final model.

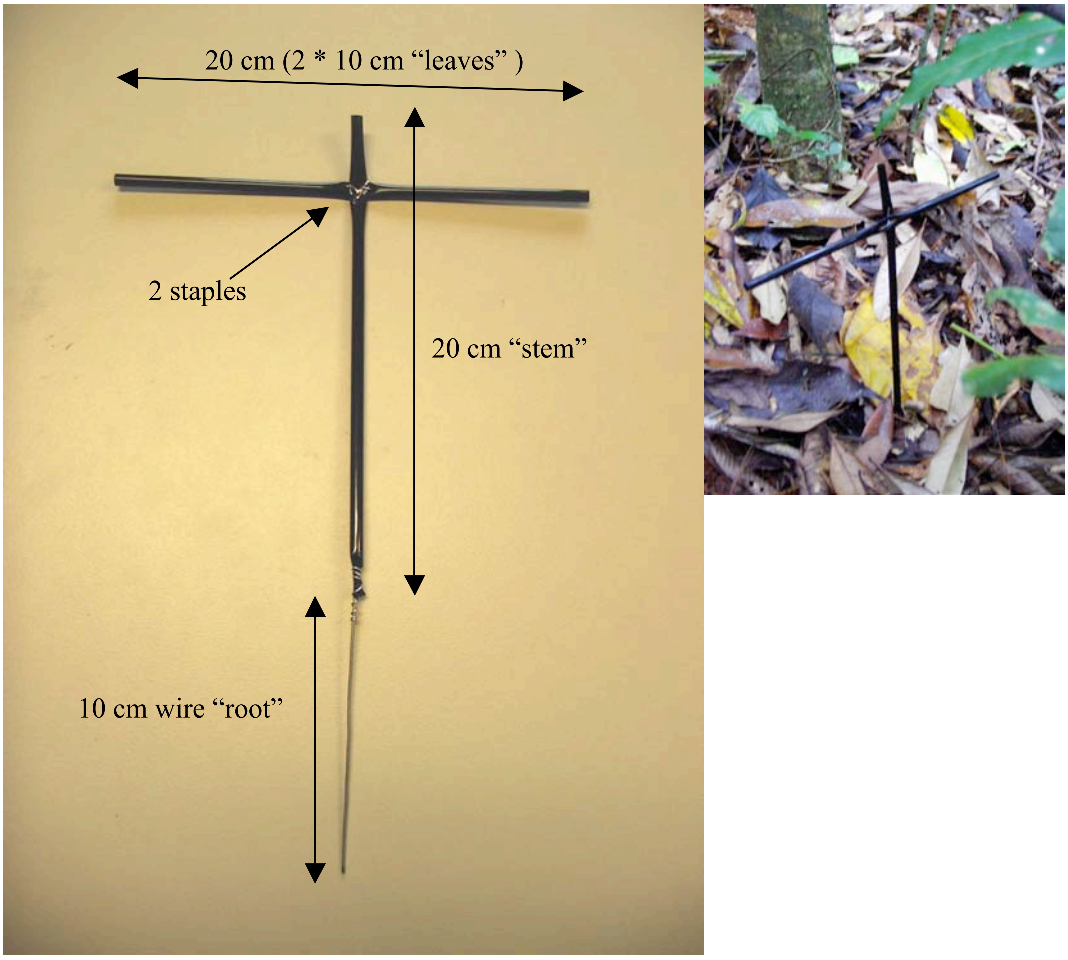


Plate 6.1. An example of an “artificial seedling” used to measure the rate of physical damage to seedlings. The “root” is inserted into the ground until the base of the straw “stem” is flush with the soil surface.

6.2.3 Height:Basal Diameter Ratio of Tall Seedlings

In a follow-up to the artificial seedling experiment, the height:basal diameter ratio was calculated for the seedlings of trees, shrubs and lianas ≥ 50 cm tall that were measured in the vegetation survey (Chapter 5). An increase in the rate of physical damage (and of recovery of height lost due to physical damage) should result in a decrease in the height:diameter ratio (Peters *et al.* 2004). Thus, I was interested to see whether the height:diameter ratio of larger seedlings decreased at the forest edge, which would lend support to any increase in physical disturbance rate detected in the artificial seedling experiment.

The ability to recover from physical damage varies between species (Guariguata 1998; Gillman *et al.* 2003; Pauw *et al.* 2004). Differences in species composition between the forest edge and interior (Chapter 5) thus might potentially bias the height:basal diameter ratio of the seedling community. Two approaches were used to overcome this potential source of bias: within-species comparisons and within-functional group comparisons. Functional groups were defined according to growth form (canopy tree, understorey tree, shrub or liana) and successional status (early, intermediate or late-successional) (see Chapter 5 for further details on classification). However, due to insufficient data, the early and intermediate-successional shrub species were pooled into one category, as were all liana species. Liana seedlings were only included in the analysis if their height could be determined (ie seedlings rooted within the sampling quadrat but not climbing out-of-sight into the canopy or the understorey, Chapter 5). Data for each functional group were analysed using analysis of covariance (ANCOVA) with two fixed factors, edge type (powerline, highway and creek) and distance, and one covariate, red:far red ratio. Distance categories were pooled into three discrete groups (0 m & 4 m, 12 m & 25 m and 50 m & 100 m) for the analyses. Red:far red ratio (measured at each seedling quadrat, Chapter 5) was included as a covariate, as light availability might affect the capacity of seedlings to recover from physical disturbance and potentially influence their height:basal diameter ratio. Where red:far red ratio was not a significant covariate, it was dropped from the analysis. Data for mid-successional canopy trees, late-successional canopy trees, early- and mid-successional shrubs and lianas were *ln*-transformed to approximate normality.

Data for individual species were analysed if the species had sufficient abundance (n ≥ 2 per group) to allow either a) comparisons either between distances within one or more edge types (with distances pooled into the discrete categories described for the functional-group analyses); b) comparisons between the edges (0 m & 4 m distance category) of different types of linear canopy openings (powerlines, highways and creeks); or c) a full-factorial ANOVA with two fixed factors, edge type and distance (red:far red ratio was included as a covariate only when it was a significant covariate in an ANCOVA). Nineteen species had sufficient abundance for analysis: six species with sufficient data for edge type by distance comparisons; two species with sufficient data for edge type (0 m & 4 m) comparisons; eleven species with sufficient data for distance within edge type comparisons (with one species having separate edge type and distance comparisons). For both within-species and within-functional group analyses, data were pooled across all sites and transects for each combination of edge type and distance. All statistical analyses were performed using SPSS 11.0 for Macintosh.

6.3 Results

6.3.1 Treefalls

The number of fallen trees was higher near the forest edge than in the forest interior (Figure 6.2), when all fallen trees were examined ($F = 7.813$, df = 1, $p = 0.007$) and when the least decayed trees (decay classes 1 – 3, decay < 75%) were examined ($F = 6.895$, df = 1, $p = 0.011$). However, when the smallest fallen trees were excluded, this effect disappeared (fallen trees ≥ 10 cm diameter, $F = 1.695$, df = 1, $p = 0.197$; fallen trees < 75 % decayed and ≥ 10cm diameter, $F = 1.774$, df = 1, $p = 0.187$). The effect of edge type was not significant in any of these analyses.

Loglinear analysis revealed significant distance * diameter class ($\chi^2 = 20.230$, df = 4, $p = 0.0004$) and alive/fallen * diameter class ($\chi^2 = 20.390$, df = 2, $p < 0.0001$) interactions: there was a greater proportion of smaller trees near the forest edge than in the forest interior, a lesser proportion of smaller fallen trees than smaller living trees and correspondingly greater proportions of intermediate-sized and large fallen trees than intermediate-sized and large living trees (Figure 6.3). The effect of edge type was not significant.

Fallen trees were associated with higher values of the red:far red ratio (Table 6.1, Figure 6.4), regardless of decay class or diameter. The edge type * distance interaction observed in Chapter 4 was maintained in this analysis (Table 6.1) and there were no significant interactions involving the term tree-fall present/absent, implying that the effect of tree-falls on the understorey light environment was independent of either distance or edge type. As it is possible that the age of a tree-fall could influence the degree of overhead canopy recovery (and subsequently light availability), I tested whether there might be a higher proportion of younger tree-falls near creek edges than near anthropogenic edges (which might account for the higher light availability near creek edges), but there were no significant differences in the proportion of older and younger tree-falls between edge types (MANOVA percent < 50 % decayed and percent >50 % decayed; edge type, Pillai's Trace 0.045, $F = 1.255$, df = 2, $p = 0.293$).

Table 6.1. Relationships between tree-falls and the understorey light environment (red:far red ratio). These data are the results from ANOVAs with three fixed factors, edge type, distance and tree-fall presence; only the edge type* distance and tree-fall presence terms were significant in any of the analyses (there were no significant interaction terms involving tree-fall presence).

Tree-fall type	**Edge Type * Distance Effect**	**Tree-fall presence/absence**
All tree-falls	$F = 5.587$, df = 10, $p < 0.0001$	$F = 24.637$, df = 1, $p < 0.001$
Decay class 1 – 3	$F = 4.141$, df = 10, $p < 0.001$	$F = 22.450$, df = 1, $p < 0.001$
Decay class 1 – 2	$F = 3.077$, df = 10, $p = 0.0001$	$F = 10.681$, df = 1, $p = 0.001$
Diameter > 10 cm	$F = 5.303$, df = 10, $p < 0.001$	$F = 27.498$, df = 1, $p < 0.001$
Diameter > 10 cm and Decay class 1 - 3	$F = 3.727$, df = 10, $p < 0.001$	$F = 31.247$, df = 1, $p < 0.001$

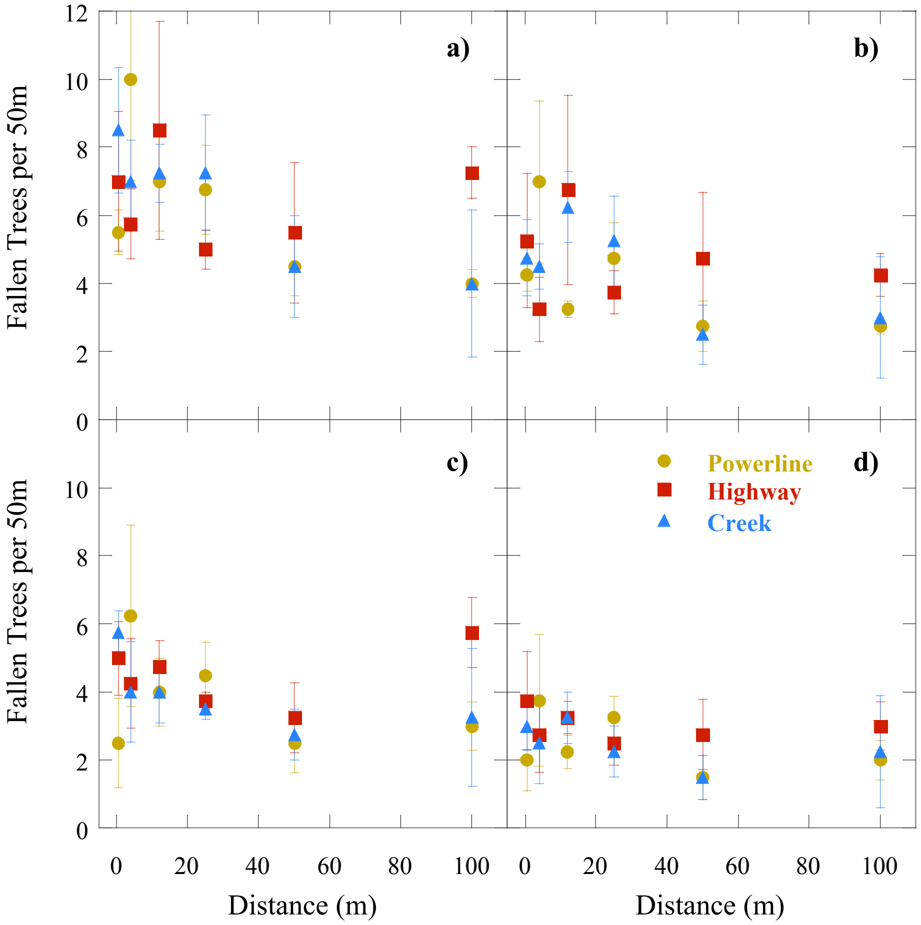


Figure 6.2. Average (± standard error) number of fallen trees per 50m; **a**) all fallen trees, **b**) fallen trees (decay class 1, 2 and 3), **c**) fallen trees > 10 cm diameter and **d**) fallen trees > 10cm diameter and within decay classes 1, 2 and 3.

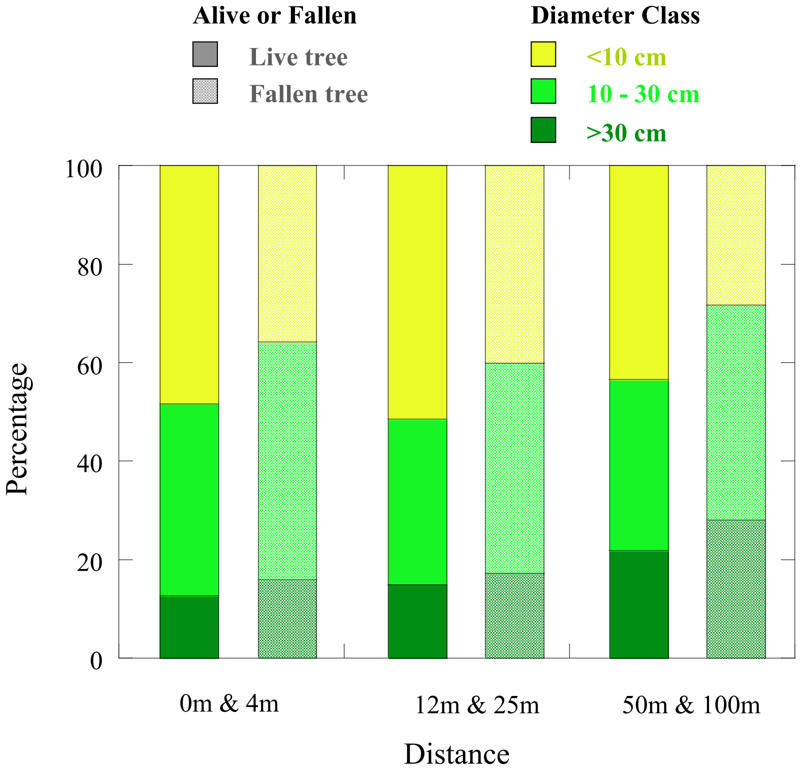


Figure 6.3. Size (diameter) class distribution of living and fallen trees. Data was pooled across all edge types and transects.

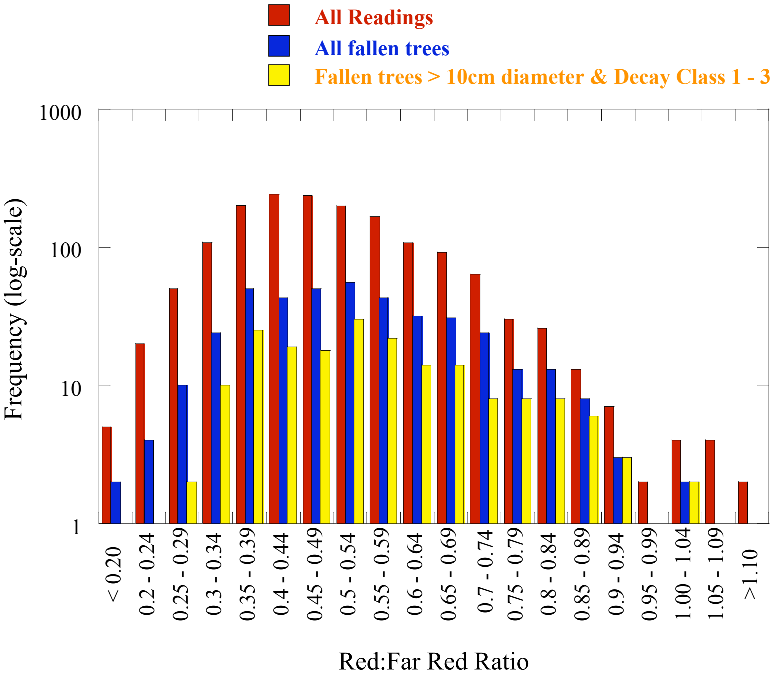


Figure 6.4. Histogram of red:far red ratio measurements, showing all measurements (red), measurements associated with fallen trees (blue; all fallen trees) and fallen trees with diameter > 10cm and less than 75% decayed (yellow).

6.3.2 Artificial Seedling Experiment

The backward conditional binomial regressions revealed that the probability of individual artificial seedlings being damaged increased with increasing red:far red ratio and decreased with distance from highway edges (Table 6.2, Figure 6.5) but decreased with increasing red:far red ratio and increased with distance from creek edges (Table 6.2), although in both cases the red:far red effect was greater than the distance effect. Neither red:far red ratio nor distance from the edge affected the probability of artificial seedling damage near powerline edges (Table 6.2).

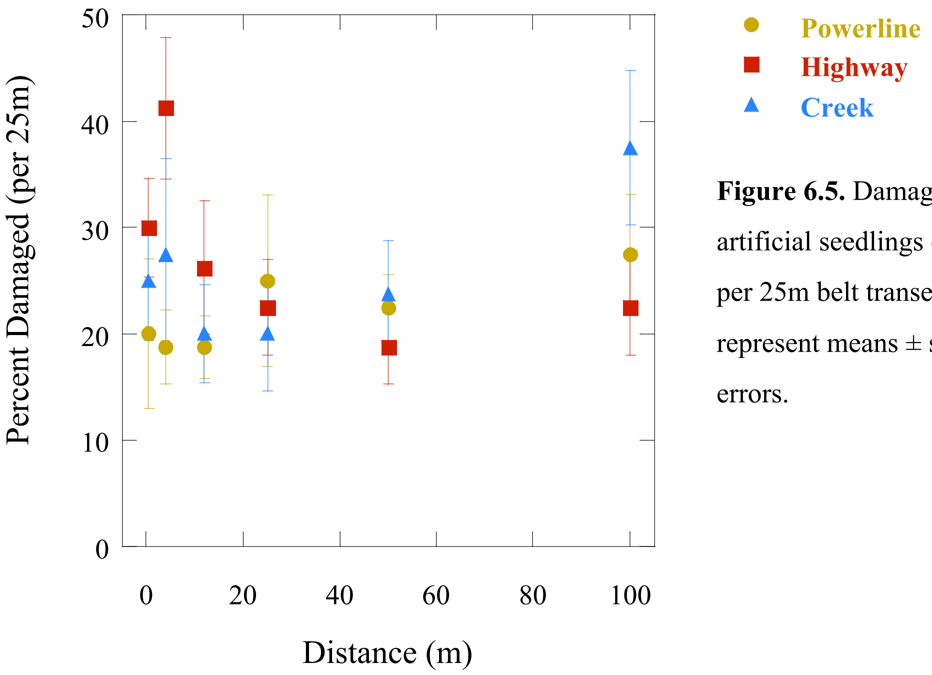


Figure 6.5. Damage to artificial seedlings (percent per 25m belt transect). Data represent means ± standard errors.

Table 6.2. Backwards conditional binomial logistic regression. Significant terms are highlighted in bold (and marginally significant terms are highlighted in italics). Non-significant terms were not included in the final model.

Edge type	**Covariate**	**B**	**Wald Statistic**	**df**	***P***	**Included in final model?**
Powerline	Distance	0.005	2.378	1	0.123	No
	Red:Far Red	1.411	2.764	1	*0.096*	No
Highway	Distance	-0.006	3.840	1	**0.050**	Yes
	Red:Far Red	1.350	5.169	1	**0.023**	Yes
Creek	Distance	0.008	6.573	1	**0.010**	Yes
	Red:Far Red	-2.243	3.441	1	*0.064*	Yes

6.3.3 Height:Basal Diameter of Tall Seedlings

Of the nine functional groups analysed, only early- and mid-successional shrub seedlings displayed a significant relationship between distance from the edge and the height:basal diameter ratio of tall seedlings (Table 6.3). Late-successional understorey tree seedlings displayed a significant interaction between distance from the edge and edge type (Table 6.3; Figure 6.6c). The height:basal diameter ratio of late-successional understorey tree seedlings was lower near powerline edges and higher near highway edges, which was not consistent with the observed patterns of artificial seedling disturbance (which did not vary with distance from powerline edges and were elevated near highway edges). In contrast, the height:basal diameter ratio of early- and mid-successional shrub seedlings was lower near highway edges than in the forest interior (Table 6.3; Figure 6.6d), which is consistent with the elevated physical disturbance observed near highway edges in the artificial seedling experiment. Two functional groups displayed significant edge type effects: the height:basal diameter ratio of mid-successional canopy tree seedlings was lower near highways than near powerlines or creeks (Table 6.3; Figure 6.6a), which may be consistent with the observed artificial seedling disturbance rates near highway edges, but was lowest near creek edges for late-successional canopy tree seedlings (Table 6.3; Figure 6.6b), which is not consistent with the patterns observed in the artificial seedling experiment.

Of the nineteen species with sufficient abundance for within-species analysis, thirteen displayed no significant relationships between the height:basal diameter ratio and either edge type or distance from the edge (Table 6.4). Of the five species which displayed significant relationships between distance from the edge and the height:basal diameter ratio, the height:basal diameter ratio was lower near the powerline edge for 2 species, higher near the powerline edge for 1 species, lower near the highway edge for 1 species and lower near both the highway and powerline edges for 1 species (Table 6.4). Of the edge comparisons (0 m & 4 m) between linear canopy opening types, 1 species displayed a lower height:basal diameter ratio near powerline edges than near highway edges (Table 6.4). The consistency of these results with the patterns expected from the artificial seedling experiment (ie height:basal diameter ratio lower near highway edges in distance comparisons and lower for highways than creeks or powerlines in edge type comparisons) was analysed with Sign tests (consistent patterns assigned a positive sign, neutral patterns a neutral sign and opposing patterns a negative sign; this analysis tests whether there are significantly more positive signs than expected by chance), but was not significant (functional groups; distance, $p = 1.000$, edge type, $p = 1.000$; individual species, distance, $p = 0.625$, edge type, $p = 0.500$).

Table 6.3. Height:basal diameter ratio patterns for different functional groups of seedlings ≥ 50cm tall. The number of seedlings in each functional group is given in parentheses.

Functional Group	**Edge Type**	**Distance**	**Red:far red ratio (covariate)**	**Edge Type * Distance**
Canopy trees				
Early –successional (21)	n.s.	n.s.	n.s.	n.s.
Mid-successional[b] (66)	$F = 2.819$, df $= 2$, $p = 0.068$	n.s.	$F = 14.388$, df $= 1$, $p < 0.001$[c]	n.s.
Late-successional[b] (223)	$F = 4.484$, df $= 2$, $p = 0.012$	n.s.	n.s.	n.s.
Understorey trees				
Early-successional (23)	n.s.	n.s.	n.s.	n.s.
Mid-successional (105)	n.s.	n.s.	n.s.	n.s.
Late-successional (234)	$F = 3.929$, df $= 2$, $p = 0.021$	n.s.	n.s.	$F = 3.631$, df $= 4$, $p = 0.007$
Shrubs				
Early- and mid-successional[a] (68)	n.s.	$F = 3.147$, df $= 2$, $p = 0.05$	n.s.	n.s.
Late-successional (145)	n.s.	n.s.	n.s.	n.s.
Lianas[b] (121)	n.s.	n.s.	n.s.	n.s.

[a] Highway and powerline edges only.

[b] *ln*-transformed prior to analysis.

[c] Pearson correlation, $r = -0.437$, $p < 0.001$.

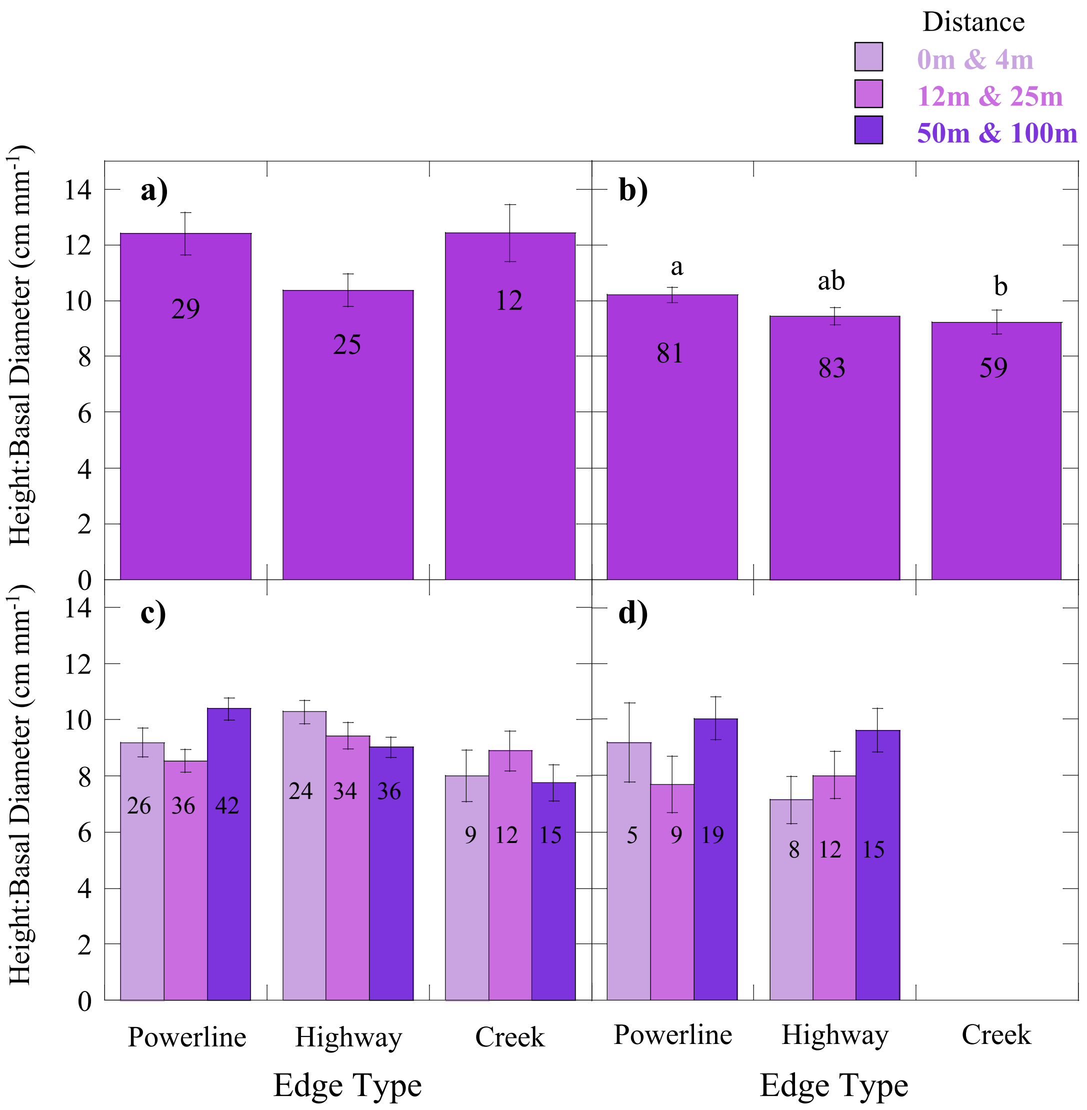


Figure 6.6. Height:Basal Diameter ratio for different functional groups of seedlings ⩾50cm tall. **a**) Mid-successional canopy trees, **b**) late-successional canopy trees, **c**) late-successional understorey trees and **d**) early- and mid-successional shrubs. In panel **b**), different letters indicate significant differences as the $p < 0.05$ level (Bonferroni post-hoc test). Sample sizes are given by the numbers within each bar.

Table 6.4. Patterns of height:basal diameter ratios for individual species. Values are means ±standard errors, with *n* given in parentheses. Analyses were performed using either two-way ANOVA (distance by edge type comparisons), one-way ANOVA (distance comparisons), Pearson correlations (distance comparisons) or independent-samples *t*-tests (edge type or distance comparisons).

Species	**0m & 4m**	**12m & 25m**	**50m & 100m**	**Significant Effects**
Canopy Trees				
Beilschmiedia volckii				
Creek	na	7.47 ±0.87 (3)	7.51 ±0.49 (4)	n.s. (distance)
Endiandra monothyra				
Powerline	na	11.34 ±1.54 (3)	7.63 ±0.61 (3)	$t = 2.239$, df = 4, $p = 0.089$ (distance)
Highway	6.73 ±0.94 (2)	na	7.54 ±1.34 (4)	n.s. (distance)
Litsea leefeana				
Powerline	10.38 ±1.18 (6)	9.46 ±1.47 (2)	11.40 ±0.61(3)	n.s. (distance)
Neolitsea dealbata				n.s. (edge type)
Powerline	14.61 ±1.06 (10)	na	na	
Highway	12.69 ±1.23 (8)	na	na	
Understorey Trees				
Aglaia tomentosa				
Powerline	na	9.19 ±0.95 (6)	10.77 ±0.69 (6)	n.s. (distance)
Highway	11.17 ±0.67 (4)	9.85 ±1.13 (7)	9.09 ±0.52 (7)	n.s. (distance)
Apodytes brachystylis				
Highway	8.47 ±0.5 (9)	9.36 ±0.69 (8)	10.41 ±0.41 (6)	Pearson correlation $r = 0.445$, $p = 0.033$ (distance)
Brombya platynema				
Highway	na	8.96 ±0.80 (6)	10.47 ±0.97 (7)	n.s. (distance)

Species	0m & 4m	12m & 25m	50m & 100m	Significant Effects
Haplostichanthus sp. Topaz				
Powerline	5.01 ±0.47 (2)	na	9.57 ±0.55 (3)	*t* = -5.799, df = 3, *p* = 0.01 (distance)
Highway	9.35 ±0.21 (2)	7.77 ±0.74 (6)	7.31 ±0.63 (4)	n.s. (distance)
Niemeyera prunifera				n.s. (distance and edge type)
Powerline	9.01 ±2.76 (2)	8.89 ±0.87 (9)	10.33 ±0.80 (12)	
Highway	9.31 ±0.60 (3)	10.28 ±0.71 (5)	8.38 ±0.94 (4)	
Creek	10.04 ±0.50 (2)	6.64 ±na (1)	7.81 ±0.96 (5)	
Pittiviaster haplophylla				
Powerline	7.96 ±0.67 (5)	8.27 ±1.08 (5)	na	n.s. (distance)
Rockinghamia angustifolia				
Powerline	6.17 ±1.31 (4)	9.35 ±0.59 (4)	na	*t* = -2.217, df = 6, *p* = 0.068 (distance)
Tetrasynandra laxiflora				
Powerline	9.73 ±1.49 (5)	na	na	n.s. (edge type)
Highway	10.42 ±0.62 (5)	na	na	
Wilkiea sp. Barong				
Highway	6.50 ±1.51 (3)	6.54 ±0.27 (2)	7.07 ±0.50 (5)	n.s. (distance)
<u>Shrubs</u>				
Ardisia brevipedata				
Powerline	6.18 ±0.76 (6)	na	na	*t* = -2.408, df = 8, *p* = 0.043 (edge type)
Highway	8.76 ±0.63 (4)	8.35 ±1.53 (6)	na	n.s. (distance within highway)

Species	**0m & 4m**	**12m & 25m**	**50m & 100m**	**Significant Effects**
Attractocarpus hirtus				Distance (powerline and highway), *F* = 3.408, df = 2, *p* = 0.04
Powerline	8.21 ±1.26 (4)	7.73 ±1.01 (9)	10.10 ±0.78 (19)	
Highway	7.63 ±1.04 (6)	8.06 ±0.84 (12)	9.78 ±0.82 (14)	
Creek	na	9.02 ±0.86 (4)	9.55 ±1.32 (5)	n.s. (distance within creek)
Diosyrros sp. Millaa Millaa (LJW 515)				
Powerline	na	8.40 ±0.78 (4)	7.78 ±0.82 (10)	n.s. (distance)
Highway	6.24 ±0.86 (9)	6.41 ±0.57 (6)	8.47 ±1.06 (3)	n.s. (distance)
Creek	7.44 ±2.86 (2)	5.82 ±0.45 (3)	6.89 ±1.02 (6)	n.s. (distance)
Ixora baileyana				n.s. (distance and edge type)
Powerline	9.84 ±3.38 (2)	10.72 ±1.38 (3)	8.37 ±0.41 (9)	
Highway	7.99 ±1.33 (3)	9.06 ±0.90 (5)	8.92 ±0.69 (6)	
Creek	8.12 ±1.06 (4)	9.13 ±2.18 (4)	8.86 ±1.00 (13)	
Pseuduvaria villosa				
Highway	8.04 ±1.77 (4)	8.82 ±0.78 (3)	6.67 ±0.99 (3)	n.s. (distance)
Lianas				
Carronia protensa[a]				n.s. (distance and edge type)
Powerline	na	11.32 ±1.99 (6)	10.41 ±1.09 (7)	
Highway	na	8.69 ±0.33 (4)	8.33 ±0.33 (3)	
Creek	na	9.72 ±1.95 (7)	9.54 ±0.09 (3)	

[a] *ln*-transformed to approximate normality

6.4 Discussion

6.4.1 Tree Falls

The number of fallen trees was higher near the edges of linear canopy openings than in the forest interior. The type of linear canopy opening did not affect this relationship. This pattern was maintained when the most decayed tree-falls were excluded but not when the smallest tree-falls were excluded; this may be due to the greater proportion of small tree-falls near the forest edge (Figure 6.3). Fallen trees, regardless of decay class or size, were associated with higher values of the red:far red ratio, although this pattern was strongest for larger and less decayed tree-falls (Figure 6.4).

These results are consistent with the hypothesis that tree-fall disturbance may be elevated near the edges of linear canopy openings, in a way similar to that observed near the edges of tropical forest fragments (eg Camargo and Kapos 1995; Laurance 1997a; Laurance *et al.* 1997), although not to the same extent. The diameter-class distribution of fallen trees appears to follow the diameter-class distribution of living trees with distance from the forest edge, although smaller tree-falls were under-represented at all distances (Figure 6.3). This suggests that neither small nor large trees were at a disproportionate risk of tree-fall mortality near the forest edge; the higher proportion of small tree-falls near the edge was merely a reflection of the higher proportion of small living trees near the forest edge.

These tree-fall data represent a "snap-shot" pattern of the abundance of fallen trees, rather than a study of long-term tree-fall mortality rates. Further longitudinal studies would be required to determine the true mortality risk to individuals of varying size, especially if the differences in the absolute values of mortality rates were small (Laurance *et al.* 2000; Nascimento and Laurance 2004). The under-representation of small tree-falls may arise from lower mortality rates or from a disproportionate loss of smaller tree-falls due to decomposition. However, mortality rates are generally greater for smaller individuals (Coomes *et al.* 2003), while studies of decomposition rates in tropical forest fragments have tended to find that rates of leaf litter decomposition are unaffected by or elevated near the forest edge (Didham 1998; Rubinstein and Vasconcelos 2005; Vasconcelos and Laurance 2005) and decomposition rates of woody debris are higher near the forest edge (Nascimento and Laurance 2004). If these results are also applicable in my study area, then small tree-falls would be systematically under-represented near the forest edge, which would suggest that the actual tree-fall edge gradient is steeper (rather than shallower) than that detected in this study. However, long-term studies of the actual rates of tree-fall mortality are required to fully address these questions.

Tree-falls were associated with higher red:far red ratio values on average, although not all high red:far red readings were associated with an individual tree-fall. The range of red:far red values associated with tree-falls was quite wide, although, not surprisingly, this range was slightly narrower (biased towards higher values) for larger and more recent tree-falls (Figure 6.4). However, some of the larger and more recent tree-falls were still associated with relatively low red:far red values (0.25 – 0.4). It is possible that either 1) a significant proportion of these trees fell a long time ago, allowing sufficient time for overhead canopy recovery, or 2) that at least some of these "tree-falls" were actually the broken remains of trees that died standing (and thus caused minimal canopy disturbance) or 3) that some proportion may have caused damage only to the sub-canopy, rather than to the canopy itself. Tree-fall disturbance does not appear to explain the differences in average red:far red ratio values between creek edges and anthropogenic edges (Chapter 4, Figure 4.8). Tree-fall numbers were not higher near creek edges, the size distribution of fallen trees did not differ between creek edges and anthropogenic edges and the proportion of more recent tree-falls did not differ between creek edges and anthropogenic edges. These differences might perhaps be explained by the lower density of sub-canopy trees near creek edges (Chapter 5) or by differences in floristic community composition between creek edges and anthropogenic edges (Chapter 5; eg a higher proportion of early-successional understorey and canopy trees near creek edges than anthropogenic edges). Gaps in the forest sub-canopy can decrease the leaf area index and increase light availability in the forest understorey, and are generally much more common than full canopy gaps (Connell *et al.* 1997). Alternatively, periodic flooding may disturb the forest canopy (or sub-canopy) near creek edges but remove much of the fallen timber.

6.4.2 Artificial Seedling Experiment

Physical disturbance to artificial seedlings was elevated near highway edges but not near powerline or creek edges. Creek edges, in fact, displayed a slight positive relationship between physical damage and distance from the edge (Table 6.2, Figure 6.5). Vasconcelos and Luizao (2004) found that litterfall was elevated near the edges of forest fragments in central Amazonia, partly due to increased production of leaves. If a similar mechanism were operating here, artificial seedling damage should have correlated negatively with red:far red ratio (which is negatively correlated with leaf area index). This negative correlation was observed near creek edges but not near powerline edges or highway edges; for highway transects, damage was positively correlated with red:far red ratio. A possible explanation for this contradictory result might be the presence (or absence) of "protective" understorey vegetation such as lianas or shrubs (Mack 1998; Gillman and Ogden 2005) (the absence of which could contribute to the positive correlation between damage and red:far red ratio observed for highway transects). However, the percent of damaged artificial seedlings (per 25 m line) was not negatively correlated with the abundance of lianas (2 – 5 cm diameter) near highways [Spearman correlation 0.264, $p = 0.070$; this marginal positive correlation may simply reflect the fact that both liana abundance (Chapter 5) and artificial seedling damage are positively correlated with red:far red ratio], powerlines (Spearman correlation 0.116, $p = 0.433$) or overall (Spearman correlation 0.065, $p = 0.483$) but was negatively correlated with the abundance of shrubs (< 2 cm dbh) near highways (Spearman correlation –0.477, $p = 0.001$) but not near powerlines (Spearman correlation 0.305, $p = 0.035$) or overall (Spearman correlation –0.082, $p = 0.328$). Thus, shrubs may have a protective effect on highway transects, although it is curious that they did not appear to have a similarly protective effect on either powerline or creek transects. Indeed, as shrub abundance was lower near powerline and creek edges than highway edges (Chapter 5), a more severe rate of artificial seedling damage would be expected near powerline and creek edges than was observed, were shrubs genuinely offering protection from physical damage. Surveys of the vegetation immediately above each artificial seedling might allow further elucidation of any such "protective" effects.

An alternative explanation for the elevated damage to artificial seedlings near highway edges but not powerline or creek edges is the more desiccating microclimate of highway edges (Chapter 4). Air temperature and vapour pressure deficit were elevated in the understorey near highway edges in both wet and dry seasons and canopy temperature was elevated near highway edges in the wet season. These altered microclimatic conditions may place greater moisture stress on vegetation near the highway edge, potentially increasing the amount of litterfall (Vasconcelos and Luizao 2004), and thus increasing damage to artificial seedlings (Gillman *et al.* 2004). However, due to time constraints, this experiment was run for a relatively short period of time (6 months *vs.* 1 year, Clark and Clark 1989 and Scariot 2000) and did not cover the majority of the dry season. Repetitions of this study should include concomitant measurements of litterfall and deadwood fall (Gillman *et al.* 2004), to examine these hypotheses.

If rates of seedling physical damage are genuinely elevated near highway edges, however, this may have implications for the composition of the seedling community. If species that are more susceptible to physical damage suffer higher mortality, species with greater resilience or resistance to physical damage may be favoured near highway edges (Guariguata 1998; Gillman *et al.* 2003; Pauw *et al.* 2004; Peters *et al.* 2004). I am not aware of any studies of the responses of seedlings or saplings to physical damage in Australian rainforests, but in neotropical rainforests, the ability to recover from damage has been related to greater allocation to roots and/or storage organs (Pauw *et al.* 2004; Peters *et al.* 2004), which in turn has been suggested to relate (at least indirectly) to increased shade-tolerance (Pauw *et al.* 2004). Studies of Australian rainforest tree seedlings have found greater shade-tolerance in seedlings with non-photosynthetic (storage) cotyledons (Osunkoya 1996), but no clear patterns in relation to root:shoot ratio (Osunkoya *et al.* 1994). There is clearly a need for more research into the fundamental ecological properties of Australian rainforest seedlings.

6.4.3 Height:Basal Diameter Ratio of Tall Seedlings

Suppression of tall seedling stature is expressed in a reduced height:basal diameter ratio (Peters *et al.* 2004). To be consistent with the results obtained in the artificial seedling experiment, firstly the height:basal diameter ratio should have been lower near highway edges than in the forest interior, unaffected by distance from the edges of powerlines and either unaffected by distance from creek edges or slightly higher near creek edges relative to the forest interior. Secondly, in comparisons of the edges (0 m & 4 m) of powerlines, highways and creeks, the height:basal diameter ratio should have been lowest near highway edges. Only one of the nine functional groups and two of the seventeen individual species examined for distance comparisons displayed the expected distance patterns. Similarly, only one of the nine functional groups and none of the eight individual species examined for edge type differences displayed the expected edge type patterns. Sign tests of the consistency of these results with the expected patterns (from the artificial seedling experiment) indicated that these patterns were not statistically significant (ie there were not significantly more positive results than expected to arise by chance) and thus these data do not support a more general increase in the frequency of physical damage near the forest edge.

Therefore, the elevated disturbance rate observed near highway edges in the artificial seedling experiment could be an artefact. Alternatively, damage to artificial seedlings might not be correlated with the rates of damage and recovery of actual seedlings. As several other researchers have successfully used artificial seedlings to assess the rate of physical disturbance to seedlings and saplings (eg Clark and Clark 1989; Mack 1998; Scariot 2000; Gillman *et al.* 2004; Gillman and Ogden 2005), it seems unlikely that the experiment was completely inaccurate. It is possible that the species examined do not consistently display a reduced height:basal diameter ratio when recovering from physical damage or that the sample sizes used were inadequate. For example, although more than 90 % of damaged seedlings in unburnt rainforest in Smithfield Conservation Park (near Cairns in north-eastern Queensland) resprouted, only 40 % did so from the broken stem, rather than from the stem base or root suckers (Marrinan *et al.* 2005). However, the almost complete absence of any consistent signal in the data tends to suggest that there were no systematic differences in the rates of physical disturbance to seedlings between the forest edge and the forest interior. It is possible that the damage detected near highway edges was insufficient to cause significant trauma to seedlings. For instance, if a significant proportion of artificial seedling damage was caused by animal trampling, differences between the resilience of artificial seedlings and real seedlings to trampling might result in patterns of seedling stature being uncorrelated with rates of artificial seedling disturbance (eg Gilman *et al.* 2002). However, the rate of animal disturbance to artificial seedlings tends to increase with increasing abundance and/or diversity of large (≥ 1 kg) animals (Mack 1998; Drake and Pratt 2001; Roldan and Simonetti 2001). The relative paucity of large animals in Australian rainforests (Connell *et al.* 2005) suggests that animal trampling is unlikely to make a very large contribution to physical disturbance rates of artificial seedlings (*cf.* Mack 1998, Papua New Guinea). Further research on the vulnerability of rainforest seedlings in north-eastern Queensland to damage by falling debris and leaf litter and on the ability of seedlings to recover from such damage would be required to determine whether or not the elevated rates of physical disturbance detected in the artificial seedling experiment are of ecological significance.

6.4.4 Physical Disturbance and Linear Canopy Openings

Linear canopy openings appeared to alter some aspects of the physical disturbance regime in the adjacent rainforest. The abundance of fallen trees was elevated near the forest edge, although whether or not this represented an increase in rates of tree mortality near the forest edge remains to be determined. Small-scale physical disturbance, as measured with artificial seedlings, was elevated near highway edges, but this does not appear to have left any consistent signal in the stature of tall seedlings near the forest edge.

Although tree-falls were associated with higher understorey light availability (red:far red ratio), not all high light measurements were associated with fallen trees (Figure 6.4); of the high red:far red ratio measurements (≥ 0.8), 66% were associated with tree-falls (or were near tree-falls that did not fall within the tree-fall survey), and the remaining readings all occurred within open patches near the forest edge (60% near highway edges, 15% near powerline edges and 25% near creek edges). Such open patches near highway edges were associated with dense thickets of *Rubus alceifolius* or intrusions of the grass *Urochloa maxima* into the edge, sometimes in association with signs of disturbance due to highway maintenance or infrastructure (Chapter 5). Open patches near powerline edges were similarly dominated by exotic grasses or the scrambler *Lantana camara* (Chapter 5). This suggests the possibility that these weeds may have colonised older tree-fall gaps (caused by either increased tree-fall mortality or disturbance due to maintenance activities) and perhaps have hindered their regeneration (Reynolds 1994; Gentle and Duggin 1997; Gascon *et al.* 2000; Schnitzer *et al.* 2000).

The abundance of fallen trees was elevated within approximately 50 m of the forest edge and disturbance to artificial seedlings was elevated within 25 – 50 m of highway edges; this distance corresponds almost exactly to the edge distance of elevated living tree abundance (Chapter 5) and altered red:far red ratio (Chapter 4). It is conceivable that the elevated number of fallen trees is merely a reflection of the elevated number of living trees near the forest edge and that tree mortality rates are not affected by proximity to linear canopy openings. Long-term studies of tree dynamics would be required to determine whether or not this is the case. The large patches of scrambling weeds near highway edges suggest that either disturbance to the forest edge should be minimised during highway maintenance activities or that some form of weed control program may be required to facilitate the regeneration of native species in these gaps near the forest edge; trials may be needed to determine the effectiveness and feasibility of these options and roadside vegetation should be monitored to determine whether the colonisation of tree-fall gaps on highway edges represents a genuine, long-term problem.

6.5 Conclusions

Three questions were addressed in this chapter, with regard to the edges of linear canopy openings: 1) is tree-fall disturbance elevated near the forest edge and is this affected by edge type? 2) is physical damage to seedlings elevated near the forest edge and is the rate of damage different between different edge types? And 3) does physical disturbance correlate with light availability?

In regard to the first question, the abundance of fallen trees was higher near the forest edge than in the forest interior, but did not differ among edge types. With regards to the second question, physical damage to artificial seedlings was elevated near highway edges, but living seedlings did not display a consistent pattern of stature suppression near the forest edge. With respect to the third question, tree-fall disturbance was associated with (but was not the sole cause of) increased light availability in the forest understorey, and correlations between light availability and small-scale seedling disturbance were inconsistent between the three edge types (and may potentially be complicated by the effects of “protective” vegetation). The presence of large gaps in the canopy near highway edges that have been colonised by scrambling weeds suggests that further monitoring of these weed patches is needed, to determine whether specific management actions are required to allow the regeneration of native species in these patches on highway edges.

I recommend the following lines of enquiry for further study:

1) The frequency of canopy gaps near linear canopy openings and in the forest interior could be assessed using aerial photographs of the study area. If photographs are available which span a time period of a number of decades (preferably covering the entire period of the existence of an anthropogenic linear feature), changes in the frequency of canopy gap formation near linear canopy openings could be examined. In the absence of long-term monitoring plots, this approach appears to offer the best way to assess changes in canopy disturbance associated with linear infrastructure over time.

2) The artificial seedling experiment could be repeated, using more regular census intervals, over a longer period of time and in conjunction with a concurrent survey of the amount and types of litterfall and debris fall. The vegetation immediately above each artificial seedling could also be surveyed, to determine whether certain species or functional groups may lessen or enhance the risk of damage to artificial seedlings.
3) Fundamental research into the vulnerability of the seedlings and saplings of different species in the Wet Tropics to physical disturbance, as well as their relative capacity to recover from traumatic physical damage, is required. Additionally, natural variability in the rates of seedling physical damage in undisturbed interior forest in the Wet Tropics requires further attention.
4) Modelling of the influence of wind within linear canopy openings. Studies of the patterns of windshear along the edges of forest fragments have helped to elucidate the mechanisms behind increased tree-fall disturbance at fragment edges (eg Somerville 1980, *cited in* D'Angelo *et al.* 2004) and similar studies might assist in understanding the mechanical stresses imposed by wind at the edges of linear canopy openings.

Chapter Seven: Seedling Survival and Growth

7.1 Introduction

Patterns of seedling recruitment and mortality beneath the rainforest canopy determine the composition of the pool of available species from which subsequent generations of plants will grow (Whitmore 1996; Capers *et al*. 2005). Although spatial patterns of seedling recruitment may be at least partly random (Brokaw and Busing 2000), the physiological tolerances and niche requirements of different species also influence the dynamics of seedling communities at different locations beneath the forest canopy (Brokaw and Busing 2000; Capers *et al.* 2005).

One of the most widely recognised axes of variation is the pioneer to climax species continuum (Whitmore 1996; Turner 2001). Pioneers and non-pioneers are separated firstly on the basis of whether or not the seeds are capable of germinating in shade as pioneer seeds require higher light levels to germinate (Whitmore 1996). Subsequently, species separate out along a continuum between those which display high growth rates in microsites with relatively high light levels but also suffer high mortality in shaded microsites and those species that can persist for long periods in deep shade but display low plasticity in growth performance in response to increased light availability (Kitajima 1994; Condit *et al.* 1996; Whitmore 1996; Kobe 1999; Wright *et al.* 2003). Most species are intermediate between these two extremes (Condit *et al.* 1996; Osunkoya 1996; Agyeman *et al.* 1999; Nascimento *et al.* 2005).

Other factors influencing the recruitment and mortality of seedlings in the environmentally heterogeneous forest understorey include susceptibility to pathogen infection (Augspurger 1984; Coley and Barone 1996), ability to withstand or to recover from physical damage (Clark and Clark 1991; Guariguata 1998; Gillman *et al.* 2003; Pauw *et al.* 2004), drought tolerance (Engelbrecht and Kursar 2003; Bunker and Carson 2005) and susceptibility to herbivory pressure (Coley and Barone 1996; DeMattia *et al.* 2006). Species' individual responses to variation in each of these parameters within the rainforest understorey may determine which of the range of environments in which they germinate that they can survive (Webb and Peart 2000).

Patterns of seedling recruitment, growth and mortality may be affected by the altered light availability, moisture stress and canopy disturbance near the edges of forest fragments (Kapos 1989; Williams-Linera 1990a; Chen *et al*. 1993; Chen *et al.* 1995;

Turton and Freiburger 1997; Newmark 2001). In tropical pre-montane rainforest in Panama, seedling growth, mortality and recruitment increased near forest edges within 8 months of edge creation, although the edge community was dominated by existing seedlings and saplings, rather than newly germinated seedlings or pioneers (Williams-Linera 1990b). In contrast, within the first 15 months after edge creation in Amazonian lowland rainforest, seedling growth rates and pioneer seedling recruitment increased within 10 m of fragment edges, although seedling mortality rates were not altered (Sizer and Tanner 1999). Over time, however, the abundance of shade-tolerant tree seedlings declined near these fragment edges (Benitez-Malvido 1998) and the species richness of recruiting tree seedlings was lower near fragment edges than in continuous forest (Benitez-Malvido and Martinez-Ramos 2003b).

Forest edges may also affect trophic interactions involving plant seedlings. For example, in temperate deciduous forest in the United States, Meadow Vole predation of tree seedlings is highest at the forest edge, whilst White-tailed Deer seedling predation is highest in the forest interior. Thus, near the edge, species preferred by voles suffer higher herbivory, whilst species that are browsed by both voles and deer do not experience a clear change in herbivory pressure (Cadenasso and Pickett 2000). Similarly, at subtropical rainforest – pasture boundaries on the Lamington Plateau in south-eastern Queensland, seedling herbivory by Red-necked Pademelons is highest within a few metres of the forest edge and the greatest damage is suffered by those species most preferred by pademelons (Wahungu *et al.* 1999, 2002). Therefore, changes in trophic interactions at forest edges depend upon the habitat associations of the different members of the herbivore community and upon their dietary preferences, which are influenced at least to some extent by the physical and chemical properties of the leaves of each plant species (Coley and Barone 1996). In contrast, the rate and amount of herbivore damage to the leaves of seedlings did not differ between the edge and the interior of tropical lowland rainforest in Chiapas, Mexico although the incidence of leaf fungal infection was higher near the forest edge (Benitez-Malvido and Lemus-Albor 2005).

In this chapter, I examined whether the survival and growth of early-, intermediate- and late-successional tree seedlings were altered near the edges of linear canopy openings or among edge types (powerlines, highways and creeks). I also examined whether seedling herbivory increased near the edges of linear canopy openings and whether this differed among species with differing successional status.

7.1.1 Research Questions

The following questions were addressed in this section of the project:

1) Are the survival and growth of seedlings of species from different successional classes (and thus different physiological tolerances) affected by distance from the edges of linear canopy openings and by the type of linear canopy opening (powerline, highway and creek)?
2) Is vertebrate herbivory pressure greater near the forest edge? Does this differ among edge types and among different seedling successional classes?

In regard to my first question, I predicted that early successional species would experience greater survival and growth near the edges of linear canopy openings, whilst late-successional species would experience lower survival (and possibly slower growth) near the forest edge and intermediate species would display an intermediate pattern. With respect to the second question, I predicted that vertebrate herbivory pressure would be greater near the edges of linear canopy openings than in the forest interior, particularly for early-successional species, which may have leaves with fewer chemical and structural defences than late-successional species (Coley and Barone 1996).

7.2 Materials and Methods

7.2.1 Study Species

Seeds of early, mid and late-successional tree species were collected in December 2003 and January 2004. Seeds were collected under Queensland Environmental Protection Agency permits WISP00673802 and WITK00672502 and Queensland State Forests permit ATH 02/015. Species selection was opportunistic, as many rainforest trees display “mast fruiting”, with high fruit production in some years and very low fruit production in others (Connell *et al.* 2005). The mid-successional species *Antirrhea tenuiflora* (Rubiaceae), *Diploglottis smithii* (Sapindaceae), *Dysoxylum pettigrewianum (*Meliaceae) and *Dysoxylum muelleri* (Meliaceae) were collected in the Wooroonooran National Park and South Johnstone State Forest (Table 7.1). Seeds were brought back to the Cairns campus of James Cook University where they were soaked in cold water for 24 – 48 hours (to eliminate seed-boring insects; advice from N. Tucker), before the flesh (or aril) was removed (to improve germination; advice from N. Tucker). Seeds were planted into trays of sterile potting mix [mixture of potting mix with added dolomite (~500 g per m^3 potting mix) and slow release fertiliser with N:P:K ratio of 16:4:4 (Osmocote ~1 kg per m^3 potting mix); advice from N. Tucker], and lightly covered with quincan gravel (volcanic scoria; advice from N. Tucker). Trays of seedlings were placed in shade-houses at the Cairns campus of James Cook University with automatic watering systems set to a watering frequency of approximately once every 10 – 15 minutes. Seedlings that germinated in the shade-house were transplanted into individual pots (5 cm * 5 cm * 10 cm depth) between 9 and 17 April, 2004.

Although seeds of the early-successional species *Omalanthus novo-guineensis* (Euphorbiaceae) were also collected, these failed to germinate. In addition, seeds of late-successional tree species could not be located, despite extensive searching. This left only the seedlings of intermediate species available for the experiment. To overcome this limitation, seedlings of two early-successional tree species [*Alphitonia petriei* (Rhamnaceae) and *Omalanthus novo-guineensis* (Euphorbiaceae)] and two late-successional tree species [*Argyrodendron peralatum* (Sterculiaceae) and *Syzygium gustavioides* (Myrtaceae)] were purchased from the Eacham Shire Nursery (near Malanda on the Atherton Tablelands) (Table 7.1) on the 1st of July 2004. These seedlings were grown in the open air from seed sourced within the Atherton Tablelands region.

Table 7.1. Study species. Data on growth habit, successional status, fruit type and dispersal mode are taken from Cooper and Cooper 1994, Tucker and Murphy 1997, Tucker 2001 and Hyland *et al*. 2003. Fruit size is divided into three categories (following Tucker and Murphy 1997): small (S, width < 1.0 cm), intermediate (I, width 1.0 - 2.0 cm) and large (L, width > 2.0 cm). Crawford's Lookout (17° 36' 29" S, 145° 47' 30" E), Palmerston Highway (17° 37' 16" S, 145° 48' 10" E) and Henrietta Creek (17° 36' 31" S, 145° 46' 26" E) are on the eastern edge of Wooroonooran National Park and K-tree road (~ 17° 37' 00" S, 145° 45' 00" E) is a forestry road in the South Johnstone State Forest. N = number of seedlings used in the experiment.

Species (Family)	**Growth Habit**	**Successional Status**	**Fruit Type (Size)**	**Dispersal**	**Seed Source Mode**	**Collection Date**	**N**
Omalanthus novo-guineensis (Warb.) Schum (Euphorbiaceae)	Tree (20 m)	Early	Dehiscent, seed arillate	Biotic	Eacham Shire Nursery	n/a	128
Alphitonia petriei C.T. White & Braid (Rhamnaceae)	Tree (40 m)	Early	Capsule (S)	Biotic	Eacham Shire Nursery	n/a	61
Antirrhea tenuiflora Benth. (Rubiaceae)	Tree	Intermediate	Simple, fleshy (S)	Biotic	Crawford's Lookout	6 - 10, January, 2004	64
Diploglottis smithii S.T. Reynolds (Sapindaceae)	Tree (15 m)	Intermediate	Dehiscent, seed arillate (L)	Biotic	K-tree road	3 - 9 December, 2003	320
Dysoxylym pettigrewianum F.M. Bailey (Meliaceae)	Tree (35 m)	Intermediate	Dehiscent, seed arillate (L)	Biotic	Henrietta Creek	6 - 10 January, 2004	128
Dysoxylum muelleri Benth. (Meliaceae)	Tree (35 m)	Intermediate	Dehiscent, seed arillate (L)	Biotic	Palmerston Highway	6 - 10 January, 2004	254
Argyrodendron peralatum (Bailey) Edlin ex J.H. Boas (Sterculiaceae)	Tree (canopy)	Late	Winged, samara (L)	Wind	Eacham Shire Nursery	n/a	64
Syzygium gustavioides (Bailey) B. Hyland (Myrtaceae)	Tree (40 m)	Late	Nut, simple (L)	Biotic	Eacham Shire Nursery	n/a	64

7.2.2 Research Design

The purpose of this section of the project was to determine whether the survival and growth of seedlings from early-, mid- and late-successional species were affected differently by distance from the edges of linear canopy openings, the type of linear canopy opening (powerline, highway and creek) and the presence or absence of vertebrate herbivory pressure. To this end, seedlings were planted at different distances (2, 12, 25, 50 and 100 m; and –10 m on powerline transects) along the transects described in Chapter 3 (Figure 7.1). However, due to low germination rates in some species, there were only sufficient seedlings available for half of the 12 transects; thus, only the site 2 transects were used for this part of the project. To measure the effect of vertebrate herbivory on seedling survival and growth and whether this varies with distance from the forest edge, half of the seedlings were planted inside herbivore exclusion cages, which were constructed from wooden posts and wire mesh (6 * 6 mm mesh size, 0.63 mm gauge) (Plate 7.1; Figure 7.2). This mesh width was chosen to exclude most vertebrate herbivores without substantially reducing light availability to seedlings within this "caged" treatment. This gave a total of 3 edge types * 2 transects * 5 distances * 2 herbivory treatments = 60 seedling plots (+ 4 extra plots within the powerline clearing). As light availability is a major determinant of seedling growth rates (Whitmore 1996), the red:far red ratio was measured at breast height (see Chapter 4), directly above each seedling plot (Figure 7.1), towards the end of the experiment (24th June – 1st July, 2005).

Seedlings were transplanted from the shadehouse into the field between the 30th of June and the 6th of August, 2004 (Table 7.2); seedlings were planted in a random arrangement within each "caged" or "open" plot and watered in as required. Censuses of seedling survival and growth were performed approximately every 4 weeks, between August 2004 and August 2005. At each census, each seedling was checked to determine whether it was still alive and the height of the apical bud (to the nearest 0.5 cm) was measured.

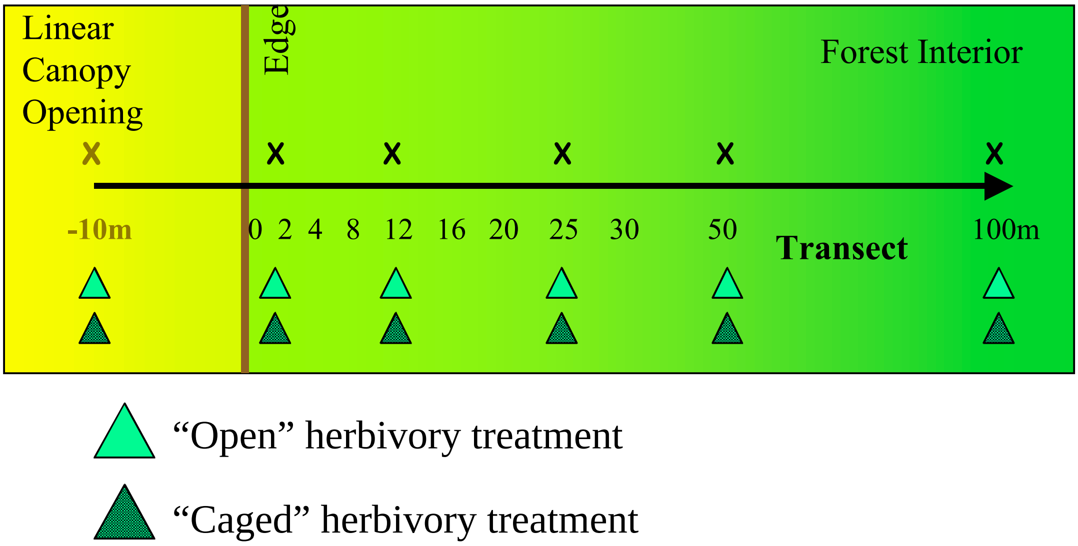


Figure 7.1. The set-up for the seedling experiment. Seedlings were planted at each distance marked with an “X”. Distances marked in beige were only measured on the powerline transects. At each distance, two seedling plots were established; one “caged” treatment, to exclude vertebrate herbivores and one “open” treatment.

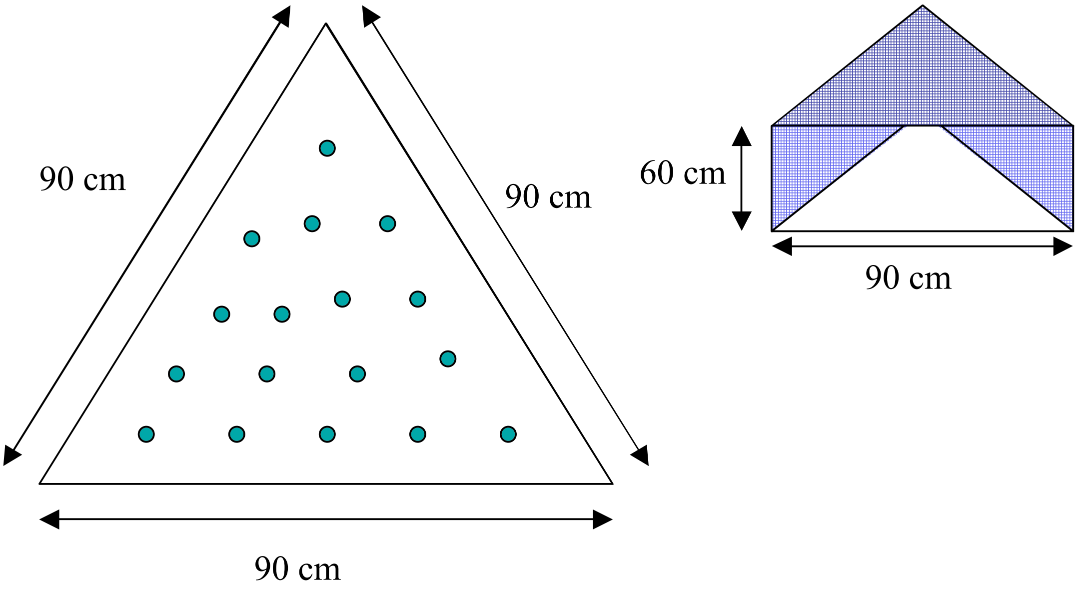


Figure 7.2. The design of the herbivore-exclusion cages. Cages were built around a triangular base (90 cm equilateral triangle) with a height of 60 cm. Three wooden posts (painted with mould-resistant paint) were placed at the three corners of the triangle and the wire mesh was wrapped around them. Seedlings were spaced at least 10 cm apart (and at least 10 cm from the edge of the mesh).

Plate 7.1. Herbivore-exclusion cages at 12 m (foreground) and 2 m (background) from the powerline edge. The matched "open" plots are located approximately 5 m to the right of each of these cages. Accumulated litter was cleared from the tops of all cages at each seedling census. The wire cages were constructed so that they could be lifted off the three wooden stakes to allow seedling measurements.

Table 7.2. Planting dates. Exceptions to the main planting dates are given in parentheses.

Edge Type	Transect	Planting Date
Powerline	One	22 July 2004 (-10 m: 27 July 2004)
	Two	27 July 2004
Highway	One	16 July 2004
	Two	7 July 2004 (Open: 9 July 2004)
Creek	One	30 June 2004 (*Omalanthus*, *Alphitonia*, *Argyrodendron* and *Syzygium*: 6 August 2004)
	Two	6 August 2004

7.2.3 Statistical Analysis

Due to uneven replication (1 seedling per plot; *Alphitonia*, *Argyrodendron*, *Syzygium*: 2 seedlings per plot: *Omalanthus*, *Dysoxylum pettigrewianum*; 4 seedlings per plot: *Dysoxylum muelleri*; 5 seedlings per plot: *Diploglottis smithii*), each species was analysed separately. Relative growth rates were calculated from the slope of the regression of *ln*(height) over time (in days) for each individual seedling. A simple linear regression was used as this offered the best fit for the range of growth behaviours displayed (Figure 7.3) and the r^2 for these regressions was generally high (0.45 – 0.8). However, because a large proportion (68.7%) of seedlings displayed zero growth, a second, binomial growth measure was evaluated (0 = no growth or negative growth rate, 1 = positive growth rate). The survival time of a seedling was recorded as the time (in days) between the date it was planted into the field experiment and the census at which it was last recorded alive (seedlings which remained alive at the end of the experiment were assigned a survival time equal to this entire period).

Seedling survival was assessed for each species. Three techniques were used:

1) ANCOVA of final percent survival (with fixed factors edge type, distance, and herbivory treatment and the covariate red:far red ratio) for *Diploglottis smithii* and *Dysoxylum muelleri*;
2) Backwards conditional binomial logistic regressions of final survival [dichotomous dependent variable is survival (0 = dead, 1 = alive), and the independent variables edge type, distance, herbivory treatment and red:far red

ratio] for *Argyrodendron peralatum*, *Antirrhea tenuiflora* and *Dysoxylum pettigrewianum*; and

3) Kruskal-Wallis tests on survival time for *Omalanthus novo-guineensis*, *Alphitonia petriei* and *Syzygium gustavioides*.

Seedlings within the powerline clearing (-10 m) were not included in these analyses.

Seedling growth was analysed for each species using backwards conditional binomial logistic regressions, with the dichotomous dependent variable being binary growth (0 = no growth or negative growth rate, 1 = positive growth rate) and independent variables edge type, distance, herbivory treatment and red:far red ratio. Seedlings within the powerline clearing (-10 m) were not included in these analyses. Discrete variables with more than two values, such as edge type (with values ‘powerline’, ‘highway’ and ‘creek’) were transformed into two dichotomous variables for binomial logistic regressions; each of these variables has values of ‘1’ and ‘0’ and has been designed to differentiate powerline and creek transects (edge 1) and highway and creek transects (edge 2). Creek transects were designated as the ‘0’ value for both variables as the greatest microclimatic contrasts (Chapter 4) and the greatest differences in plant community composition (Chapter 5) were between creek edges and anthropogenic edges. All statistical analyses were performed using SPSS 11.0 for Macintosh.

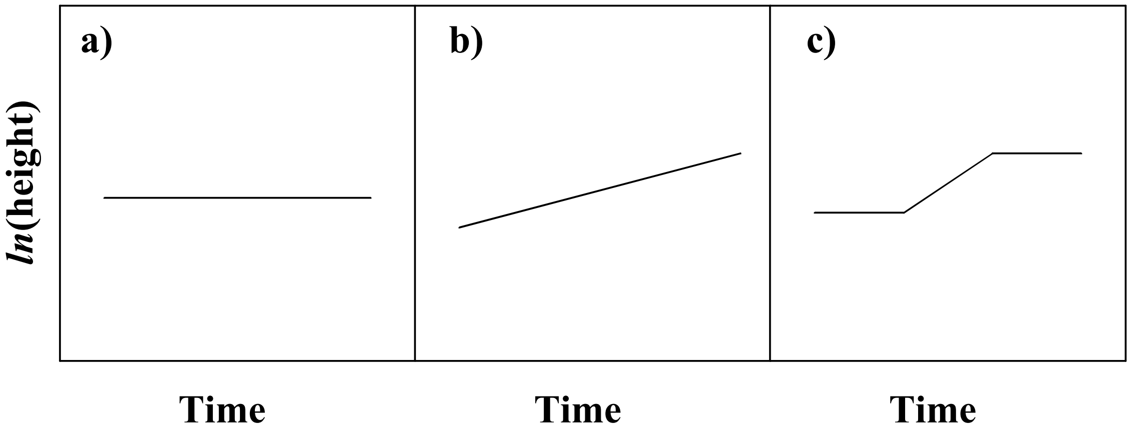


Figure 7.3. Growth patterns displayed by seedlings: **a**) no growth, **b**) linear growth and **c**) “stepped” growth.

7.3 Results

7.3.1 Seedling Survival

Overall percent survival of seedlings of *Diploglottis smithii* was affected by the exclusion of vertebrate herbivores. Survival was lower in “open” plots and the difference between “caged” and “open” plots was greatest on creek transects, least on powerline transects (Table 7.3; Figure 7.4a) and greater in the forest interior than on the forest edge (Table 7.3; Figure 7.4b). Overall percent survival of *Dysoxylum muelleri* increased with increasing red:far red ratio (Table 7.3; Figure 7.4f), was lower along creek (52.50 ± 8.49 %) transects than powerline (67.50 ± 6.04 %) or highway (65.00 ± 8.39 %) transects (Table 7.3; Figure 7.4d) and was lower in “open” (49.17 ± 6.51 %) than in “caged” (74.17 ± 5.29 %) herbivory plots (Table 7.3; Figure 7.4 d, e).

Overall survival of *Antirrhea tenuiflora* seedlings increased with increasing red:far red ratio (Figure 7.5c), was lower in “caged” than in “open” herbivory plots and was less likely along highway transects than along creek transects (Table 7.4; Figure 7.5a). Likewise, overall survival of *Dysoxylum pettigrewianum* seedlings increased with increasing red:far red ratio (Figure 7.5f) but was more likely along highway transects than along creek transects (Table 7.4; Figure 7.5d). Survival of *Argyrodendron peralatum* seedlings also increased with increasing red:far red ratio (Figure 7.5j) but was less likely along powerline transects than creek transects (Table 7.4; Figure 7.5g) although both of these effects were only marginally significant.

Survival time, rather than overall survival, of seedlings of *Omalanthus novo-guineensis*, *Alphitonia petriei* and *Syzygium gustavioides* was assessed as the overall survival of seedlings of these species was very low. Higher light availability (red:far red ratio) increased the survival time for *Omalanthus* but not *Alphitonia* or *Syzygium* seedlings (Table 7.5; Figure 7.6c, f, i). *Omalanthus* seedlings survived longer and the difference between “caged” and “open” survival times was greater along creek transects than along highway or powerline transects (Table 7.5; Figure 7.6a). In addition, there was a marginally significant distance by herbivory treatment interaction (Table 7.5), which was caused by longer survival of “caged” seedlings than “open” seedlings at 12 and 25 m from the forest edge (Figure 7.6b). Significant effects of edge type and edge type * herbivory on the survival time of *Alphitonia* and *Syzygium* seedlings (Table 7.5; Figure 7.6d, g) were caused by greater variability in survival times along creek transects (variability in survival time decreased from creek to highway to powerline transects).

However, there were no clear patterns in the influence of herbivory pressure on the survival of these species.

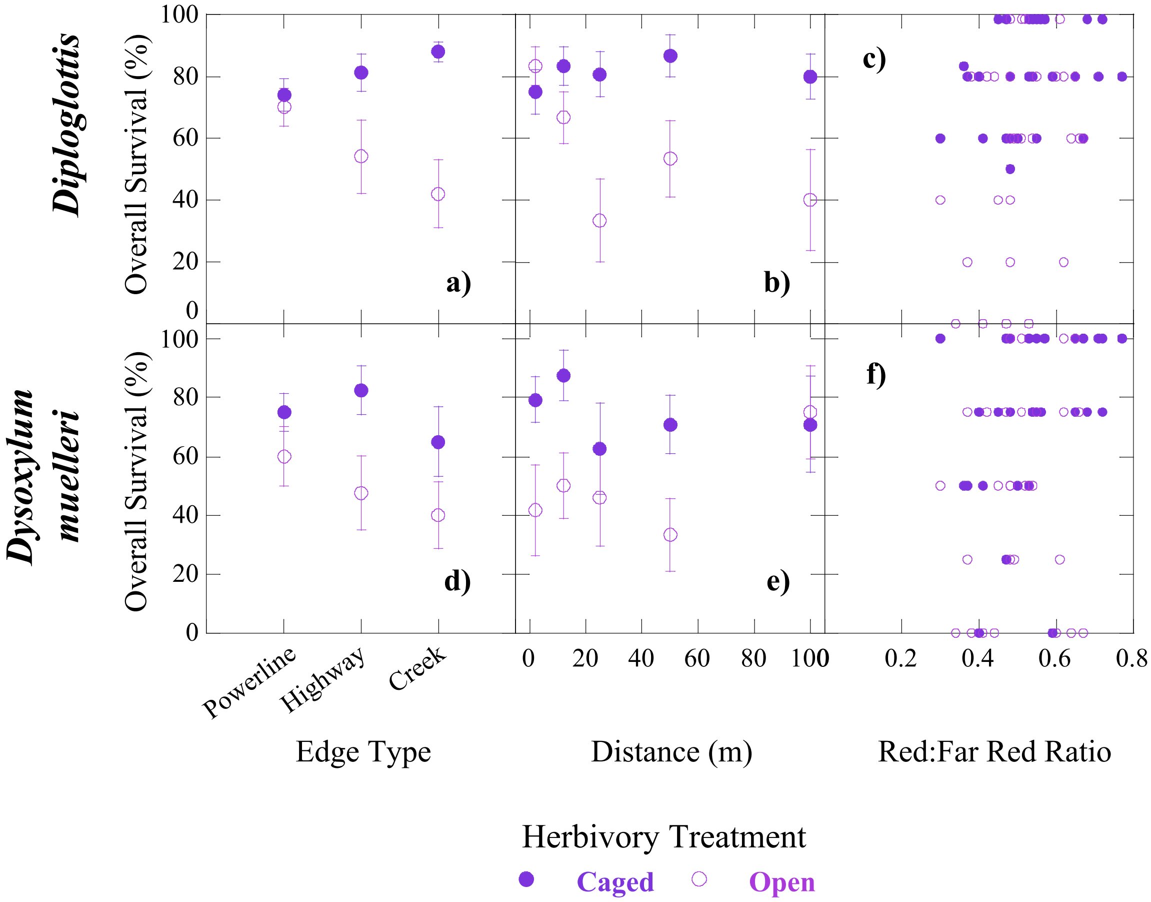


Figure 7.4. Variation in overall percent survival of *Diploglottis smithii* and *Dysoxylum muelleri* seedlings among edge types (**a** and **d**), with distance from the edges of linear canopy openings (**b** and **e**) and with light availability (red:far red ratio; **c** and **f**). Seedlings protected from vertebrate herbivores (“caged” herbivory treatments) are shown in filled symbols and seedlings exposed to vertebrate herbivores (“open” treatment) are shown in open symbols. Values are means ± 1 S.E.

Table 7.3. Overall percent survival for *Diploglottis smithii* (n = 5 replicate plants per plot) and *Dysoxylum muelleri* (n = 4 replicate plants per plot). Data were analysed with ANCOVA. Seedlings within the powerline clearing (-10 m) were not included in these analyses. Significant results ($\alpha < 0.05$) are highlighted in bold and marginally significant results ($\alpha < 0.10$) are highlighted in italics.

Species	**Variable**	***F***	**df**	***p*-value**
Diploglottis smithii	Red:far red (covariate)	2.652	1	0.114
	Edge type	1.307	2	0.286
	Distance	2.055	4	0.113
	Herbivory	16.899	1	**< 0.001**
	Edge type * distance	0.928	8	0.509
	Edge type * herbivory	4.048	2	**0.028**
	Distance * herbivory	2.919	4	**0.038**
	Edge type * distance * herbivory	1.090	8	0.398
Dysoxylum muelleri	Red:far red (covariate)	5.182	1	**0.030**
	Edge type	3.191	2	*0.056*
	Distance	1.543	4	0.216
	Herbivory	6.321	1	**0.018**
	Edge type * distance	1.864	8	0.105
	Edge type * herbivory	0.344	2	0.712
	Distance * herbivory	1.115	4	0.368
	Edge type * distance * herbivory	0.282	8	0.967

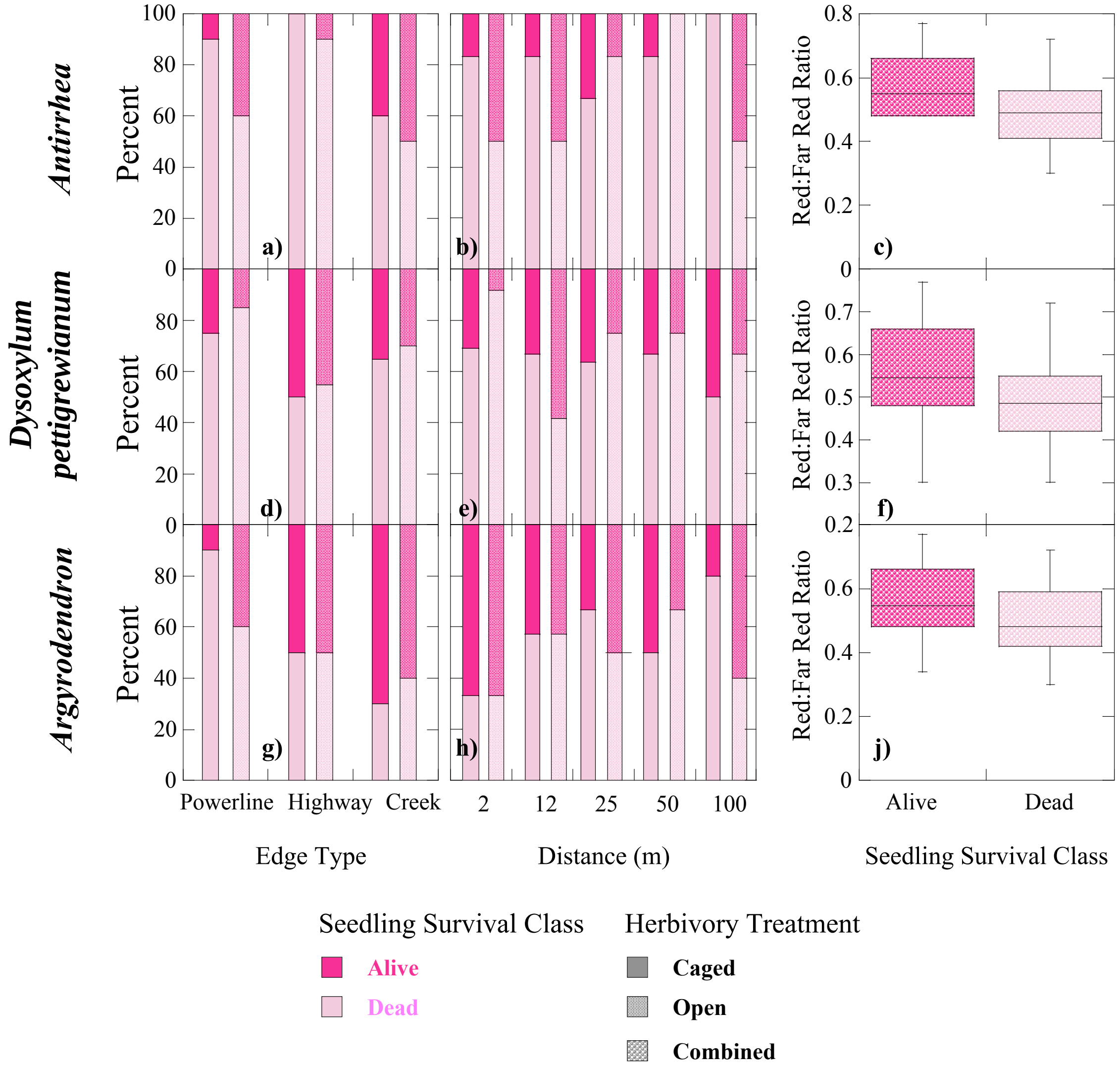


Figure 7.5. Variation in the overall survival of seedlings of *Antirrhea tenuiflora*, *Dysoxylum pettigrewianum* and *Argyrodendron peralatum*. Proportions of seedlings surviving and deceased at the end of the seedling experiment varied among edge types (**a**, **d** and **g**), with distance from the edges of linear canopy openings (**b**, **e** and **h**), with light availability (red:far red ratio; **c**, **f** and **j**) and between seedlings protected from (filled symbols) and exposed to (hashed symbols) vertebrate herbivores.

Table 7.4. Backwards-conditional binomial regressions for overall survival for *Antirrhea tenuiflora* (n = 1 replicate plant per plot), *Dysoxylum pettigrewianum* (n = 2 replicate plants per plot) and *Argyrodendron peralatum* (n = 1 replicate plant per plot). Species and edge types were analysed separately. Only variables that were included in the final models are shown. Seedlings within the powerline clearing (-10 m) were not included in these analyses. Significant results (α < 0.05) are highlighted in bold and marginally significant results (α < 0.10) are highlighted in italics.

Species	**Variable**	**B**	**Wald**	**df**	***p*-value**
Antirrhea tenuiflora¶	Red:far red	9.186	6.338	1	**0.012**
	Herbivory	1.565	4.002	1	**0.045**
	Edge type[1]	2.336	4.349	1	**0.037**
Dysoxylum pettigrewianum†	Red:far red	5.204	7.099	1	**0.008**
	Edge type[2]	-1.147	7.053	1	**0.008**
Argyrodendron peralatum‡	Red:far red	4.240	2.792	1	*0.095*
	Edge type[3]	1.215	3.799	1	*0.051*

¶ Model χ^2 = 17.867, df = 3, $p < 0.001$ and 83.3% classification accuracy.

† Model χ^2 = 12.928, df = 2, $p = 0.002$ and 73.3% classification accuracy.

‡ Model χ^2 = 8.841, df = 2, $p = 0.012$ and 70.0% classification accuracy.

[1] This edge type effect differentiates highway transects from creek transects. This positive term indicates that survival was more likely along creek transects than along highway transects.

[2] This edge type effect differentiates highway transects from creek transects. This negative term indicates that survival was more likely along highway transects than along creek transects.

[3] This edge type effect differentiates powerline transects from creek transects. This positive term indicates that survival was less likely along powerline transects than along creek transects.

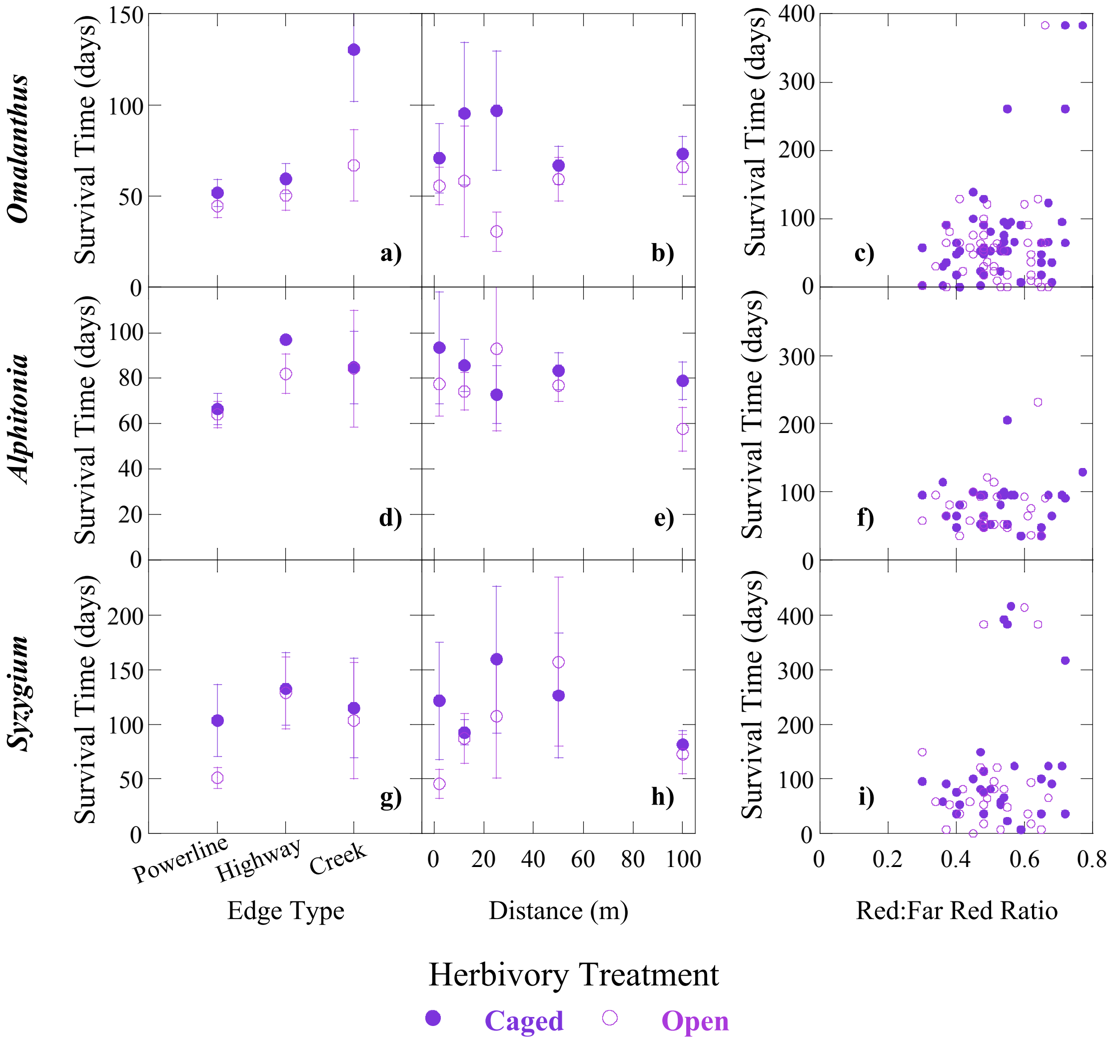


Figure 7.6. Variation in the survival time (in days) for seedlings of *Omalanthus novo-guineensis, Alphitonia petriei* and *Syzygium gustavioides*. Survival time varies among edge types (**a**, **d** and **g**), with distance from the edges of linear canopy openings (**b**, **e** and **h**), with light availability (red:far red ratio; **c**, **f** and **i**) and between seedlings protected from (filled symbols) and exposed to (open symbols) vertebrate herbivores. Values for **a**, **b**, **d**, **e**, **g** and **h** are means ± 1 S.E. Note the different scale on the y-axes of panels **c**, **f** and **g**.

Table 7.5. Kruskal-Wallis tests of factors affecting the survival time of seedlings of *Omalanthus novo-guineensis*, *Alphitonia petriei* and *Syzygium gustavioides*. Seedlings within the powerline clearing (-10 m) were not included in these analyses. Significant results ($\alpha < 0.05$) are highlighted in bold and marginally significant results ($\alpha < 0.10$) are highlighted in italics.

Species	**Variable**	χ^2	**df**	***p*-value**
Omalanthus novo-guineensis	Edge type	5.065	2	*0.079*
	Distance	8.409	4	*0.078*
	Herbivory	1387.5§	1	**0.030**
	Edge type * distance	15.404	14	0.351
	Edge type * herbivory	11.155	5	**0.048**
	Distance * herbivory	16.096	9	*0.065*
	Edge type * distance * herbivory	32.662	29	0.292
	Red:far red¶	0.225‡	na	**0.013**
Alphitonia petriei	Edge type	10.551	2	**0.005**
	Distance	1.673	4	0.796
	Herbivory	321.0§	1	0.177
	Edge type * distance	20.167	14	0.125
	Edge type * herbivory	13.567	5	**0.019**
	Distance * herbivory	5.375	9	0.800
	Edge type * distance * herbivory	32.963	29	0.279
	Red:far red¶	0.031‡	na	0.817
Syzygium gustavioides	Edge type	11.739	2	**0.003**
	Distance	2.108	4	0.716
	Herbivory	326.5§	1	0.143
	Edge type * distance	16.829	14	0.265
	Edge type * herbivory	14.661	5	**0.012**
	Distance * herbivory	4.930	9	0.840
	Edge type * distance * herbivory	24.569	29	0.700
	Red:far red¶	0.157‡	na	0.240

¶ Spearman correlations between survival time and red:far red ratio were performed separately to the Kruskal-Wallis tests.

‡ Spearman's rho. §Mann-Whitney U statistic.

7.3.2 Seedling Growth

Seedlings of *Omalanthus novo-guineensis* were more likely to experience positive growth rates along creek transects than along powerline or highway transects (Table 7.6; Figure 7.7a). Very few *Alphitonia petriei* seedlings experienced positive growth rates and neither edge type, distance from linear canopy openings, herbivory treatment nor red:far red ratio influenced the likelihood of seedlings displaying positive growth rates in this species (Table 7.6; Figure 7.7d, e, f). The probability of seedlings of *Antirrhea tenuiflora* experiencing positive growth rates increased with increasing red:far red ratio (Figure 7.7i) and was higher along creek transects than along highway transects (Table 7.6; Figure 7.7g) although these effects were only marginally significant. The probability of *Diploglottis smithii* seedlings experiencing positive growth rates increased with increasing red:far red ratio (Figure 7.7l) and was greater along creek transects (Table 7.6; Figure 7.7j). In contrast, although the probability of *Dysoxylum muelleri* seedlings experiencing positive growth rates increased with increasing red:far red ratio (Figure 7.7r), this probability decreased along creek transects relative to powerline and highway transects (Table 7.6; Figure 7.7p). *Dysoxylum pettigrewianum* seedlings were influenced only by light availability; the probability of positive growth rates increased with increasing red:far red ratio (Table 7.6; Figure 7.7o). *Argyrodendron peralatum* seedlings were more likely to experience positive growth rates along creek transects than along powerline transects (Table 7.6; Figure 7.7s). There were no *Syzygium gustavioides* seedlings that experienced positive growth rates.

Although the effect of distance from the edges of linear canopy openings did not contribute significantly to the probability of seedlings of any species experiencing positive growth, there were non-significant trends for three species. A higher proportion of seedlings of the mid-successional species *Antirrhea tenuiflora* and *Diploglottis smithii* experienced positive growth rates within 12 to 25 m of the forest edge than in the forest interior and a lower proportion of seedlings of the late-successional species *Argyrodendron peralatum* experienced positive growth rates within 25 m of the forest edge than in the forest interior (Figure 7.7).

Although differences in the probability of seedlings experiencing positive growth rates along powerline transects relative to highway transects were not specifically tested, no overall patterns emerged. Three species were slightly more likely to experience positive growth rates along powerline transects and four species were slightly more likely to experience positive growth rates along highway transects (Figure 7.7).

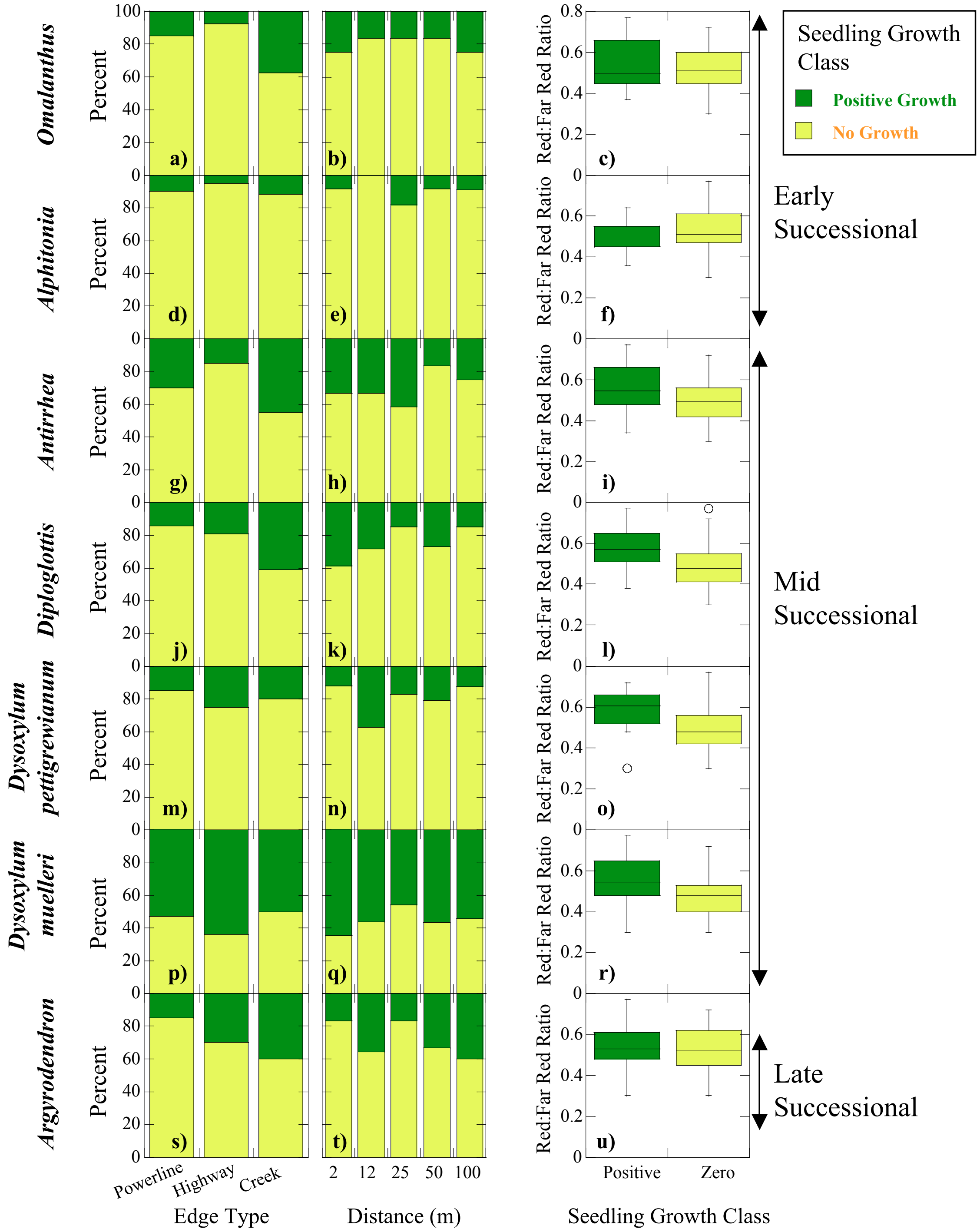


Figure 7.7. Variation in the proportion of seedlings which experienced positive growth rates (green symbols) or no growth (yellow symbols) differs among edge types (**a**, **d**, **g**, **j**, **m**, **p** and **s**), with distance from the edges of linear canopy openings (**b**, **e**, **h**, **k**, **n**, **q** and **t**) and usually increases with increasing light availability (red:far red ratio; **c**, **f**, **i**, **l**, **o**, **r** and **u**). No *Syzygium gustavioides* seedlings experienced positive growth beneath the rainforest canopy.

Table 7.6. Backwards-conditional logistic binomial regressions for growth rate (0 = no growth or negative growth rate, 1 = positive growth rate). Species and edge types were analysed separately. Only variables that were included in the final models are shown. Seedlings within the powerline clearing (-10 m) were not included in these analyses. Significant results ($\alpha < 0.05$) are highlighted in bold and marginally significant results ($\alpha < 0.10$) are highlighted in italics.

Species	**Variable**	**B**	**Wald**	**df**	***p*-value**
Omalanthus novo-guineensis[¶]	Edge 1[a]	1.224	4.947	1	**0.026**
	Edge 2[b]	2.001	8.577	1	**0.003**
Alphitonia petriei	Constant only	na	na	na	na
Antirrhea tenuiflora[‡]	Red:far red	4.870	2.976	1	*0.085*
	Edge type[b]	1.132	2.464	1	0.116
Diploglottis smithii[§]	Red:far red	6.041	18.247	1	**< 0.001**
	Edge 1[a]	1.018	7.277	1	**0.007**
	Edge 2[b]	0.737	4.494	1	**0.034**
Dysoxylum pettigrewianum[fi]	Red:far red	6.887	8.914	1	**0.003**
Dysoxylum muelleri[¢]	Red:far red	8.649	31.615	1	**< 0.001**
	Edge 1[c]	-0.754	4.165	1	**0.041**
	Edge 2[d]	-1.282	10.851	1	**0.001**
Argyrodendron peralatum[¥]	Edge type[a]	1.115	2.478	1	0.115
Syzygium gustavioides	No positive growth experienced			na	na

¶ Model $\chi^2 = 12.044$, df = 2, $p = 0.002$ and 80.0% classification accuracy.

‡ Model $\chi^2 = 6.633$, df = 2, $p = 0.036$ and 71.7% classification accuracy.

§ Model $\chi^2 = 42.101$, df = 3, $p < 0.001$ and 77.0% classification accuracy.

fi Model $\chi^2 = 9.916$, df = 1, $p = 0.002$ and 78.3% classification accuracy.

¢ Model $\chi^2 = 42.389$, df = 3, $p < 0.001$ and 63.0% classification accuracy.

¥ Model $\chi^2 = 2.825$, df = 1, $p = 0.093$ and 71.7% classification accuracy.

[a] This edge type effect differentiates powerline transects from creek transects. This positive term indicates that growth was more likely along creek transects than along powerline transects.

[b] This edge type effect differentiates highway transects from creek transects. This positive term indicates that growth was more likely along creek transects than along highway transects.

[c] This edge type effect differentiates powerline transects from creek transects. This negative term indicates that growth was less likely along creek transects than along powerline transects.

[d] This edge type effect differentiates highway transects from creek transects. This negative term indicates that growth was less likely along creek transects than along highway transects.

7.3.2.1 Seedling Growth Within the Powerline Clearing

Due to low replication, seedling survival and growth within the powerline clearing were not analysed quantitatively; results are presented for qualitative comparison only. Survival was lower in plots on the southern side of the powerline clearing (compared to the northern side) for all species. Survival also tended to be lower in "open" plots than in "caged plots" for all species. Averaged across plots on the northern and southern sides of the powerline clearing, seedling relative height growth rates were generally higher in "caged" plots than in "open" plots and were higher for the pioneer species *Omalanthus novo-guineensis* than the other pioneer species, *Alphitonia petriei*, or any of the mid- and late-successional species (Figure 7.8).

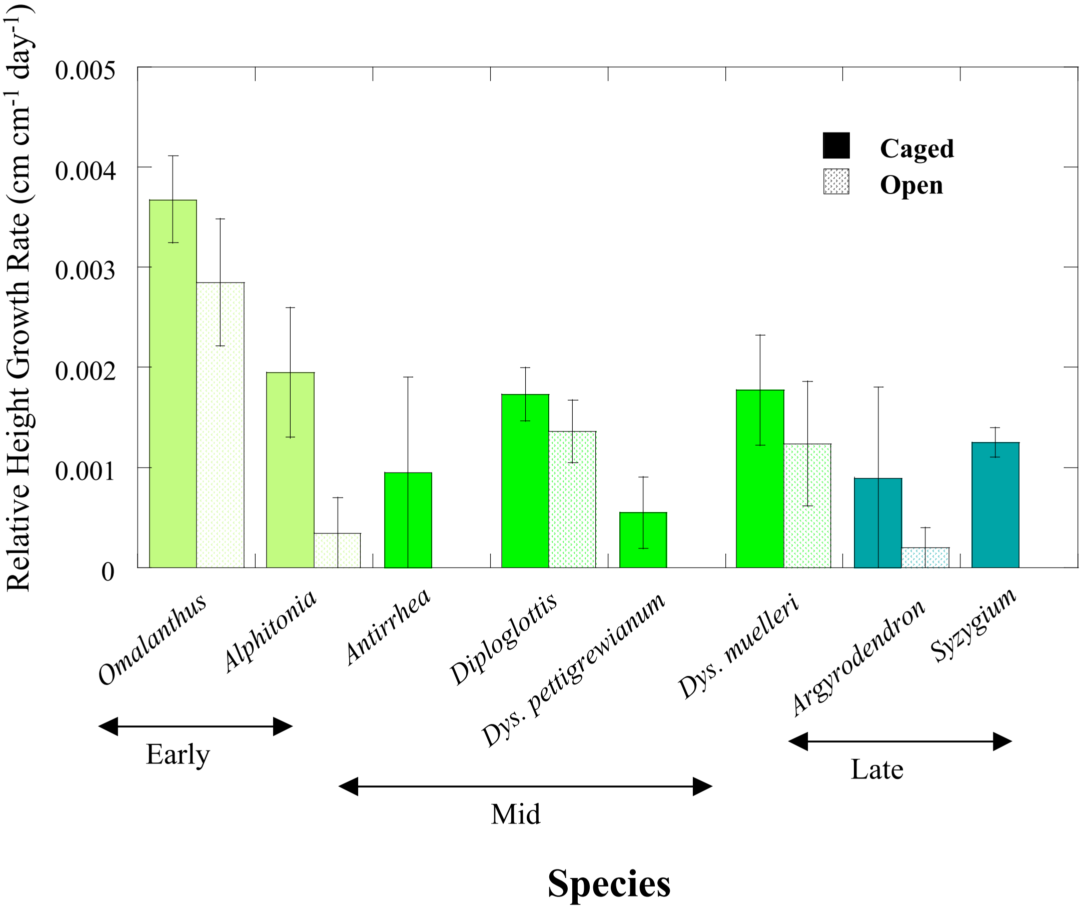


Figure 7.8. Seedling relative height growth rates (cm cm^{-1} day^{-1}) for "caged" and "open" plots within the powerline clearing (-10 m), for early- (*Omalanthus novo-guineensis* and *Alphitonia petriei*), mid- (*Antirrhea tenuiflora*, *Diploglottis smithii*, *Dysoxylum pettigrewianum* and *Dysoxylum muelleri*) and late-successional (*Argyrodendron peralatum* and *Syzygium gustavioides*) species. Values are means and standard errors.

7.4 Discussion

7.4.1 Are the Survival and Growth of Early-, Mid- and Late-Successional Tree Seedlings Differentially Affected by Distance from Linear Canopy Openings?

There was no clear relationship between distance from the edges of linear canopy openings and the survival and growth of seedlings of species from different successional classes. The early-successional species, *Omalanthus novo-guineensis* and *Alphitonia petriei*, did not display the expected increases in survival and growth rate near the edges of linear canopy openings although survival and growth of *Omalanthus* seedlings were favoured at higher light levels and along creek edges (which had both higher light availability and lower moisture stress; Chapter 4). In fact, *Omalanthus* seedlings survived only in microsites with the highest light availability (creek edges and within the powerline clearing). The *Alphitonia* seedlings obtained from the Eacham Shire Nursery were root-bound and it is possible that the poor performance of these seedlings in the field may have been caused by poor initial health. The performance of *Omalanthus* seedlings is consistent with the higher proportion of light-demanding species found near creek edges relative to anthropogenic edges (herbs, understorey tree seedlings and canopy tree seedlings; Chapter 5) and seems likely to be due to the higher light availability near creek edges (Chapter 4).

Survival and growth of seedlings of the late-successional species, *Argyrodendron peralatum* and *Syzygium gustavioides*, were not significantly affected by distance from the forest edge, but higher light availability increased the survival of *Argyrodendron* seedlings and, at creek edges, survival and growth of *Argyrodendron* seedlings were greater than that experienced along powerline transects. In addition, there was a slight, non-significant trend towards decreased probability of positive *Argyrodendron* seedling growth within 25 m of the edges of linear canopy openings (Figure 7.7f). Very few *Syzygium* seedlings survived and none experienced positive growth rates such that the poor performance of these seedlings may have masked any trends in the data. Declines in the abundance of late-successional tree seedlings have been detected at the edges of tropical forest fragments in Brazil (Benitez-Malvido 1998) and north-east Queensland (Turton and Freiburger 1997) but were not found near fragment edges in pre-montane forest in Panama (Williams-Linera 1990a). In this study (Chapter 5), the abundance of late-successional canopy tree seedlings declined near powerline and highway edges but not near creek edges. The greater survival and growth of *Argyrodendron* seedlings along creek transects relative to powerline edges are consistent with these edge type effects (Chapter 5), but the lack of significant distance effects on seedling survival or growth is not. These data suggest that physiological tolerance of environmental conditions may not be the sole mechanism influencing the abundance of late-successional tree seedlings near powerline and highway edges. Other possible mechanisms might include increased competition from other species (eg herbs, lianas or early- or mid- successional tree seedlings) and altered disturbance regimes associated with athropogenic edges (eg maintenance), although the increased seedling survival along creek transects relative to powerline transects and the positive effect of red:far red ratio on seedling survival suggest that microclimatic conditions probably do play an important role.

Amongst the mid-successional species, seedling survival and growth increased with increasing light availability for all species except *Diploglottis smithii*, for which survival was affected only by herbivory exposure (although growth still increased with higher light availability). Distance from the edges of linear canopy openings did not significantly affect the survival or growth of any species although there were slight, non-significant increases in the proportion of *Antirrhea tenuiflora* and *Diploglottis smithii* seedlings experiencing positive growth rates within 12 – 25 m of edges (Figure 7.7h and k). Creek edges promoted survival and/or growth for two species (*Diploglottis smithii* and *Antirrhea tenuiflora*) but reduced the growth of *Dysoxylum muelleri* and the survival of *Dysoxylum pettigrewianum* seedlings. These contrasting responses of the two *Dysoxylum* species to light availability and creek edges (which had higher light levels and lower moisture stress than anthropogenic transects; Chapter 4), suggest that these species may have been more vulnerable to pathogen infection in the moister air and higher herbivory pressure near creek edges as demonstrated by significant edge type * herbivory treatment interactions for survival of *Diploglottis* and *Omalanthus* (Figure 7.4a and Figure 7.6a). In support of this hypothesis, Garcia-Guzman and Dirzo (2001) have shown that herbivore wounding of leaves increases fungal pathogen infection. Alternatively, the greater survival of several other species along creek edges may have increased the competition between seedlings along creek edges. However, as *Dysoxylum muelleri* survival responded negatively to and *Dysoxylum pettigrewianum* survival was unaffected by herbivory exposure (and the resulting lower number of surviving seedlings in exposed “open” seedling plots), it seems unlikely that seedling competition was a major factor contributing to the negative effect of creek edges on the performance of these species. In contrast, the positive survival response of *Antirrhea* seedlings to the exposed herbivory treatment suggests that this species may have been negatively affected by competition with other surviving seedlings.

The lack of any significant relationships between distance from the edges of linear canopy openings and the survival and growth of early-, mid- or late-successional seedlings may have been a result of the generally low light level beneath the forest canopy. Red:far red ratio is correlated with the log of percent canopy transmittance (Capers and Chazdon 2004), meaning that the light levels measured in this study would have varied between 1% and ~4%, relative to light intensity above the forest canopy, with occasional patches up to ~8%, especially along creek transects (see regression of red:far red and % canopy transmittance in Capers and Chazdon 2004). At the lower light levels, many species may be at or near their light compensation points and small increases in light level will have strong effects on seedling survival although the range of light levels may be too small to allow growth rate and competitive differences between early-, mid- and late-successional species to be fully expressed (Agyeman *et al.* 1999; Kobe 1999; Poorter 1999). Even the higher light levels experienced along creek edges may not be sufficient to allow the maximum growth rates of any tree species (Agyeman *et al.* 1999; Kobe 1999; Poorter 1999). This suggests that the forest edges near these linear canopy openings have become sufficiently "sealed" (Harper *et al.* 2005) to prevent the future establishment of clear successional patterns of regeneration with distance from the forest edge, although the higher light levels along creek edges may allow the persistence of early- as well as mid- and late-successional species.

7.4.2 Is Vertebrate Herbivory Pressure Greater Near the Forest Edge?

Within the rainforest understorey, herbivory exposure affected the seedling survival, although not the growth rates, of half of the species included in this study (*Omalanthus novo-guineensis, Diploglottis smithii, Dysoxylum muelleri* and *Antirrhea tenuiflora*). Survival was higher for "caged" (protected) *Dysoxylum muelleri* seedlings but lower for "caged" *Antirrhea tenuiflora* seedlings. Neither of these species displayed a change in herbivory pressure with distance from the edges of linear canopy openings. In contrast, herbivory pressure (the difference in seedling survival between "caged" and "open" seedling plots) was affected by distance from the forest edge for seedlings of the pioneer species *Omalanthus novo-guineensis* and the mid-successional species

Diploglottis smithii. *Omalanthus* seedlings at 12 and 25 m survived for longer in "caged" plots than in "open" plots whilst the survival of seedlings at other distances was not affected by herbivory exposure. This effect was driven by longer survival time of "caged" seedlings at these distances along creek transects rather than highway or powerline transects (Figure 7.4). The increased survival time along creek edges is likely to be due to higher light availability and possibly to decreased moisture stress (Chapter 4). Therefore, the difference between exposed and protected seedlings may not indicate greater herbivory pressure near the forest edge than in the forest interior, given that overall seedling survival is less likely in the lower light environments of the forest interior (Table 7.5; Chapter 4). However, Red-legged Pademelons (*Thylogale stigmatica*) are known to browse on *Omalanthus* seedlings within powerline clearings (Nigel Tucker *pers. comm.*) and are attracted to forest edges by the abundant grasses available in clearings (Vernes *et al.* 1995). Thus it is possible that this change in herbivory with distance is genuine although the presence of flowing water, rather than grass, may attract Pademelons or other mammals to creek edges.

The effect of herbivory exposure on the survival of *Diploglottis smithii* seedlings was greater in the forest interior than within 12 m of the edges of linear canopy openings (Figure 7.4). This result contradicts my initial prediction that herbivory pressure would be greater near the forest edge than in the forest interior. However, the distributions of principal herbivore species relative to the forest edge, in combination with changes in palatability of foliage, are likely to determine the spatial pattern of herbivory pressure experienced by plant seedlings (Coley and Barone 1996; Cadenasso and Pickett 2000).

Possible seedling herbivores in the study region include the Long-nosed Bandicoot (*Perameles nasuta*), the Red-legged Pademelon (*Thylogale stigmatica*), the Fawn-footed Melomys (*Melomys cervinipes*), the Giant White-tailed Rat (*Uromys caudimaculatus*), the Bush Rat (*Rattus fuscipes*) and the Cape York Rat (*R. leucopus*) (Strahan 1995). *Melomys* abundance is known to increase whilst the abundances of *R. fuscipes* and *R. leucopus* decrease near the edges of powerline clearings and highways (Goosem and Marsh 1997; Goosem 2000). *Uromys* abundance does not appear to be affected by proximity to linear canopy openings (Goosem and Marsh 1997) but decreases in smaller rainforest fragments (Laurance 1994; Harrington *et al.* 2001). The conical diggings of *P. nasuta* (Strahan 1995) were observed near powerline, highway and creek edges in this study (*pers. obs.*) and this species may favour smaller fragments and forest edges (Harrington *et al.* 2001; Vernes *et al.* 2001). The home range of *T. stigmatica* near rainforest edges includes a diurnal forest interior range and a nocturnal forest edge range where grasses and seedlings within and beyond the forest edge are intensively browsed (Vernes *et al.* 1995). The closely related subtropical species, *T. thetis*, also forages heavily on grasses and seedlings near rainforest edges (Wahungu *et al.* 1999, 2000).

Alternatively, it is possible that the main seedling predators may not be mammals. For example, Orange-footed Scrub Fowl (*Megapodius reinwardt*), Brush Turkeys (*Alectura lathami*) or Chowchillas (*Orthonyx spaldingii*) may uproot seedlings while digging through leaf litter on the forest floor (Theimer and Gehring 1999). *M. reinwardt* and *A. lathami* are able to persist in all but the smallest (< 1 - 4.5 ha) rainforest fragments while *O. spaldingii* is frequently absent in fragments < 32 ha on the nearby Atherton Tablelands (Warburton 1997). This suggests that *M. reinwardt* and *A. lathami* may be less sensitive to fragmentation and possibly more tolerant of edge conditions that dominate small fragments (eg Laurance *et al.* 2002) than *O. spaldingii*; however, *O. spaldingii* has been observed within 50 m of highway and creek edges in the study area (*pers. obs.*).

If the principal seedling predators of *Diploglottis smithii* are species which decline near the forest edge (eg *R. fuscipes* and *R. leucopus* or *O. spaldingii*), this may explain the lower herbivory-related mortality in this species near forest edges. Conversely, if the main seedling predator of *Omalanthus novo-guineensis* is an edge-preferring species (eg pademelons are known to browse on young *Omalanthus* seedlings within powerline clearings; Nigel Tucker *pers. comm.*), this may explain the marginally significant herbivory exposure effect observed along creek transects for this species. It may also be that invertebrates (eg snails, insects) or pathogens influenced the patterns observed in this study. For example, in tropical lowland rainforest in Chiapas, Mexico, the incidence of leaf fungal infection was higher near the forest edge than in the forest interior (Benitez-Malvido and Lemus-Albor 2005) and, in temperate forest in north America, insect herbivory was higher on the forest edge than within the forest for one seedling species but not for three others (Meiners *et al.* 2000). Further study is required to determine the identity and spatial distribution of seedling predators, or other biological agents of seedling mortality (eg insects, pathogens) and their influence on the survival of seedlings near the edges of linear canopy openings within the Wet Tropics World Heritage Area of north-eastern Australia.

7.4.3 Synthesis

If the altered microclimatic conditions near the edges of linear canopy openings (Chapter 4) were to lead to a clear change in the successional status of recruiting tree seedlings (eg Benitez-Malvido 1998; Sizer and Tanner 1999), the survival and growth of the seedlings of earlier-successional species ought to be greater than those of later-successional species near the forest edge, with the pattern reversed in the forest interior. Unfortunately, the high percentage of seedlings that did not exhibit any height growth, and the low replication for some species, prevented a comparative analysis of relative growth rates between early-, mid- and late-successional species at different distances from the forest edge to the forest interior. Thus, the relative growth performance (and potentially competitive ranking) of species with different successional status could not be assessed. However, the generally low light levels experienced in the forest understorey (equivalent to ~ 1 – 4 % canopy transmittance), probably would have precluded the development of significant differences in growth rates (Agyeman *et al.* 1999; Kobe 1999; Poorter 1999); dominance at these light levels is more likely to be determined by inter-specific differences in mortality rates (Agyeman *et al.* 1999; Kobe 1999).

The only clear patterns between successional status and seedling mortality were the distinction between the survival of the pioneer species *Omalanthus novo-guineensis* and the survival of all mid- and late-successional species. *Omalanthus* seedlings survived only in plots with the highest light availability (12 – 25 m from creek edges and within the powerline clearing) whilst mid- and late-successional species survived across the entire light and edge distance spectrum beneath the rainforest canopy. Herbivory pressure was also not clearly related to successional status. Although half of the species in this study were affected by exposure to herbivory, the only successional pattern discernible was the lack of herbivory effects on the seedling survival or growth of late-successional species. The only clear change in herbivory pressure with distance from the forest edge was the decrease in herbivory-related mortality of *Diploglottis smithii* seedlings near the edge (Figure 7.4b).

These data do not provide clear support for a shift in the relative seedling performance of earlier- and later-successional species near the edges of linear canopy openings. In one respect, the increased survival time of protected ("caged" herbivory treatment) *Omalanthus* seedlings near creek edges is broadly consistent with the higher proportion of early-successional canopy tree species observed in the standing vegetation in those sites (Chapter 5). In contrast, the lack of a distance effect on the seedling survival or growth of mid-successional species is not consistent with the observed increase in the proportion of mid-successional species in the standing vegetation near anthropogenic edges (Chapter 5). It is possible, however, that an indirect edge effect is responsible for the increase in mid-successional species near the edges of anthropogenic edge clearings. In this study, the growth rates of all four mid-successional species responded positively to increased red:far red ratio (light availability) and this ratio was higher in the forest interior than between 4 m and 25 m of powerline and highway edges (Figure 4.8). As the nutritional value of foliage tends to increase with plant growth rate (Coley and Barone 1996), a combination of more nutritious seedling foliage and a forest-interior distribution of the principal herbivore species may have led to heavier mortality of mid-successional seedlings in the forest interior than near the forest edge (observed for *Diploglottis smithii* seedlings). This would indirectly favour the survival of mid-successional species near the edges of linear canopy openings.

Alternatively, these data may indicate that the mechanisms that produced the successional patterns observed in the standing edge vegetation are no longer influencing the dynamics of newly recruited seedlings. Microclimatic edge effects tend to be strongest immediately after edge creation (Kapos *et al.* 1997) and decrease over time as plant growth responds to the increased light availability and the edge becomes “sealed” (Didham and Lawton 1999; Harper *et al.* 2005). The current powerline and highway edges are approximately 15 years old and microclimatic edge gradients may no longer be strong enough to promote altered successional composition in newly-germinated tree seedlings. However, the positive effect of creek edges on the survival of pioneer species and the growth of several other species suggest that microclimatic edge gradients, particularly the strong gradients in light availability found at this more dynamic type of edge (Chapter 4) are sufficient to influence the dynamics of the seedling community near creeks.

There is also a question of time frame; the seedling community may take several years to establish. Seedling recruitment rates over 6 years in fragmented and continuous tropical forest in the central Amazon were not sufficient to re-establish the understorey seedling community in plots experimentally cleared of existing seedlings (Benitez-Malvido and Martinez-Ramos 2003a, b). The relatively short time span (1 year) of this study may not be sufficient to demonstrate the full range of variation in microclimate, herbivory pressure, seed fall and seedling recruitment and mortality that cumulatively shape the species composition of the seedling community near the forest edge. However, the decrease in herbivory pressure observed for *Diploglottis smithii* seedlings near the forest edge suggests that alterations in trophic interactions between seedlings and herbivores may be occurring for at least some species at the edges of linear canopy openings and the potential for such effects to alter the composition of the seedling pool requires further attention.

7.5 Conclusions

Two questions were addressed in this section of the project:

1) Are the survival and growth of tree seedlings with different successional status affected by distance from the edges of linear canopy openings and by the type of linear canopy opening (powerline, highway and creek) in different ways?
2) Is vertebrate herbivory pressure greater near the forest edge and does this differ among edge types and among different seedling successional classes?

In response to the first question, the survival and growth of seedlings from species from different successional classes did not display clear relationships with distance from the edges of linear canopy openings. Although seedling survival and growth rates of most species were positively influenced by increasing light availability, light levels beneath the forest canopy may have been too low to allow the development of transitions in the successional status of tree seedlings between the forest edge and the forest interior. However, whilst pioneer seedlings survived only in the environments with highest light availability (creek edges and within the powerline clearing), mid- and late-successional seedlings were able to survive over the entire span of distances between the forest edge and the forest interior.

In response to the second question, although seedlings of three species displayed greater survival when protected from vertebrate herbivory within the rainforest understorey, only one species displayed a significant ($\alpha < 0.05$) change in herbivory pressure with distance from the edges of linear canopy openings, and this change was opposite in direction to that predicted: herbivore-related morality was higher in the forest interior than near the edges of linear canopy openings for seedlings of the mid-successional species *Diploglottis smithii*. Reductions in growth rate in response to vertebrate herbivory pressure were only observed within the powerline clearing rather than in the rainforest understorey.

I recommend the following line of enquiry for further study:

This experiment should be repeated with greater replication (greater replication per species, a higher number of species and more plot replication per transect) and fewer distances per transect to allow direct comparisons between the growth and mortality rates of different species and a correlation of these rates with seedling foliar chemistry. A possible design might include a comparison of the edge (2 – 12 m) with the forest interior (100 m), for all three edge types (powerlines, highways and creeks), with the same two herbivory exposure treatments used in this study ("caged" and "open") although with slightly greater spacing between seedlings to avoid any possible density effects on seedling growth and survival (eg the positive response of *Antirrhea tenuiflora* seedlings to herbivore exposure). The number of plots per transect could be doubled (ie 2 * 2 distances * 2 herbivory treatments) and the replication per species could be increased (eg 5 replicate plants per species per plot). The number of species could be increased to 3 species per successional class (early, mid or late) to provide a broader representation within each class (especially if the three species covered the span of seed size within each successional class). The purpose of this experiment would be similar to that of this project; to determine whether the relative performance (measured via relative height growth rate and seedling survival) of seedlings from species with different successional status differs with distance from the edges of linear canopy openings (and among linear canopy opening types). The experiment would also test whether herbivory pressure varies differentially among species with distance from the forest edge and whether any patterns in herbivory are related to changes in the leaf foliar chemistry (eg nutritional value, concentration of secondary metabolites, structural thickening) of seedlings growing at different distances from the forest edge.

Chapter Eight: General Discussion and Conclusions

8.1 Introduction

The research questions addressed in this thesis were:

1) Do linear canopy openings produce horizontal edge gradients (in microclimate, vegetation structure and composition, and physical disturbance) in the adjacent rainforest understorey?
2) Do these edge gradients differ among edge types?

Initially, I predicted that linear canopy openings would generate edge gradients in microclimate and vegetation and that the width of the linear canopy opening would be the main determinant of the strength and penetration distance of these edge gradients. Thus powerlines, as the widest linear clearing, would be associated with the strongest edge gradients; whilst highways and creeks, being of similar width, would have similarly strong edge effects although the presence of flowing water might dampen gradients in vapour pressure and complicate vegetation gradients near creek edges. I also predicted that the degree of edge 'sealing' [the extent to which vegetation fills the open space between the ground surface and the forest canopy at an edge (Harper *et al.* 2005)] would influence edge gradients such that more sealed edges would experience lesser edge gradients (eg Didham and Lawton 1999). As edge sealing is often determined by the time elapsed since edge creation, I predicted that the edge gradients associated with the anthropogenic linear clearings (15 – 50 years old, with current edges 15 years old) would be more severe than those associated with creeks (eg Parendes and Jones 2000).

Results presented in this thesis support the prediction that linear canopy openings are associated with edge gradients in microclimate and vegetation but indicate that the extent and severity of edge gradients are not simple functions of either edge width or natural versus anthropogenic origin. These results will be briefly reviewed in the following section and the broader implications will be discussed in the remainder of the chapter.

8.1.1 Review of Main Results

Four aspects of rainforest ecology were explored in this thesis: variation in the understorey microclimate, vegetation structure and composition, physical disturbance and the survival and growth of rainforest tree seedlings. The main findings for each of these sections are summarised below.

8.1.1.1 Microclimatic Variation

Rainforest understorey microclimate was significantly altered near the edges of linear canopy openings (Table 8.1). Traverse measurements revealed that light intensity was elevated near the forest edge and this increase was greatest and extended furthest along creek edges. Air temperature and vapour pressure deficit were elevated near powerline edges in the dry season and near highway edges in both wet and dry seasons but were lowered near creek edges in the wet season. Canopy temperature was elevated near highway edges and lowered near powerline edges in the wet season. Soil moisture was lower near creek edges than in the forest interior although this appeared to be a result of higher sand content in soil near creek edges. The alterations in temperature and vapour pressure deficit seem likely to be the result of differences in relative fluxes of latent and sensible heat within linear canopy openings. In particular, the bitumen surface of highways would not allow the same rate of wet season evapotranspiration as the grassy vegetation within powerline clearings, which in turn does not match the evaporation of flowing water within the perennial creek in both wet and dry seasons. Thus, the relative partitioning of heat into latent heat (and therefore the degree of evaporative cooling) is likely to be greatest near creek edges, intermediate (and seasonal) near powerline edges and least near highway edges. Greater light intensity and reduced soil moisture (and associated increased sand content of soil) near creek edges may be due to a more open edge structure near creeks as compared to anthropogenic edges, possibly maintained by periodic flooding of creek edges.

Table 8.1. Summary of effects detected near the edges of linear canopy openings. Increases (↑), decreases (↓) or no change (—) near edges are indicated (extent of edge effects are given in parentheses).

		Edge Type	
Effect	**Powerlines**	**Highways**	**Creeks**
Microclimatic Variation			
Light Availability			
Red:far red ratio	↑ (0.5 m) ↓ (4 – 50 m)	↑ (0.5 m) ↓ (4 – 50 m)	↑ (50 m)
Photosynthetically Active Radiation	↑ (< 20 m)	↑ (< 20 m)	↑ (50 m)
Air Temperature	↑ (20 m, dry season)	↑ (< 20 m)	↓ (50 m, wet season)
Vapour Pressure Deficit	↑ (< 20 m, dry season)	↑ (< 16 m)	↓ (4 – 50 m, wet season)
Canopy Temperature	↓ (~20 m, wet season)	↑ (< 30 m, wet season)	—
Soil Moisture	—	—	↓ (< 20 m)
Wind speed (data logger)	↑ (< 50 m)	↑ (< 50 m)	↑ (50 m)
Existing Community Composition			
Stem density	↑ (< 50 m)	↑ (< 25 – 50 m)	↑ (< 50 m)
Tree size	↓ (< 25 – 50 m)	↓ (< 25 – 50 m)	↓ (< 25 – 50 m)
Basal area and above-ground biomass	—	—	—
Liana abundance	↑	↑	↑
Weeds	↑ (0.5 m)	↑ (12 m)	↑ (~12 m)
Native grasses	↑ (0.5 m)	↑ (12 m)	↑ (25 m)
Ferns	—	—	↑ (< 50 m)
Herbs	↑ (< 12 m)	—	↑ (< 12 m)
Shrubs	↓ (< 25 m)	—	↓ (< 100 m)
Understorey tree composition	To < 12 m	To < 25 m	To < 100 m
Canopy tree composition	To < 100 m	To <50 – 100 m	To <50 - 100 m
Physical Disturbance			
Tree falls	↑ (< 50 m)	↑ (< 25 – 50 m)	↑ (< 50 m)
Seedling physical damage	—	↑ (< 25 m)	↓ ?
Seedling Survival and Growth			
Early-successional species	—	—	↑
Mid-successional species	—	—	↑ (some species)
Late-successional species	—	—	↑

Data logger measurements of diurnal variation in air temperature, vapour pressure deficit and wind speed revealed that the diurnal ranges of air temperature and vapour pressure deficit were greater in the dry season than the wet season (with the exception of air temperature ranges near powerline transects, which were similar in both seasons). Diurnal variation was also greater at the very edge of the forest near powerlines and highways but did not vary significantly with distance from creek edges. Measurements also showed that edge gradients in air temperature and vapour pressure deficit tended to be greater on hot, clear days and between the hours of 10:00 and 16:00. Gradients in air temperature sometimes reversed near powerlines at night, particularly on cold, clear nights whilst edge gradients in air temperature and vapour pressure deficit were generally weak or absent near creek edges. Wind speeds were very low within the forest; indeed, the predominant wind speed measured was 0 km hr^{-1}. However, the maximum wind speed measured (which was correlated with the proportion of measurements > 0 km hr^{-1}) was higher near the forest edge than in the forest interior, greater in the dry season than in the wet season and greater near creek edges than powerline or highway edges. Again, these wind speed results seem likely to be a due to a more open edge structure near creeks than near powerlines or highways.

Measurements of the red:far red ratio, which is highly correlated with canopy transmittance and overall light availability (Capers and Chazdon 2004), revealed higher light availability near creek edges than near powerline or highway edges. The proportion of high light readings (≥ 0.70, a value observed to be associated with gaps in the canopy layer) was elevated within 12 m of all edge types, indicating that the proportion of the forest beneath canopy gaps is greater near the edge than in the forest interior and does not differ among edge types. Differences in average red:far red values between anthropogenic edges and creek edges may be due to a greater degree of edge ‘sealing’ near powerline and highway edges (producing a less open edge structure and greater vegetation density near these edges) than near creek edges, which are periodically disturbed by flooding. Flood disturbance may also lower foliage density near creek edges by removing smaller trees and saplings (lower density of saplings and trees 5 – 10 cm dbh along creek transects, Chapter 5) and thus lowering the foliage density of the forest understorey and/or subcanopy. Differences in plant species composition between creek edges and anthropogenic edges (Chapter 5) may also influence the amount of light transmitted through the forest canopy.

8.1.1.2 Vegetation Structure and Composition

Vegetation structure and species composition were significantly affected by both edge proximity and edge type (Table 8.1). Densities of trees, saplings and lianas were elevated near the edges of linear canopy openings and there were greater proportions of small (5 – 10 cm dbh) and intermediate-sized (10 – 30 cm dbh) trees and a lower proportion of large (≥ 30 cm dbh) trees near the forest edge than in the forest interior. However, neither the basal area nor the above-ground biomass of trees ≥ 5 cm dbh were reduced near the forest edge. Absolute densities of saplings were less and lianas greater along creek transects than powerline or highway transects. Creek transects also had a lower proportion of small trees and a greater proportion of large trees than powerline or highway transects.

Despite the greater density of trees, saplings and lianas near the forest edge, species diversity of large (≥ 5 cm dbh) and small (< 2 cm dbh) stems was not elevated near the forest edge although the diversity of stems 2 – 5 cm dbh was elevated near the forest edge. Intrusion of exotic species was not responsible for these discrepancies among stem size classes.

Functional group composition was altered near the forest edge and among edge types. Weed species were restricted to the very edge (0.5 m) of the forest near powerlines, to very bright gaps within 12 m of highway edges and to within 12 m of creek edges, though at very low abundances. The abundance of native grass species was greatest near the forest edge and this effect was particularly pronounced near creek edges. The abundance of herbaceous species was greater and the abundance of understorey shrub species less near the forest edge, particularly along powerline and creek transects. Creek edges also had an elevated abundance of terrestrial ferns.

The abundances of canopy tree saplings and adults were elevated near the forest edge although absolute numbers of canopy tree saplings were lower along creek transects than powerline or highway transects. In contrast, the abundances of trees and saplings of understorey tree species were not elevated near the forest edge relative to the forest interior. The abundances of seedlings of canopy and understorey tree species were also unaffected by edge proximity. Within understorey tree species, the proportion of early-successional individuals increased towards the forest edge and this effect was stronger for creek edges than powerline or highway edges. The proportion of late-successional individuals decreased towards the forest edge, particularly along creek transects. Additionally, along creek transects the proportions of late- and early-successional individuals differed among adults, saplings and seedlings such that the proportion of late-successional individuals decreased and the proportion of early-successional individuals increased with decreasing size class. Powerline and highway transects displayed the opposite pattern. Amongst canopy tree species, the proportion of early-successional individuals was greater and the proportion of late-successional individuals less near the forest edge but the greatest declines in proportions of late-successional individuals were observed near anthropogenic edges rather than creek edges. Additionally, the proportion of mid-successional individuals increased near the edges of powerlines and highways, with this increase greatest near powerline edges. The proportion of late-successional individuals decreased and the proportion of mid-successional individuals increased between adults and juveniles, with these changes being greatest along powerline transects and least along creek transects. The proportion of early-successional individuals generally decreased between adults and juveniles although edge gradients among seedlings were still apparent along creek transects. These changes in successional composition amongst understorey and canopy tree species suggest that recruitment of early-successional species is still occurring near creek edges but may be declining near powerline and highway edges whilst the recruitment of mid-successional canopy tree species is greatest near anthropogenic edges (particularly powerline edges).

Edge gradients in functional group composition were largely correlated with edge gradients in light availability (red:far red ratio). Within the smallest size class (< 2 cm dbh), the size class for which correlations were measured, the abundances of functional groups that increased near the edge were also positively correlated with red:far red ratio whilst species that declined near the edge were negatively correlated with red:far red ratio. The exceptions to this pattern were seedlings of early-, mid- and late-successional canopy tree species.

There was no indication of a reduction in the abundance of species with large (> 2.0 cm width), biotically-dispersed diaspores near the edges of linear canopy openings. This suggests that at least one of the dispersers of these fruits does not avoid the edges of linear canopy openings (eg the Southern Cassowary, *Casuarius casuarius*). There was an increase in the abundance of species with small (< 1.0 cm width), biotically-dispersed diaspores near the edge, perhaps due to the increased proportion of early-successional species near the edge. Within the smallest size class (< 2 cm dbh), the abundance of species with small, abiotically-dispersed diaspores also increased near the edges of linear canopy openings, possibly due to slightly elevated wind speeds near the edge as well as transport of propagules by water (creek edges) or traffic (highway edges).

8.1.1.3 Physical Disturbance

Aspects of the physical disturbance regime appeared to be altered near the edges of linear canopy openings (Table 8.1). There were greater numbers of fallen trees near the edges of powerlines, highways and creeks but larger trees (≥ 30 cm dbh) were not disproportionately represented among fallen trees at the forest edge. Not surprisingly, fallen trees were associated with higher light levels (measured via the red:far red ratio) although there was no interaction between this effect and either distance from the forest edge or edge type. In contrast, small-scale disturbance to seedlings through falling leaf litter and canopy debris was not consistently greater near the forest edge than in the forest interior. Although the rate of small-scale disturbance, as measured with artificial seedlings, was elevated near highway edges, there was no consistent reduction in the stature of taller (≥ 50 cm) seedlings near the edge as might be expected amongst seedlings suffering greater rates of physical trauma (*cf.* Peters *et al.* 2004). Whilst the elevated rate of damage to artificial seedlings near highway edges might be a result of greater moisture stress, perhaps as a result of elevated wet season canopy temperatures and year-round increases in understorey vapour pressure deficit near highways (Chapter 4), the lack of any consistent signal in seedling stature suggests that this effect may not significantly influence the seedling community. Further studies of small-scale seedling disturbance and long-term measurements of tree mortality rates are required to determine the full significance of these patterns.

8.1.1.4 Seedling Survival and Growth

Proximity to the edges of linear canopy openings did not produce the predicted patterns in seedling survival, growth and herbivory in seedlings planted into experimental plots along powerline, highway and creek transects (Table 8.1). My initial hypothesis was that survival and growth of seedlings of early- and possibly mid-successional species would be greater near the forest edge than in the forest interior while the seedlings of late-successional species would display the opposite pattern. I also predicted that herbivory pressure from vertebrate species would be higher near the forest edge than in the forest interior as a consequence of altered faunal edge communities (Goosem and

Marsh 1997; Goosem 2000). However, although the pioneer species *Omalanthus novo-guineensis* survived only in the highest-light microsites (along creek edges and within the powerline clearing), there were no significant effects of distance from the edge on the survival or growth of any species in this experiment. Indeed, very few seedlings in this experiment experienced positive growth rates although the likelihood of positive growth was generally greater along creek transects than along powerline or highway transects and tended to increase with increasing light availability (red:far red ratio). Seedling survival also tended to increase with increasing light availability.

Although seedling survival was generally greater when seedlings were protected from vertebrate herbivory, vertebrate herbivory pressure was not significantly increased near the forest edge than in the forest interior. Indeed, in the one species (*Diploglottis smithii*, a mid-successional species) which did experience a significant effect of distance on herbivory pressure, herbivory pressure on seedling survival was *lower* near the forest edge than in the forest interior, directly contradicting my initial hypothesis.

8.2 Patterns and Processes Near the Edges of Linear Canopy Openings

Linear canopy openings are associated with a number of edge effects in the understorey microclimate and vegetation community of the surrounding rainforest. The nature and extent of these edge effects appear to be functions of edge structure (particularly the degree of edge sealing) and the physical properties of the linear canopy openings themselves.

Edge structure is influenced by edge age and by processes that assist or hinder the process of edge sealing (Gascon *et al.* 2000). Immediately after edge creation, the edge has the vertical structure of the original undisturbed forest but, over time, the vegetation community responds to increased light levels and empty space between the ground and the canopy becomes filled with a ‘wall’ of saplings, small trees, lateral branches, vines, shrubs and seedlings (Didham and Lawton 1999; Laurance *et al*. 2002; Harper *et al.* 2005). Such sealed edges may experience smaller microclimatic edge effects and fewer intrusions of matrix species into the forest (Didham and Lawton 1999; Cadenasso and Pickett 2000, 2001) than the initial, more open forest edge. However, processes that either prevent edges from sealing or break down established vegetation structure near the edge can leave the forest exposed to more severe edge effects for prolonged periods of time (Gascon *et al*. 2000). For example, the intrusion of fire

(Didham and Lawton 1999) or exotic plant species (Gascon *et al.* 2000) that interfere with plant regeneration or gap succession can maintain a more open edge structure in rainforest fragments.

In this study, edge structure was more ‘open’ near creeks than near powerlines or highways. Light levels (PAR and red:far red ratio, Chapter 4) and maximum wind speeds were increased and these effects penetrated further into the forest at creek edges (Figure 4.6) whilst there were fewer saplings and small trees near creek edges than near powerline or highway edges (Chapter 5). In contrast, anthropogenic edges were more sealed, with lower red:far red ratios indicating higher leaf area indices (ie greater foliage volumes). Current anthropogenic edges are approximately 15 years old, which is sufficient time for edges in other tropical (Williams-Linera 1990a; Kapos *et al.* 1997) and temperate (Harper *et al.* 2005) forest ecosystems to become sealed. The current age of the creek edge, however, is uncertain. Although the creek itself has certainly been present for a considerable period of time, the frequency and severity of stand-level disturbance (eg flooding, cyclone disturbance) is not known in detail. Anecdotal evidence suggests that moderate to severe flooding may occur irregularly, with return intervals of less than 5 to 10 years (Richard Carrigan, National Parks Ranger, *pers. comm.*) while two tropical cyclones have passed over the area within the last thirty years (Cyclone Winifred, a category 3 cyclone, passed over the region in 1986 and the eye of Severe Tropical Cyclone Larry, a category 5 cyclone, passed over the study area on 20th March 2006, subsequent to the data collection for this thesis). Only minor flooding of the creek, with water not reaching beyond the very edge of the creek bank, was observed during the three years of this study but this period of time also included an unusually severe drought (2002 – 2003) in north-eastern Australia, associated with a moderate *El Nino* event (Marrinan *et al.* 2005). The sandier texture of soil near creek edges suggests that flood waters may occasionally reach to between 4 and 50 m from the edge of the creek bank (*pers. obs.*). Irregular disturbance by floodwaters thus appears to have the potential to influence the dynamics of the vegetation, through either complete or partial stand destruction.

The structure and composition of vegetation near rivers in other tropical and temperate forests are affected by flood frequency, height and duration (Salo *et al.* 1986; Gregory *et al.* 1991; Worbes *et al.* 1992; Korning and Balslev 1994; Ferreira and Stohlgren 1999; Robertson and Augspurger 1999; Bendix and Hupp 2000; Nilsson and Svedmark 2002; Wittmann *et al.* 2004). Vegetation closer to the main river channel, which is affected more frequently by flooding than vegetation further from the main channel, may be younger (Worbes *et al.* 1992; Robertson and Augspurger 1999; Van Pelt *et al.* 2006) and often more structurally open (Robertson and Augspurger 1999; Guilherme *et al*. 2004; Wittmann *et al.* 2004; Van Pelt *et al.* 2006) than forest further upslope. In the Amazon River basin, forest which is close to the river may be flooded for a large part of the year (up to 260 days per year; Worbes *et al.* 1992; Ferreira and Stohlgren 1999) and often has lower species diversity, younger stand ages, higher tree mortality rates and more successional tree species than forest which is not flooded or is flooded for shorter periods of time (Worbes *et al.* 1992; Korning and Balslev 1994; Ferreira 1997; Ferreira and Stohlgren 1999; Guilherme *et al*. 2004). Flooding may also influence vegetation near streams in temperate forest (Hibbs and Bower 2001; Russell and McBride 2001) although few studies have explored the influence of stream flooding on tropical rainforest vegetation (eg Ferreira and Stohlgren 1999). Data presented in this study suggest that even irregular flooding may influence the vegetation community near stream edges in tropical rainforest, reducing the number of saplings and small trees and thereby reducing understorey and/or subcanopy foliage density (higher red:far red ratio, Figure 4.8). Consequent greater penetration of light and wind into the forest understorey and more open edge structure near the creek favours the establishment of more light-demanding, early-successional species (Chapter 5, Chapter 7) near creek edges than near anthropogenic edges. However, neither the number of fallen trees (Chapter 6, Figure 6.2) nor the percentage of the understorey that was beneath a canopy gap (Chapter 4, Figure 4.9) was greater near creek edges than anthropogenic edges although both parameters were elevated near the forest edge relative to the forest interior. This suggests that flooding effects, if any, exerted a greater influence on the forest understorey and subcanopy than on larger trees in the forest canopy.

Alternatively, it is possible that the elevated abundance of lianas near creek edges, as compared to powerline and highway edges (Chapter 5, Figure 5.9), maintains a more open edge structure by interfering with the processes of succession near creek edges (eg Schnitzer *et al.* 2000; Guilherme *et al*. 2004). In rainforest on Barro Colorado Island, Panama, approximately 7.5% of tree-fall gaps were found to be in a state of ‘stalled succession’, with lianas dominating the vegetation community and suppressing the regeneration of canopy trees (Schnitzer *et al.* 2000). Some palm species were also observed to be associated with altered successional pathways in tree-fall gaps (Schnitzer *et al.* 2000). Similarly, in tropical semideciduous riparian forest in south-eastern Brazil, a species of understorey woody bamboo (*Merostachys riedeliana*) was associated with increased tree mortality rates, especially for small trees (Guilherme *et al*. 2004). In my study sites, the overall abundance of lianas was elevated near creek edges relative to anthropogenic edges (Chapter 5, Figure 5.9). As lianas are generally observed to increase mortality rates of tropical trees and saplings (Putz 1984; Schnitzer and Bongers 2002; Schnitzer *et al*. 2005), the elevated abundance of lianas near creek edges may be responsible for the more open edge structure and the lower numbers of saplings and small trees near creek edges as compared to anthropogenic edges. However, as liana abundance is itself often positively associated with higher levels of forest disturbance (Putz 1990; Laurance 1991; Laurance *et al.* 2001a; Schnitzer and Bongers 2002) and with elevated light levels (Putz 1990; Hegarty 1991; Laurance 1991; Dewalt *et al*. 2000; Schnitzer and Bongers 2002), it is possible that elevated liana abundance near creek edges may be both a cause and a consequence of higher physical disturbance and more open edge structure near creek edges (*cf.* Laurance *et al.* 2001a).

Although the greatest contrasts in edge structure were between creek edges and anthropogenic edges, powerline and highway edges did display subtle differences in edge structure. Whilst the proportion of understorey red:far red measurements beneath canopy gaps (red:far red ≥ 0.70) did not differ between powerline and highway edges, the spatial arrangement of these measurements did. Larger canopy gaps dominated by weedy vegetation (eg the exotic scramblers *Rubus alceifolius* and *Lantana camara* and/or exotic grasses such as *Urochloa maxima*) were more frequent near highway edges than near powerline edges (Chapter 6). This suggests the possibility that exotic species were interfering with regeneration (*cf.* Reynolds 1994; Gentle and Duggin 1997; Gascon *et al.* 2000) near highway edges, possibly to a greater extent than near powerline edges. Although differences in exotic propagule pressure between highways and powerlines may contribute to this pattern, it seems likely that other edge differences are also involved, given that exotic species dominate powerline clearings as well as highway verges. The most likely explanation may be differences in the frequency of human edge disturbance. Forest edges along powerline corridors have not been disturbed by humans since the early 1990s and the forest may even have begun to expand into the powerline clearing (Dr Miriam Goosem, *pers. comm.*) whereas highways are subject to regular slashing of grass, removal of pioneer trees near the edge and other maintenance activities. Exotic species, which are often adapted to high light conditions for germination and survival, may require disturbance to invade evergreen tropical rainforest (Fine 2002). Whether or not differences in the frequency of edge disturbance are contributing to differences in the influence of exotic species on plant regeneration near powerline and highway edges remains speculative and requires further examination.

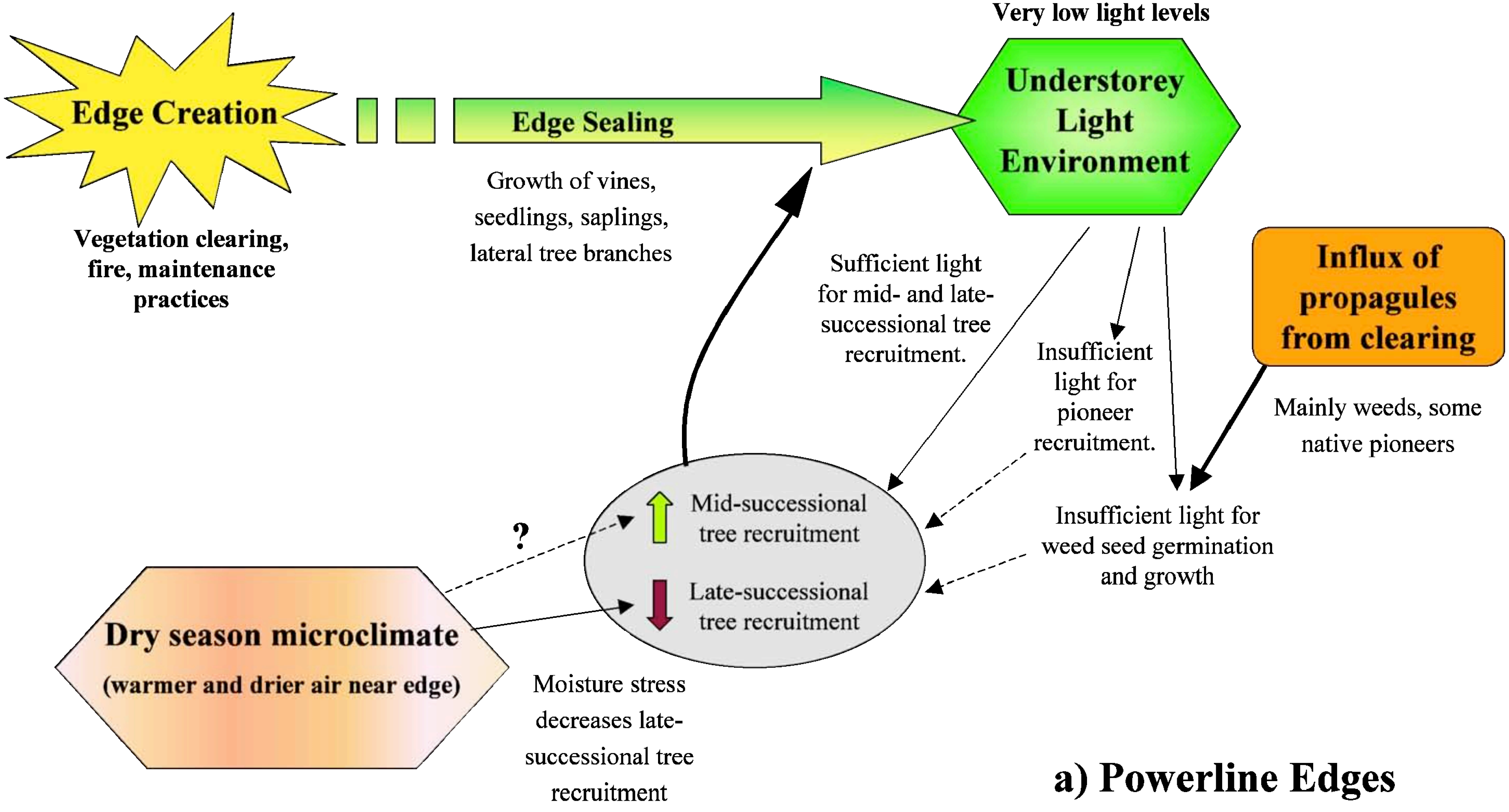
Despite the more open edge structure near creeks, microclimatic edge effects were more severe near highways and powerlines. Air temperature and vapour pressure deficit were elevated near powerline edges in the dry season and highway edges in both wet and dry seasons whilst air temperature and vapour pressure deficit were unaffected near creek edges in the dry season and slightly lowered in the wet season. Canopy temperatures were altered only near anthropogenic edges in the wet season. These differences between edge types may be the result of differences in evaporative cooling within powerline clearings and highways and creeks (Chapter 4) and indicate that the characteristics of the linear canopy opening itself can exert an influence on the edge gradients experienced in the adjacent forest. In particular, these data indicate that greater evaporative cooling within a linear canopy opening (ie partitioning of heat energy into latent heat rather than sensible heat) will reduce moisture and temperature stress experienced at the forest edge.

The analogous effect in traditional forest fragmentation studies is the ‘matrix effect’ (or edge contrast effect). Generally, the greater the contrast between the conditions in the matrix and in the forest, the more severe the edge effects experienced in the forest will be (Mesquita *et al.* 1999; Gascon *et al.* 2000; Jules and Shahani 2003; Harper *et al.* 2005; Kupfer *et al.* 2006). Matrix effects have mostly been studied in relation to biological effects such as the moderation of edge gradients in species richness and composition, tree mortality rates and the penetration of non-forest and/or exotic species (eg Gascon *et al.* 1999, 2000; Mesquita *et al.* 1999; Jules and Shahani 2003; Antongiovanni and Metzger 2005; Laurance *et al.* 2006; Nascimento *et al.* 2006). Observations that external weather conditions affect the severity and extent of microclimatic edge effects in temperate (Chen *et al.* 1995) and tropical (Giambelluca *et al*. 2003) forest support the supposition that matrix conditions also influence abiotic edge effects (eg Malcolm 1998; Mesquita *et al.* 1999; Harper *et al.* 2005; Kupfer *et al.* 2006; Nascimento *et al.* 2006).

In this study, the nature of the linear canopy openings may have influenced the biological edge effects experienced in the adjacent rainforest both indirectly, through differences in abiotic edge effects (*cf*. ‘biotic edge effects,’ Murcia 1995) and directly, through differences in propagule pressure. Indirect effects of altered edge microclimate may have included the changes in the relative abundances of different functional groups of plants observed near the edges of linear canopy openings, with general increases in earlier-successional groups and declines in late-successional groups near the forest edge (Chapter 5) as well as the marked increase in juveniles of mid-successional canopy tree species near anthropogenic edges, particularly powerline edges (Chapter 5). These shifts in vegetation community composition are likely to reflect the responses of species with different physiological requirements (ie differing environmental niches) to altered microclimate near the forest edge (Chapter 4, Chapter 5). Correlations between light availability (red:far red ratio) and the seedling abundance of many functional groups support this proposition (Chapter 5, Table 5.8).

Direct effects of differences in propagule pressure may relate to differences in the ability of each type of linear canopy opening to function as a conduit for the dispersal of native and exotic plant species. Propagules of both native and exotic species can disperse along creek lines via flowing water although the contribution of such dispersal to species composition along watercourses in the study area is not known. In temperate forests, propagule dispersal by water can increase the species richness of riparian and streamside forests (Nilsson *et al.* 1994; Honnay *et al*. 2001; Jansson *et al.* 2005) and it is likely that this process also contributes to the plant community along watercourses in north-eastern Queensland. In contrast with watercourses, which may disperse both native and exotic species, depending upon upstream sources of propagules, powerline clearings and highway verges are dominated by exotic species (Chapter 5). Very few native species were encountered within powerline clearings or along highway verges (Chapter 5) and it is likely that these linear clearings served as conduits for the dispersal of mainly exotic species rather than native species (eg Goosem 1997; Forman and Alexander 1998; Parendes and Jones 2000; Hansen and Clevenger 2005). The presence of high traffic volumes along the Palmerston Highway may have provided a source of propagule pressure in addition to that associated with dispersal from established roadside exotic vegetation (eg Forman and Alexander 1998; Christen and Matlack 2006). Broad differences in propagule pressure between anthropogenic and natural linear canopy openings may underlie the greater abundance of exotic species near highway edges as compared to creek edges although it is likely that differences in edge structure and edge disturbance are behind the differences in the penetration distance of weeds beyond the forest edge near creeks, highways and powerlines. These effects, however, were not directly examined in this study and further research is required to test these hypotheses.

The overall picture that emerges from these data is of a variety of processes occurring in combination within different types of linear canopy openings in tropical rainforest (Figure 8.1 a, b, c). Periodic flood disturbance may be maintaining a more open edge structure near creeks while evaporation from flowing water within the creek buffers the forest against increases in air temperature and moisture stress. The resulting microclimate of high light availability and low moisture stress appears to favour the survival and growth of species sensitive to drought stress (eg ferns and fern allies, Chapter 5) and to allow the continued recruitment of light-demanding, early-successional plant species while not limiting recruitment of mid- or late-successional species through moisture stress (Chapter 5, Chapter 7). In contrast, the grassy vegetation within powerline clearings appears to allow evaporative cooling in the wet season (when evapotranspiration rates of grasses are highest, Sturman and Tapper 1996) to a much greater degree than in the dry season while the bitumen surface of the highway may not allow a high level of evaporative cooling in either the wet or dry season. These reductions in evaporative cooling may result in greater temperature and moisture stress near the forest edge (*cf.* Malcolm 1998; Giambelluca *et al.* 2003) which, in turn, may alter the species composition of the plant community by favouring the survival of drought-tolerant species over drought-susceptible species (Condit *et al.* 1996; Engelbrecht and Kursar 2003; Bunker and Carson 2005), a distinction which may also favour the survival of exotic species (Fine 2002). Also in contrast to the more open structure of creek edges, the sealed edges near highways and powerlines have reduced the penetration of light and wind into the forest understorey (Chapter 4), to the extent that the recruitment of early-successional tree species has been reduced near these edges (Chapter 5, Chapter 7). Edge disturbance during highway maintenance, however, may be allowing light-demanding, exotic species to colonise and dominate canopy gaps near highway edges, potentially interfering with the regeneration of canopy species (*cf.* Reynolds 1994; Gentle and Duggin 1997; Gascon *et al.* 2000; Schnitzer *et al.* 2000) in a process which might eventually compromise the integrity of the forest edge (*cf.* Gascon *et al.* 2000). Further research is required to confirm these hypotheses and to investigate the influence of exotic species on edge regeneration near highway clearings.



a) Powerline Edges

Figure 8.1.

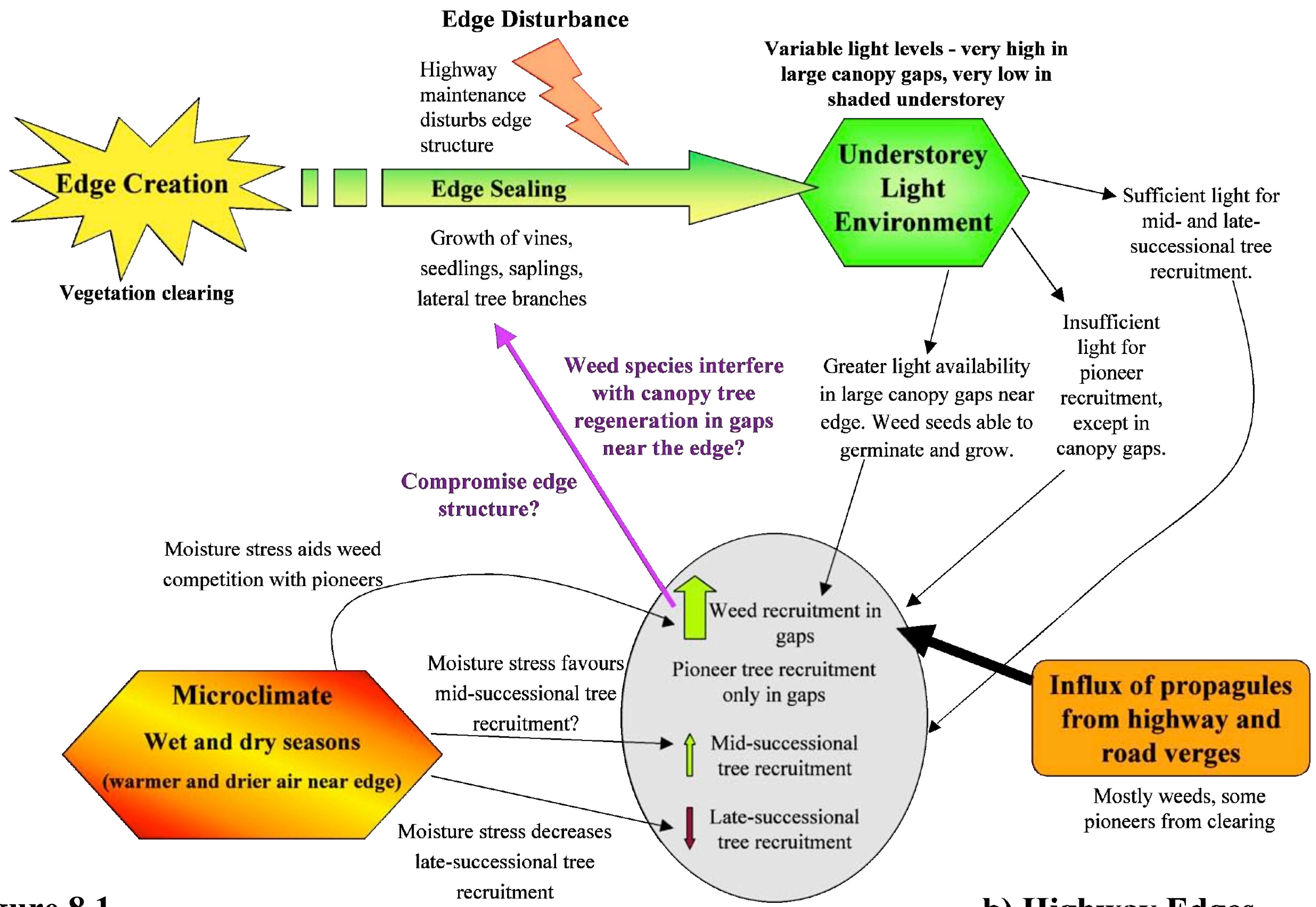


Figure 8.1.

b) Highway Edges

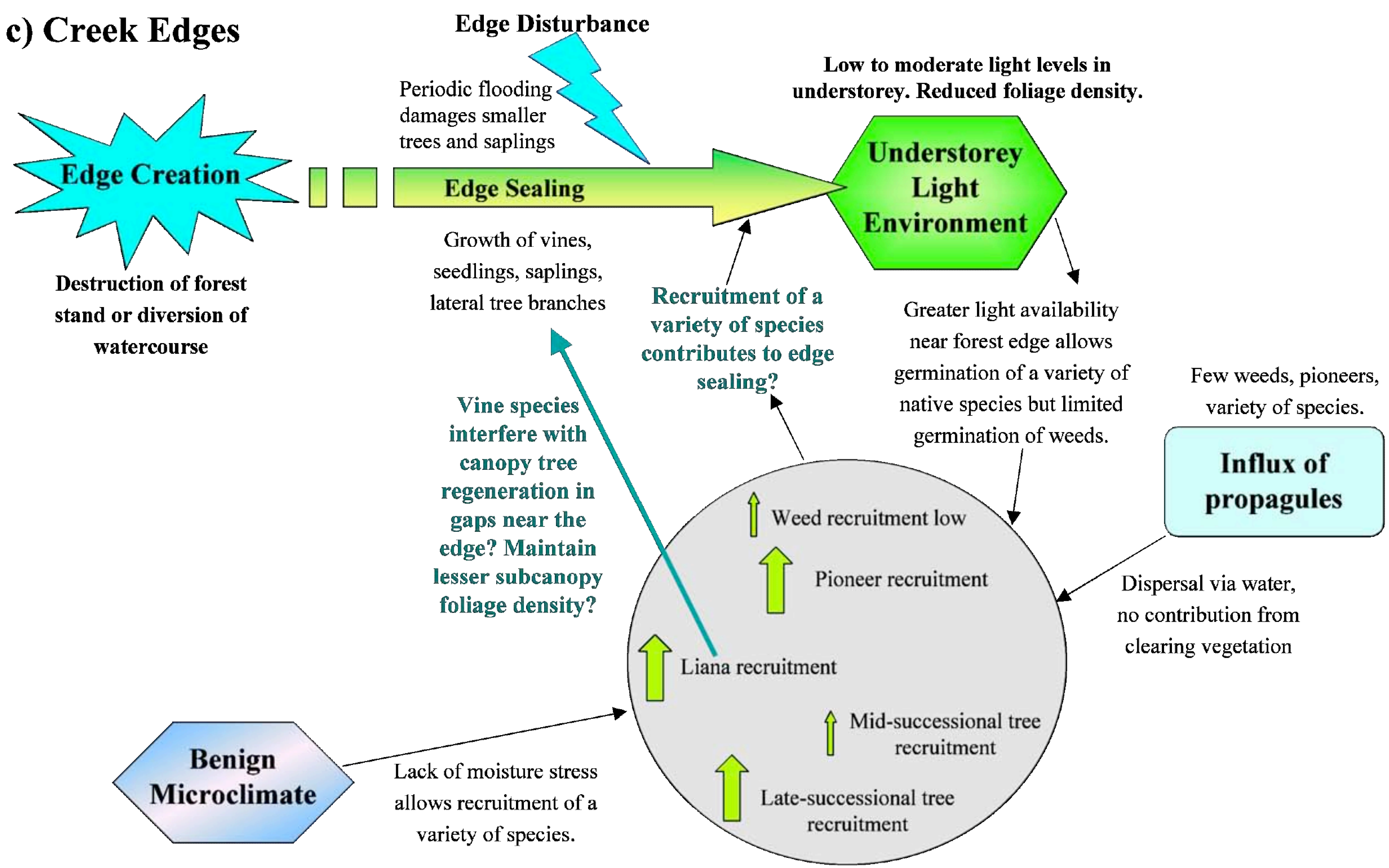


Figure 8.1. Conceptual diagram of processes operating at **a**) powerline edges, **b**) highway edges and **c**) creek edges in rainforest in north-eastern Queensland.

8.3 Potential Consequences for Ecological Processes

Linear clearings for human infrastructure are an increasingly common and widespread landscape feature within forest ecosystems (Goosem 1997; Marsh and Beckman 2004). Although the area of forest cleared for these features may be relatively small, the area of disturbed forest edge generated by these clearings may potentially be much larger and spatially widespread, reducing the area of undisturbed forest, even within otherwise intact forest reserves. In the Wet Tropics World Heritage Area of north-eastern Queensland, 1316 ha of rainforest have been cleared for a 320 km length of powerlines and 608 ha of rainforest have been cleared for a 1427 km length of highways and other roads (Trott *et al.* 1996, Goosem 1997). If the approximate distance of edge effects produced by powerline clearings is 25 m, a rough calculation of the area of altered edge forest associated with powerline clearings is 320 km * (2 * 25 m) = 1600 ha, an area at least as great as that directly lost for powerline clearings. Similarly, if an edge distance intermediate between that observed in this study (~25 m) and Seigenthaler and Turton's (2000) study of unsealed roads (3 – 11 m) is used (15 m), the area of altered edge forest associated with highways and other roads within the Wet Tropics World Heritage Area may be in the vicinity of 1427 km * (2 * 15 m) = 4281 ha or, approximately, seven times the area of rainforest cleared for the roads themselves. Although these estimates are only first approximations, they provide an indication of the potential extent of rainforest alteration associated with artificial linear canopy openings and are consistent with Skole and Tucker's (1993) observation that the area of disturbed edge forest within a fragmented ecosystem may approach or even exceed the area of direct forest loss.

The implications of these data for rainforest vegetation dynamics near watercourses are less clear. Edge gradients in microclimate, vegetation structure and plant species composition were detected near creeks in this study, indicating that watercourses do have an important influence on the adjacent vegetation community in this region, probably similar to the effects of watercourses on riparian vegetation in other tropical and temperate regions (eg Salo *et al.* 1986; Worbes *et al.* 1992; Nilsson *et al.* 1994; Ferreira 1997; Ferreira and Stohlgren 1999; Robertson and Augspurger 1999; Bendix and Hupp 2000; Honnay *et al.* 2001; Guilherme *et al.* 2004; Wittman *et al.* 2004; Van Pelt *et al.* 2006). The influence of watercourses on vegetation dynamics is, however, dependent on the size of the watercourse, the volume and variability of flows, the frequency and duration of flood events and the horizontal extent and severity of flooding of riparian or streamside vegetation (Salo *et al.* 1986; Gregory *et al.* 1991; Worbes *et al*. 1992; Ferreira 1997; Robertson and Augspurger 1999; Bendix and Hupp 2000; Nilsson and Svedmark 2002; Van Pelt *et al.* 2006). The creek investigated in this study (Henrietta Creek) is a third order stream in the North Johnstone River catchment, a region which receives an annual rainfall of approximately 3000 – 4000 mm, within the wetter range (although not the very wettest) of climates in the Wet Tropics region (Turton *et al*. 1999). At the study sites, the creek was 16 – 30 m wide and without overhead canopy cover. Many streams in the region are smaller than the creek studied in this thesis and may thus exert a lesser influence on the surrounding vegetation (Nilsson *et al.* 1994; Ferreira and Stohlgren 1999; Honnay *et al.* 2001) although, as small (2 – 4 m wide) streams are associated with microclimatic edge gradients in temperate forest (Brosofske *et al.* 1997), it is still possible that smaller streams will influence the surrounding vegetation in tropical rainforests. Conversely, the larger streams and rivers within the study region will likely experience greater volumes of water flow and possibly more frequent flooding, and may thus exert a stronger influence on the dynamics of the nearby vegetation community (eg Salo *et al.* 1986; Nilsson *et al.* 1994; Ferreira and Stohlgren 1999; Honnay *et al.* 2001). Further research is required to explore the effects of watercourses of varying size and across the range of precipitation and topography within rainforests in north-eastern Australia on the dynamics and composition of the adjacent vegetation community.

Linear clearings for human infrastructure have previously been found to alter the abundance and distribution of small (Burnett 1992; Goosem and Marsh 1997; Goosem 1997, 2000, 2002, 2004) and medium-sized mammals (Peter Byrnes, *unpublished data*) and to influence understorey microclimate (Seigenthaler 1999; Seigenthaler and Turton 2000) in rainforest in north-eastern Queensland. This study has demonstrated that the structure and composition of the vegetation community is also altered near the edges of linear canopy openings. Together, these results present a growing body of evidence which indicates that internal fragmentation within rainforests poses threats additional to those associated with broad-scale rainforest fragmentation (eg Laurance 1991, 1994, 1997; Harrington *et al*. 1997, 2001; Turton and Freiburger 1997; Warburton 1997) and can further reduce the area of undisturbed habitat even within large tracts of remaining forest.

8.4 Conclusions

I initially predicted that linear canopy openings would be associated with edge gradients in microclimate and vegetation and that the width of linear canopy openings and the degree of edge sealing would be the main determinants of the strength and penetration distance of these edge gradients. Thus I predicted that powerlines, as the widest linear clearing, would be associated with the strongest edge gradients; whilst highways and creeks, being of similar width, would have similarly strong edge effects. I also predicted that creeks, which have been present in the landscape for a much longer period of time than anthropogenic linear clearings (powerline and highway 15 – 50 years old, with current edges 15 years old), would have more sealed forest edges than powerlines or highways and thus experience lesser edge gradients (eg Didham and Lawton 1999; Parendes and Jones 2000).

Data presented in this thesis supported the prediction that linear canopy openings are associated with edge gradients in microclimate and vegetation but did not support the simple prediction that edge gradients would be greatest near powerlines, of intermediate strength near highways and least near creeks. The nature, extent and seasonality of microclimatic edge gradients were dependent upon the physical properties of the linear canopy openings themselves such that greater evaporative cooling from flowing water in the creek buffered rainforest near creek edges from the more desiccating conditions experienced in rainforest near highway and powerline edges. The seasonality of evapotranspiration within the grassy powerline clearings produced greater evaporative cooling in the wet season than the dry season, and thus reduced microclimatic edge gradients near powerline edges in the wet season. In contrast, the bitumen surface of the highway did not allow a great amount of evaporative cooling in either season and microclimatic edge gradients were thus equally severe near highway edges in both seasons. Additionally, periodic flooding disturbance appears to reduce the degree of edge sealing near creeks, allowing a greater penetration of wind and light into the forest understorey near creek edges. In contrast, regular highway maintenance activities may disturb the forest edge and allow the penetration of weed species into the rainforest near highways. Weed species may in turn interfere with the regeneration of canopy tree species in large gaps near highway edges, potentially further compromising the structure of the forest edge. These different abiotic edge gradients and disturbance regimes near powerlines, highways and creeks favoured the recruitment and persistence of different successional groups of species, which may further influence the structure of vegetation at the forest edge. Thus, a number of processes combine to produce the edge gradients observed near the edges of powerlines, highways and creeks in rainforest in north-eastern Australia.

8.4.1 Directions for Future Research

Numerous questions about the effects of linear canopy openings on rainforest plant ecology still remain to be addressed. Firstly, a number of processes (plant species demographics, tree-fall mortality rates, flood disturbance) have been inferred from ‘snap-shot’ (single point in time) data. These processes should be measured directly, via long-term monitoring, to confirm whether the inferences drawn from the data presented in this study are correct. Similarly, the flow regime of the creek, including the frequency, extent and severity of flooding, should be measured directly to determine the influence of watercourses on adjacent vegetation communities. The influence of lianas on vegetation dynamics near creek edges should also be investigated to determine the relative contributions of periodic flood disturbance and liana competition on the stand dynamics of streamside vegetation.

Secondly, the influence of ‘top-down’ effects of fauna on floristic community dynamics and diversity needs further investigation. Although the data presented in this thesis do not provide strong support for such effects, only indirect methods were used to explore them. Potential changes in plant – animal interactions near forest edges should be investigated directly. For example, although the abundance of plant species with large, biotically-dispersed diaspores was not reduced near forest edges, implying that the dispersers of these seeds may not preferentially avoid the edge, it is not known whether average dispersal distances are affected. If either primary dispersal or secondary dispersal distances (or directions) are altered near the forest edge, this might alter the seed shadow of plant species near the forest edge (eg Ness 2004). If seed dispersal distances from parent trees are reduced, the overall recruitment of species which experience strong Janzen-Connell (Janzen 1970; Connell 1971) survivorship effects may be lowered (*cf.* Cordeiro and Howe 2003) while, conversely, species which do not experience strong reduction in recruitment beneath parent trees may increase in abundance at the expense of other species (*cf.* Wright and Duber 2001). Either possibility could affect the species composition and diversity of the plant community near the forest edge and deserve further attention. Additionally, although the abundances of small mammals (Burnett 1992; Goosem and Marsh 1997; Goosem 1997, 2000, 2002, 2004) and medium-sized mammals (Peter Byrnes, *unpublished data*) have been examined near linear canopy openings, the influence of these clearings on the abundance and distribution of frugivorous bird species has not been investigated. Similarly, both herbivore – seedling and pathogen – seedling interactions require further examination as alterations in these interactions near forest edges may also differentially affect the survival and recruitment of different plant species (eg Jules and Rathcke 1999; Wahungu *et al.* 1999, 2002; Kollmen and Buschor 2003; Benitez-Malvido and Lemus-Albor 2005; Chauvet and Forget 2005).

Finally, linear clearings may pose a barrier to the movement of rainforest species and, although such 'linear barrier effects' have been explored in mammals (Goosem 2001, 2004), they have not been investigated for plant species. Linear clearings may prevent the dispersal of plant diaspores or the passage of pollen between rainforest on either side of the clearing if the pollen or diaspore vectors (eg animals, birds, wind) are unable to cross the clearing. Research is needed to determine whether plant populations on either side of linear clearings are isolated and whether species with particular diaspore dispersal modes or pollination syndromes are more vulnerable to such isolation. Additionally, the ability of different types of linear canopy openings to serve as conduits for the dispersal of native and exotic species should be explored.

8.5 Management Implications and Recommendations

Three recommendations for the management of linear clearings within tropical rainforest emerge from this study:

1) Wherever possible, disturbance to the forest edge should be avoided, to allow a ‘sealed’ edge structure to develop and be maintained, in order to minimise the severity and penetration distance of edge effects experienced in rainforest near artificial linear canopy openings. This applies in particular to highway edges where it appears that maintenance practices might be increasing the potential for weeds to invade in canopy gaps. Maintenance practices should ideally aim to minimise disturbance to trees, other vegetation and soil at the forest edge. I also concur with the recommendation of Goosem (2004) to maintain canopy closure above roads wherever possible, in order to minimise the increase in light levels near the forest edge and therefore minimise the recruitment of weed species.
2) Where possible, the contrast between vegetation within artificial linear canopy openings and the surrounding forest should be minimised. Particular attention should be given to the ability of vegetation within linear canopy openings to maintain high rates of evapotranspiration in both wet and dry seasons and to provide a suitable habitat structure to allow the passage of native fauna and thus maintain some degree of population connectivity between rainforest on either side of the linear clearing (Goosem and Marsh 1997; Goosem 1997, 2001, 2004). Therefore encouragement of native species over weedy grasses should be considered. Use of herbicides which control grass and allow germination of low-growing natives is one option that might be explored. Maintenance regimes in powerline clearings and road verges that only remove the larger species that might cause problems to powerlines or traffic but retain the lower growing natives offer the potential to reduce microclimatic alterations adjacent to highways and powerline clearings. These regimes may even allow retention of lower canopy heights that reduce light availability and thus invasion by the most light-demanding of exotics (grasses) and the consequent weed propagule pressure on the adjacent forest. The influence of vegetation structure within linear canopy openings on wind speed and turbulence should also be investigated, and consideration of this factor should be included in the management of powerline clearings and other anthropogenic linear clearings.

3) Investigate, as a matter of urgency, possible interactions between weed species and edge disturbance on the regeneration of native plant species near highways and powerlines. Data presented in this study suggest the possibility that human disturbance to rainforest edges near highways during maintenance activities, in combination with potentially greater propagule pressure, may allow exotic species to colonise and dominate canopy gaps near highways, potentially suppressing the regeneration of native canopy species. Monitoring of the population dynamics of trees and exotic species is required to determine whether tree-fall disturbance is genuinely elevated near highway edges and, if so, the relative contributions of highway maintenance activities *vs*. edge effects (ie elevated wind disturbance, elevated moisture stress) to tree mortality rates. Monitoring of the dynamics of native and exotic plant species within canopy gaps near highway edges is also required to determine whether exotic species interfere with the regeneration of native species and hinder the processes of gap succession and canopy recovery (*cf*. Reynolds 1994; Gentle and Duggin 1997; Gascon *et al.* 2000; Schnitzer *et al.* 2000). As weed species are often light-demanding and require canopy disturbance to invade tropical rainforest (Fine 2002), canopy damage from the recent passage of Severe Tropical Cyclone Larry (20th March 2006, subsequent to the data collection for this thesis) may allow exotic species to invade rainforest adjacent to highway edges and to penetrate further into the forest than the 12 m observed in this study, especially if these species are present in the soil seed bank (weed seeds have been detected in the soil seed bank up to 25 m from powerline edges, Dr Miriam Goosem, *unpublished data*). Research is required to determine the extent of the threat that exotic species may pose for rainforest regeneration near highway clearings and to identify possible methods to ameliorate any such effects. Designs for roads that, wherever possible, retain overhead canopy cover, bridges which pass over the forest canopy (and thus avoid the need for canopy clearing), revegetation on road embankments and cuttings (Goosem 2004) as well as designs for powerlines that place the line above the forest canopy (and thus avoid the need for canopy disturbance) should be considered as these are likely to reduce the effects of linear infrastructure on forest microclimate and biota (Goosem 2004).