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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.

> Thesis submitted by Catherine Louise POHLMAN BSc (Hons) ANU in July 2006



for the degree of Doctor of Philosophy in the School of Tropical Environmental Studies and Geography James Cook University

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Abstract

Human activities have led to the loss and fragmentation of rainforest around the world's tropics and sub-tropics, whilst internal fragmentation by linear clearings has subdivided many remaining areas of rainforest, exacerbating the effects of the initial disturbance. Linear clearings for human infrastructure, including roads and powerlines, are widespread within the rainforests of the world and the Wet Tropics World Heritage Area of north-eastern Queensland in particular. Edge effects of these linear clearings have the potential to substantially increase the disturbed area within existing tracts of rainforest and affect a wide range of rainforest biota.

I examined the edge effects of two artificial linear clearings on rainforest understorey microclimate, physical disturbance regimes, vegetation structure and composition and tree seedling survival and growth. Edge effects adjacent to powerline clearings and highways were compared with those near perennial creeks, the only type of widespread natural linear canopy opening available in the complex mesophyll vine forest of the Palmerston Region in the Wet Tropics World Heritage Area of northeastern Queensland (average annual precipitation 3000 – 4000 mm).

Understorey microclimate of rainforest adjacent to highways, powerline clearings and creeks was significantly altered from that of the forest interior. Light intensity was elevated near the edges of powerline clearings, highways and creeks with the effect being strongest for creek edges. Air temperature and vapour pressure deficit were elevated near powerline clearing edges in the dry season and highway edges in both wet and dry seasons but were not elevated near creek edges in either season. In contrast, soil moisture was reduced near creek edges but remained unaltered near powerline clearing and highway edges. Air speed was not significantly related to distance from the forest edge when assessed with instantaneous measurements although slight increases in air speed were detected near the edge of the forest when diurnal patterns were assessed using data loggers. The predominant air speed throughout the study sites, however, remained at or close to 0 m s⁻¹. Canopy temperature was elevated near highway edges and lowered near powerline edges in the wet season but no edge gradients in canopy temperature were detected near creek edges in either season. These different edge gradients may be largely the result of differences in the fluxes of latent and sensible heat within each type of linear canopy opening with these data indicating

that the nature of the linear canopy opening is at least as important as the width in determining the severity and extent of microclimatic edge effects.

Variation in the understorey light environment was assessed using the red:far red ratio, which has been shown in other studies to correlate very closely with percent canopy transmittance as well as other commonly used measures of canopy cover and light availability. Average red:far red values were elevated near creek edges and reduced near powerline and highway edges although the proportion of high light measurements (≥ 0.70) was elevated within 12 m of all edge types. These data indicate that anthropogenic edges are more 'sealed' (ie have a greater foliage density near the edge) than creek edges. This more open vegetation structure near creek edges was accompanied by a decline in soil moisture (due to changes in soil texture) suggesting that periodic flooding may be one of the causative factors maintaining lower foliage density and thus a comparatively more open edge structure.

Measures of physical disturbance provided mixed results. There were greater numbers of fallen trees near the edges of powerlines, highways and creeks but no particular tree size appeared to be disproportionately at risk of tree-fall mortality. As there was also a greater number of living trees near the forest edge, it is uncertain whether the mortality rate of canopy trees truly was elevated near the forest edge. 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 $(\geq 50 \text{ cm})$ seedlings near the edge as might be expected amongst seedlings suffering greater rates of physical trauma. 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, the lack of any consistent signal in seedling stature suggests that this effect may not significantly influence the seedling community.

Vegetation structure and composition were altered near the edge of the forest, relative to the forest interior. The abundances of vines, small trees and saplings were elevated near the forest edge. Pioneer species were also more abundant near the edge, particularly adjacent to creeks. Light-demanding herbs occurred more frequently and late-successional shrubs less frequently near the forest edge than in the interior. Grasses and weeds were found almost exclusively on the very edge of the forest but were also recorded in large canopy gaps within 12 m of highway edges and at low abundance within 12 m of creek edges. Changes in the proportions of early-, mid- and latesuccessional tree species between adults and juveniles suggested that understorey light conditions were no longer suitable for the recruitment of early-successional trees near anthropogenic edges. This suggests that anthropogenic edge structure has become more sealed since these edges were created. In contrast, understorey light availability near creek edges remained sufficient for the recruitment of light-demanding pioneer species.

Proximity to the edge did not significantly affect seedling survival or growth for eight species included in a herbivore-exclusion experiment. The seedlings of pioneer species survived only in areas with high light availability (ie within the powerline clearing and near creek edges). Light availability was also the strongest determinant of the survival of seedlings of mid- and late-successional species. There was weak evidence for a decrease in herbivory pressure near the forest edge and no evidence of an effect of edge distance on seedling survival or growth. The majority of seedlings did not experience any growth in this experiment although the probability of seedlings experiencing positive growth rates increased with increasing light availability. The major differences observed in this study occurred in seedling survival rather than seedling growth, suggesting that the ability of seedlings to persist in the understorey may have been an important factor influencing the composition of the tree seedling community.

These data indicate that artificial linear clearings were associated with edge gradients in the abiotic environment of the adjacent forest and that these abiotic edge effects were the driving force behind changes observed in the plant community at the forest edge. The understorey of forest near the edges of highways and powerlines was brighter, warmer and drier than the forest interior although only slightly windier. In contrast, the edges of natural linear canopy openings did not cause elevated moisture stress but did experience elevated light availability. Analysis suggests that a combination of differences in the degree of edge 'sealing' among edge types caused by varying disturbance regimes in the clearings and differences in the physical properties of the linear canopy openings themselves (particularly in the level of evaporative cooling) were responsible for the observed biotic and abiotic edge gradients near natural and anthropogenic linear canopy openings.

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Chapter One: Introduction

1.1 Introduction

The rapid loss and fragmentation of tropical rainforests as a result of human activities are serious threats to the preservation of Earth's biodiversity (Laurance and Bierregaard 1997; Brook et al. 2003; deFries et al. 2005). Fragmentation is associated with numerous deleterious processes including the isolation of remaining forest patches and the creation of altered habitat at fragment edges (Laurance et al. 2002), which may seriously impair the ability of species reliant on undisturbed forest habitat to persist in fragmented landscapes. Studies of forest fragmentation have traditionally focused on landscapes in which large tracts of the original continuous forest have been cleared or otherwise altered for human activities leaving isolated remnants of forest surrounded by a matrix of altered habitat (Fahrig 2003; Ries et al. 2004; Harper et al. 2005). These studies have demonstrated numerous alterations in the ecology of remaining forest patches. Many species decline in abundance or are lost altogether while others increase in abundance or invade from the matrix (Gascon et al. 2000; Terborgh et al. 2001; Aponte et al. 2003; Ferraz et al. 2003), mutualisms may be disrupted (Cordeiro and Howe 2001, 2003; Guimaraes and Cogni 2002) and trophic interactions may change markedly (Terborgh *et al.* 2006). Vegetation structure and community dynamics may change substantially in forest fragments particularly near exposed fragment edges (Laurance et al. 1997, 1998a, b; Laurance 1998, 2001; Harper et al. 2005) and environmental conditions within fragments may become harsher and less favourable for the survival or growth of interior forest species (Kapos 1989; Matlack 1993). Together, these changes can lead to dramatic declines in forest biodiversity and ecosystem function in remnant forest fragments (Leigh et al. 1993; Tilman et al. 1994; Brooks et al. 1999; Beuer et al. 2002; Brook et al. 2003; Ferraz et al. 2003; Larsen et al. 2005). Fragmentation within remaining tracts of forest, however, has received comparatively little attention.

Linear clearings for road and powerline infrastructure are widespread and can substantially increase the edge length of an area of rainforest for a relatively small amount of habitat loss (Goosem 1997; Marsh and Beckman 2004). For example, in the Wet Tropics World Heritage Area of north-eastern Queensland, 1316 ha of rainforest has been cleared for 320 km of powerline easements and 608 ha has been cleared for 1427 km of roads (Trott *et al.* 1996; Goosem 1997). The edge effects of such linear clearings further reduce the area of intact rainforest over and above that already lost to clearing and fragmentation (Goosem 1997, 2000; Olander *et al.* 1998; Siegenthaler and Turton 2000; Ortega and Capen 2002; Marsh and Beckman 2004) and, as clearings for linear infrastructure are widespread in many forests, it is imperative to understand their potential impacts if these forests are to be successfully preserved (Goosem 1997). In this thesis, I will examine the edge effects of linear canopy openings on rainforest understorey microclimate and vegetation structure and composition.

Although studies have been conducted on mammalian communities (eg Burnett 1992; Goosem and Marsh 1997; Goosem 2000, 2001, 2002, 2004), little is known about the effects of roads and powerlines on the ecology of native plants in the Australian Wet Tropics. In particular, the long-term consequences of linear clearings for the understorey microclimate and the distribution and abundance of rainforest plant species in relation to such clearings are unknown (Siegenthaler 1999; Siegenthaler and Turton 2000). Alterations in microclimate differentially affect the germination, survival and growth of the seedlings of different species (Osunkoya *et al.* 1992; Osunkoya 1996; Whitmore 1996), thus any alterations in understorey microclimate near linear clearings may influence the dynamics and composition of the floristic community. Thus, in this project, I will examine the effects of such linear clearings on understorey microclimate and the vegetation community in the adjacent rainforest.

1.2 Aims

In this project, I investigated whether linear canopy openings produce microclimatic and floristic edge effects in nearby rainforest. I examined one natural (watercourse) and two artificial (powerline and highway) types of linear canopy opening. These represent some of the most common types of linear canopy openings in the Wet Tropics World Heritage Area of Australia, an area with an extensive network of clearings for linear infrastructure (Trott *et al.* 1996; Goosem 1997; Weston and Goosem 2004) where my study took place (Figure 1.1). I included watercourses in the study as these are a widespread natural type of linear canopy opening with a long evolutionary history in tropical rainforests and thus allow a comparison of the effects of anthropogenic (relatively recent) and natural internal fragmentation on the nearby rainforest. I explored the edge effects of linear canopy openings on the understorey microclimate, the composition of the floristic community, the physical disturbance regime and the survival and growth of seedlings with different light requirements in rainforest in north-eastern Australia. My overall research questions were:

- 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?

With regard to my second question, I predicted that the width of the linear canopy opening would be the main determinant of the edge effects observed in the adjacent rainforest (particularly the rainforest understorey); thus powerlines, as the widest linear clearing type, would be associated with the strongest edge gradients; whilst highways and creeks, being of similar width, would have similarly strong edge effects. It was recognised that the presence of flowing water might dampen gradients in vapour pressure and complicate vegetation gradients near creek edges. Additionally, differences in the disturbance regimes adjacent to clearings (eg regular highway maintenance vs. occasional flooding of creek edges) and propagule pressure of exotic plant species might also influence edge gradients. Also, as the severity of edge gradients is influenced by 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)], which is in turn affected by the time since edge creation, I predicted that the edge gradients associated with the anthropogenic linear clearings (15 - 50 years old, 15 - 50 years old,with current edges 15 years old) would be more severe than those associated with creeks (eg Parendes and Jones 2000).



Figure 1.1. The Wet Tropics World Heritage Area of north-eastern Queensland, Australia. This area has an extensive network of clearings for linear infrastructure. The inset shows highways, powerlines and other roads within the study region (Wooroonooran National Park and South Johnstone State Forest). Maps were prepared by Ms Tina Lawson with data from Geosciences Australia.

1.3 Outline of thesis

This thesis has been divided into the following, thematically-based chapters:

1. Introduction

2. Literature Review

A review of the relevant literature on temperate and tropical forest fragmentation and internal fragmentation with particular attention to studies focused on plants and the abiotic environment.

3. General Methodology

This chapter will present a description of the overall study design, the study area and the aspects of rainforest ecology to be explored in subsequent chapters.

4. Microclimatic Variation

This chapter will present an examination of the effects of natural and anthropogenic linear canopy openings on the spatial, seasonal and diurnal variation in the microclimate of the rainforest understorey. This will include:

- (a) traverse measurements (single point in time) during the wet season and dry season,
- (b) data logger measurements (diurnal variation) during the wet and dry seasons, and
- (c) variation in the light environment (measured via the red:far red ratio).

In part (a) the understorey light environment was examined using quantum sensors to measure the instantaneous intensity of photosynthetically active radiation (PAR; 400 - 700 nm wavelengths) in fine weather when edge gradients in all microclimatic parameters are strongest. In part (c) a red:far red sensor was used during overcast conditions when light conditions are uniform to measure the ratio of red (~ 660 nm wavelength) to far red (~ 730 nm wavelength) light to provide a better surrogate for the overall light regime experienced over time.

5. Vegetation Structure and Composition

In this chapter I will discuss a survey of the standing vegetation near powerline, highway and creek edges as compared with the forest interior. I will examine:

- (a) vegetation structure (including the distribution and abundance of groups of species with similar growth forms such as lianas, ferns, herbs, shrubs and trees),
- (b) the species composition and abundance of trees, saplings and seedlings, and
- (c) whether vegetation structure and composition are correlated with the understorey light environment.

6. Physical Disturbance

This chapter will address the question of whether physical disturbance is elevated near the forest edge. This question will be explored at two scales; tree-fall disturbance to the forest canopy and small-scale disturbance to seedlings and saplings from falling leaf litter and other canopy debris through measurements of:

- (a) the distribution of fallen trees in relation to the edge (to examine whether there is a greater number of tree falls near the edge),
- (b) an artificial seedling experiment (to assess the distribution of physical damage to seedlings caused by falling debris and leaf litter) (*cf.* Scariot 2000), and
- (c) seedling stature, measured with the height:basal diameter ratio (to determine whether seedling stature is suppressed by physical damage near the edge, *cf*. Peters *et al.* 2004),

7. Seedling Survival and Growth

In this chapter I will examine how the survival and growth of tree seedlings from species with differing successional status (and thus differing regeneration requirements) are affected by proximity to natural and anthropogenic linear canopy openings and the presence or absence of vertebrate herbivory pressure. I will examine:

- (a) the survival and growth of seedlings of selected species (with differing physiological tolerances and successional status), and
- (b) the level of vertebrate herbivory pressure on seedlings.

8. Main Discussion, Conclusions and Recommendations

In this chapter, I will discuss connections between the results presented in the previous four chapters and examine the implications of these results for the theoretical understanding of forest internal fragmentation. Management implications and recommendations for future research will be discussed.

The thesis has been written as a series of 'papers', tied together with general methods, discussion and conclusions sections, to allow me to focus on each aspect of the study individually, before considering the overall implications of the results in the main discussion section. The overall design of the project is described in Chapter 3, while specific details of the methods used to study individual aspects of the project are described in Chapters 4, 5, 6 and 7.

Chapter Two: Literature Review

2.1 Introduction

This chapter will focus on the effects of fragmentation, both external and internal, on the plant communities of temperate and tropical forest ecosystems with particular attention given to tropical rainforests. The emphasis will be on the responses of plants to the fragmentation-associated processes that occur near fragment and linear clearing edges and in isolated forest remnants, but the influence of these processes on animal taxa will also be considered where information on plant responses is scarce.

2.2 Forest Fragmentation

Human activities are increasingly leading to the loss and fragmentation of many of the Earth's natural ecosystems. Fragmentation occurs when previously continuous habitat is progressively reduced to a series of isolated habitat fragments of varying shapes and sizes, often biased towards smaller, isolated remnants in a 'matrix' of severely altered land (Whitmore 1997; deFries *et al.* 2005). Such fragmentation imposes a cost on species that is additional to the direct cost of habitat loss. For instance, in many countries tropical rainforest persists as isolated remnants surrounded by a matrix of land vastly altered for agriculture, forestry and other human land uses. Remaining large tracks of undisturbed forest are under threat from rates of clearing and forest conversion unprecedented in history (Whitmore 1997; deFries *et al.* 2005).

In the wake of fragmentation, the remaining forest remnants (patches of uncleared forest within a "matrix" of converted habitat) undergo a number of alterations in vegetation structure and community dynamics and composition. These alterations are particularly severe for smaller and/or more irregularly shaped fragments (Malcolm 1994; Lindenmayer and Peakall 2000; Laurance *et al.* 2002) as these remnants may be strongly affected by changes that occur at fragment edges in response to the altered conditions of the matrix (edge effects). Smaller fragments may also be unable to support large enough populations of some species to enable those species to persist within the fragment in the long term (eg Terborgh *et al.* 2001; Beuer *et al.* 2002; Ferraz *et al.* 2003) and species that are unable to cross the matrix between fragments will become isolated and may be reduced to a number of small, non-viable populations that could result in regional extinction in the long-term (Dudash and Fenster 2000). Fragmented

forest may also be more vulnerable to periodic drought events and to cyclones than continuous forest (Laurance 1997a, 1998; Laurance *et al.* 2001b). Additionally, interactions between remaining species may be altered, which may potentially lead to changes in the entire ecology of the forest fragment (Terborgh *et al.* 2006).

Forests may also be fragmented internally through infrastructure networks such as highway, road or powerline networks. The effects of such internal fragmentation are less well-known but may have widespread effects as networks of linear infrastructure are extensive in many regions of the world (Goosem 1997). Linear clearings may alter the abiotic environment and the distribution and abundance of species at the forest edge in a similar manner to the edge effects observed in forest fragments (Goosem 1997; Goosem and Marsh 1997) and may also isolate populations on either side of the linear clearing if individuals or diaspores are unable to successfully cross such clearings (Goosem 1997, 2004). The effects of such internal fragmentation have received less attention than the effects of landscape fragmentation *per se* but have the potential to dramatically reduce the amount of undisturbed habitat remaining in otherwise intact areas of forest.

2.2.1 Edge Effects

Interactions between the matrix and the forest occur at the boundary between the two and often lead to alterations of the physical and biological characteristics of the forest which are collectively known as "edge effects" (Murcia 1995; Kapos et al. 1997; Laurance 1997a; Turton and Freiburger 1997; Newmark 2001). In a review of the available literature, Murcia (1995) identified three types of edge effects: 1) abiotic edge effects; 2) direct biotic edge effects and; 3) indirect biotic edge effects. Abiotic edge effects are the changes that occur in the physical environment at the forest edge and may include alterations in microclimate, soil properties and physical disturbance regimes as well as the intrusion of herbicides or other pollutants or elevated noise levels near transport corridors (Forman and Alexander 1998; Gascon et al. 2000). Direct biotic edge effects occur when species are directly affected by the altered physical conditions at the edge, resulting in changes to their distributions and abundance. Indirect biotic edge effects occur when interactions between different species are altered near the forest edge and may result in disruptions to such processes as pollination and seed dispersal, higher predation rates, changes in competitive interactions and disruptions to mutualistic interactions, among others (Murcia 1995; Freidenburg 1998).

Edge effects may greatly reduce the area of undisturbed habitat within forest fragments. The extent of this reduction will depend on the extent and severity of the edge effects and, in very small fragments, there may be no undisturbed habitat remaining at all (Kapos 1989; Laurance 1997a, 2001). This places greater strain on populations of species already under threat from habitat loss and other human pressures. The study of the nature and extent of edge effects is thus of great importance for the successful conservation of biodiversity within fragmented landscapes.

2.2.1.1 Abiotic Edge Effects

The abrupt transition from forest to cleared land that occurs at an edge can lead to alterations in the physical characteristics of the forest at the edge. Cleared areas experience higher levels of solar radiation (photosynthetically active radiation), higher daytime temperatures, greater temperature extremes, higher wind velocities, lower humidity and greater evaporative demand (vapour pressure deficits) than the interior forest understorey (Murcia 1995). Exposure to the cleared matrix leads to alterations in the forest understorey microclimate at the edge and for some distance into the adjacent forest.

An immediate consequence of edge creation is an increase in light intensity in the understorey near the edge. This increase has been found to extend up to 60 m in tropical pre-montane forest in Tanzania (Newmark 2001), 15 - 25 m in pre-montane forest in Panama (Williams-Linera 1990a), 30 m in an old remnant of upland rainforest in Queensland (Turton and Freiburger 1997), 40 m in *terra firme* rainforest in Brazil (Kapos 1989), 10 m in temperate podocarp-broadleaf forest in New Zealand (Young and Mitchell 1994), 5 - 40 m in temperate deciduous forest in Illinois, USA (Gehlhausen *et al.* 2000) and up to 60 m in old-growth Douglas-fir forest in the American Pacific north-west (Chen *et al.* 1995). The distance of increased light penetration at the edge and the relative difference between edge and interior microclimates have been found to vary with edge orientation. Both parameters are greater for edges which are oriented so as to receive greater daily exposure to sunlight, particularly in forests located further from the equator (Matlack 1993; Young and Mitchell 1994; Chen *et al.* 1995; Turton and Freiburger 1997; Gehlhausen *et al.* 2000; Newmark 2001).

Increased light penetration at the edge drives changes in the entire microclimatic regime of the forest understorey. Air temperature, soil temperature, soil moisture,

relative humidity and vapour pressure deficit are all significantly affected by edges in both tropical and temperate forests (Kapos 1989; Young and Mitchell 1994; Chen et al. 1995; Turton and Freiburger 1997; Gehlhausen et al. 2000; Newmark 2001). During the daytime, air temperature increases at the edge, with elevated temperatures detected up to 180 m in temperate forests (Chen et al. 1995) and to between 15 and 94 m in tropical forests (Kapos 1989; Williams-Linera 1990a; Newmark 2001). Relative humidity decreases at the forest edge, with this decrease extending up to 10 - 240 m in temperate forests (Chen et al. 1995; Gehlhausen et al. 2000) and to between 15 and 40 m in tropical forests (Kapos 1989; Williams-Linera 1990a). Together, these changes in air temperature and relative humidity lead to a decrease in vapour pressure deficit at the forest edge (Young and Mitchell 1994; Turton and Freiburger 1997), which extends up to 60 - 83 m in tropical forests (Kapos et al. 1997; Newmark 2001). Soil temperature increases within 60 m of the edge in temperate forests (Chen et al. 1995) and 30 m of the edge in tropical forests (Turton and Freiburger 1997). Soil moisture decreases within 20 m of the edge in tropical forests (Kapos 1989) and in temperate forests shows greater variability but no decline within 15 m of the edge in old growth Douglas-fir forests (Chen et al. 1995) and declines within 15 - 60 m of fragment edges in temperate deciduous forest (Gehlhausen et al. 2000). The extent and severity of edge effects for all of these parameters vary with edge aspect, external weather conditions and time of day. Edge effects are greatest on more exposed edges, on hot, cloud-free days and between mid-morning and late afternoon, depending on the orientation of the edge (Chen et al. 1995; Turton and Freiburger 1997; Newmark 2001, 2005). During the night, edge gradients in air temperature (and, to a lesser extent, soil temperature) may reverse and gradients in relative humidity may weaken or vanish (Chen et al. 1995; Newmark 2005).

In addition to microclimatic changes driven by increased solar radiation, edges also expose forests to increased wind speed and turbulence (Laurance 2001). The distance that increased wind speeds penetrate into the forest has been directly measured in old-growth Douglas-fir forests in the American Pacific north-west and depends on external wind speed. At low wind speeds, edge distance is approximately 30 m but, at higher wind speeds, the edge distance can reach up to 240 m (Chen *et al.* 1995). Wind direction can also influence the distance that increased wind velocities penetrate into the forest (Chen *et al.* 1995). In tropical forests, the edge distance for increased wind speed has been measured indirectly through alterations in the vegetation such as increased

wind-related damage and mortality (Laurance 1997a). For example, in the Brazilian Amazon rainforest, increased wind disturbance may be responsible for substantially increased tree mortality within 100 m of the forest edge and moderate increases in mortality up to 300 m from the edge (Laurance *et al.* 1998a). Kapos *et al.* (1997) also indirectly measured a possible increase in the mixing of air between the matrix and the understorey at the forest edge through the analysis of stable carbon isotopes in understorey leaves. Increases in wind speed within the forest may also contribute to changes observed in air temperature and relative humidity at the edge (Chen *et al.* 1995; Gehlhausen *et al.* 2000). Direct measurements of wind speed are required to determine the extent of wind-related edge effects within tropical forest fragments.

Microclimatic edge effects are not fixed in time and space; both edge distance and the severity of the difference in microclimate between forest edge and interior may be highly variable (Newmark 2001). In addition to variability due to edge orientation and time of day, microclimatic edge effects may be influenced by season and by time elapsed since edge creation. Newmark (2001) found a great deal of seasonal variation in the extent and severity of edge effects on air temperature and relative humidity in tropical pre-montane forest in Tanzania. Additionally, Turton and Freiburger (1997) found that some microclimatic parameters exhibited edge effects in either the wet or dry season alone or were more pronounced in the dry season than in the wet season for a remnant of upland rainforest in Queensland, whilst Young and Mitchell (1994) found that edge gradients in air temperature and vapour pressure deficit that were present in summer disappeared in winter in temperate forest in New Zealand. Kapos et al. (1997) found that edge effects on vapour pressure deficit and soil moisture altered substantially within one and a half years of edge creation in the Brazilian Amazon rainforest. Edgeassociated reductions in vapour pressure deficit, which initially extended 60 m into the forest, had almost disappeared after 18 months. In contrast, the relationship between soil moisture and distance from the edge changed from being a simple pattern of reduction in soil moisture extending approximately 20 m into the forest to a much more complicated pattern of change extending approximately 60 m into the forest (Kapos et al. 1997). These microclimatic changes probably reflect changes in the structure of the vegetation at the forest edge over time (Williams-Linera 1990a; Kapos et al. 1997).

As forest edges age, the initially open space between the understorey and the canopy becomes "sealed" with a wall of vegetation; this may consist of saplings, herbs, shrubs, smaller trees, lateral branches of existing trees and, in tropical forests, a

profusion of lianas (Matlack 1994; Didham and Lawton 1999; Gascon et al. 2000; Mourelle et al. 2001; Laurance et al. 2002; Harper et al. 2005). In both temperate and tropical forests, sealed edges tend to experience less severe and less extensive microclimatic edge effects than edges with a more "open" vegetation structure (Matlack 1993; Didham and Lawton 1999). Decreases in the edge extent of elevated light levels, air temperature, vapour pressure deficit and lowered levels of soil and litter moisture have been observed near sealed edges in both temperate and tropical forest (Matlack 1993; Kapos et al. 1997; Didham and Lawton 1999), however, the effect of edge sealing on the penetration of elevated wind speeds has not been directly measured. Although older edges tend to become sealed over time, the intrusion of fire or exotic plant species into the forest edge may disrupt or reverse the process of edge sealing, leaving older forest edges open to the more severe and extensive edge effects experienced by younger forest edges (Didham and Lawton 1999; Gascon et al. 2000). These ongoing edge effects will influence vegetation community dynamics (Harper et al. 2005) and may determine whether or not a forest fragment is able to persist or to retain interior forest habitat over the longer term (Young and Mitchell 1994; Gascon et al. 2000).

2.2.1.2 Biotic Edge Effects

Alterations in the physical conditions at the forest edge can affect the structure of the vegetation and the distribution and abundance of species. Forest structure, rates of litterfall, rates of vegetation dynamics and above ground biomass can all be altered at the edge. These changes, combined with alterations in microclimate, may result in changes to the floristic community composition of the forest near the edge. When a forest edge is first created, vegetation structure resembles that of the forest interior; it is quite open beneath the canopy layers and understorey at the edge is fully exposed to the conditions in the matrix (Kapos 1989; Matlack 1994; Harper and Macdonald 2002). In temperate forests (particularly in north America), initial microclimatic changes at a newly-created forest edge lead to increases in tree mortality, windthrow and wind damage and fallen coarse woody debris (Burton 2002; Harper and Macdonald 2002; Harper et al. 2004). Increased tree mortality can act to further increase light intensity in the understorey, extending up to 60 m from the edge in Douglas-fir forests in Canada (Burton 2002). The initially strong microclimatic edge gradients also drive changes in community composition of plant species at the forest edge. Some interior species decrease in abundance (Matlack 1994; Fox et al. 1997; Gehlhausen et al. 2000;

Mourelle *et al.* 2001; Rheault *et al.* 2003; Nelson and Halpern 2005) while others, often light demanding, shade-intolerant species, increase in abundance (Matlack 1994; Gehlhausen *et al.* 2000; Mourelle *et al.* 2001; Honnay *et al.* 2002; Harper *et al.* 2005; Nelson and Halpern 2005). Exotic weed species found in the surrounding matrix also penetrate into the outer edge zone of the forest (Fox *et al.* 1997; Gehlhausen *et al.* 2000; Honnay *et al.* 2002). Over time, temperate forest edges become closed in by the growth of lateral and adventitious branches of trees (Matlack 1994; Mourelle *et al.* 2001). This process may take in excess of 20 years (Matlack 1994; Burton 2002; Harper and Macdonald 2002). After edge closure, microclimatic edge gradients may become less severe and extend a shorter distance into the forest (Matlack 1993, 1994). There may also be a reduction in penetration of weed species into the forest (Cadenasso and Pickett 2001).

In temperate deciduous forest in south-west Ontario, Canada and Piedmont USA, the forest canopy undergoes successional processes similar to those observed in forest gaps or in secondary succession, to replace light-demanding species favoured by the initial changes in microclimate at the edge with shade-tolerant, interior tree species (Matlack 1994; Mourelle et al. 2001). This process is facilitated by the increased interception of light by shade-tolerant trees at the edge, which further reduces the intensity of light reaching the understorey (Mourelle et al. 2001). The process may take well over 55 years but may not occur for all interior canopy tree species (Matlack 1994) and was not observed at all in one study of ancient Douglas-fir forest edges (Honnay et al. 2002). Further investigation is required to elucidate the role of windthrow in the long-term dynamics of tree species near temperate forest edges. There are some indications that wind-related tree mortality may affect certain tree species with particular tree architecture more than other species. The severity of these effects may depend on the orientation of the edge but the role of wind disturbance in the dynamics of temperate forest edges greater than 20 years old is not known (Burton 2002; Harper and Macdonald 2002).

Similar biotic edge processes are found in tropical forests. In the Brazilian Amazonian lowland *terra firme* rainforest, at the Biological Dynamics of Forest Fragments Project (BDFFP), when the forest was first cleared, the newly-formed edges experienced strong microclimatic gradients and increased wind disturbance (Kapos 1989; Rankin-de Merona and Hutchings 2001). These alterations in the abiotic environment led to an increase in dry season litterfall within 50 m of the edge, as trees shed leaves in response to increased moisture stress (Kapos 1989; Sizer *et al.* 2000). Rates of litterfall returned to background levels within 2 years of edge creation, as the forest edge was 'closed' by an increased growth of vines, lianas, understorey plants and adventitious branches of existing trees (Laurance *et al.* 1997; Laurance 1998; Sizer *et al.* 2000), although they were again elevated within 60 m of the edge during the 1997 El Nino drought-event, 12 - 15 years after edge creation (Laurance *et al.* 2001b). By 10 - 19 years after edge creation, litterfall rates were higher near fragment edges than in the forest interior (Vasconcelos and Luizao 2004) although the rate of leaf-litter decomposition did not vary between edges and the forest interior (Rubinstein and Vasconcelos 2005; Vasconcelos and Laurance 2005) and the rate of decay of coarse woody debris was higher near the edge (Nascimento and Laurance 2004).

The altered abiotic conditions of recently-cleared forest edges also led to elevated tree mortality near the edge (Rankin-de Merona and Hutchings 2001; Laurance et al. 2002). Some trees near the edge died due to increased moisture stress (Laurance et al. 2002) while others were damaged or killed by increased wind disturbance (Laurance et al. 1997, 1998a, 2001b; Rankin-de Merona and Hutchings 2001). Within the first 3 to 5 years, death and damage to smaller trees (10 - 30 cm diameter at breast height [dbh])were elevated. Trees within 20 m of the newly-formed edge were particularly prone to windthrow which, in turn, resulted in the damage and death of trees between 20 m and 40 m of the edge (extending up to 60 m into the forest although to a lesser extent) in a 'domino effect' (Rankin-de Merona and Hutchings 2001). Large trees (> 60 cm dbh) were particularly vulnerable to windthrow and experienced dramatically elevated mortality within 4 years of edge creation (Laurance 2001) and ongoing mortality long after the edge of the forest had been closed in by new growth (Laurance *et al.* 2000). The increase in tree damage and mortality resulted in an increase in the recruitment of existing saplings to trees within 3 to 5 years of edge creation (Rankin-de Merona and Hutchings 2001).

Over time (2 to 5 years), forest edges in the BDFFP were 'closed' through increased growth of plants in the understorey and lateral branches of existing trees at the edge and increases in the abundance of vines and lianas (Sizer *et al.* 2000; Laurance *et al.* 2001a; Laurance *et al.* 2002), in response to which change some microclimatic gradients became less severe but more complex (Kapos *et al.* 1997). The effects of elevated wind disturbance were still detectable at forest edges 17 years after edge creation (Laurance *et al.* 1997, 1998a). Tree mortality was strongly elevated within 100 m of the forest edge and was detectably higher than in interior forest for up to approximately 300 m with this increase being particularly severe for large trees (> 60 cm dbh) (Laurance et al. 1998a, 2000; Laurance 2001). Rates of tree damage were also elevated within 100 m of the edge as were rates of adult tree recruitment and turnover (with increases in turnover detectable up to approximately 300 m from the edge) (Laurance et al. 1998a, b; Laurance 2001). These changes were not influenced by edge aspect (Laurance et al. 1998a). This increase in the rate of tree community dynamics at the edge has implications for vegetation structure and composition. The original tall, complex forest is replaced by shorter, less structurally complex forest (Laurance 2001) and, as recruitment rate is positively correlated with the proportion of trees from successional families and negatively correlated with the proportion of trees from old growth families within these forest fragments, the forest near the edge shifts in composition from predominantly old-growth trees to an increasing dominance by successional trees (Laurance et al. 1998b). These changes in tree community dynamics have also led to a reduction in the above ground biomass of the forest within 100 m of the edge (Laurance et al. 1997).

Some of the alterations in vegetation structure found in the central Amazon (in the BDFFP) have also been found in other recently-isolated Neotropical rainforest fragments. In tropical wet pre-montane forest in Panama, after 7 years small trees (5 – 9.9 cm dbh) had increased in stem density and basal area with woody plants (< 5 cm dbh and > 2 m tall) increasing in stem density within 20 m of the forest edge. Trees > 10 cm dbh and plants < 2 m tall showed no change in stem density or basal area with distance from the edge but mortality for trees (> 5 cm dbh) was 14 times greater within 15 m of the edge than in the forest interior in the first 12 years after edge creation (Williams-Linera 1990a). The increases in stem density for small trees and woody plants were thought to be due to increased growth of existing saplings rather than the recruitment of new seedlings at the edge (Williams-Linera 1990a). In contrast to the results from the BDFFP, no changes were observed in the floristic composition near the forest edge, (with the exception of lianas, which were found almost exclusively at the very edge of the forest) and structural changes extended only 15 m - 20 m rather than to 100 m – 300 m (Williams-Linera 1990a). In another study, on a series of artificial islands created by inundation for a hydroelectric reservoir in lowland rainforest in French Guiana, four years after inundation, the frequency of small dead wood was greater than interior forest from the edge to more than 100 m whereas the volume of

dead wood was greater within approximately 30 m of the edge. These changes were thought to indicate a reduction in above ground biomass possibly similar to that found at the BDFFP in Brazil (Davies 2002). The reduction in the density of canopy trees found near temperate forest edges in British Columbia, Canada (Burton 2002), suggests that it is possible that temperate forests may also experience declines in biomass near the edge although this phenomenon requires further investigation in both tropical and temperate forests.

The future structure and species composition of forest near the edge depend upon the survival and growth of seedlings of different species. Although seedling growth and recruitment rates were elevated near forest edges within the first 8 - 15months after edge creation in both premontane forest in Panama and Amazonian forest fragments (Williams-Linera 1990b; Sizer and Tanner 1999), Williams-Linera (1990a) did not find any changes in the species composition of seedlings, saplings or adult trees with proximity to the edge within 12 years of edge creation. In contrast, in the BDFFP, the density of seedlings of shade-tolerant species near 'closed' forest edges (> 5 years old) decreased with proximity to the edge of 100 ha fragments (Benitez-Malvido 1998, 2001). There was, however, an increase in the recruitment of pioneer species near the edges of Amazonian forest fragments after the initial edge creation that was not observed near edges in premontane forest, where pioneer seedlings germinated only at edges where the soil had been disturbed (Williams-Linera 1990b; Sizer and Tanner 1999). It is possible that this disparity continued to shape the seedling community in subsequent years at both sites. Seedling herbivory did not differ with distance from the edge for the transplanted seedlings of 3 species of shade-tolerant trees but each species responded differently to fragment edges; one was unaffected, survival increased closer to the edge for the second while the third showed decreased growth near the edge (Benitez-Malvido 2001). Thus, at the BDFFP, recruitment of shade-tolerant seedlings and tree species decreased at edges of forest fragments, recruitment of successional tree species increased and tree community dynamics were elevated (Benitez-Malvido 1998; Laurance et al. 1998b, 2002; Sizer and Tanner 1999) although these changes were not found in Panama within 12 years of edge creation (Williams-Linera 1990a). There is thus the potential for some tropical forest edges to become increasingly altered from their original state through time and further investigation of long-term changes is required.
An important question is whether the biotic edge effects measured in younger fragments will persist over the longer term. Studies of older rainforest fragments on the Atherton Tablelands of north-east Queensland suggest that some biotic edge effects may still be present more than 60 years following edge creation. Laurance (1997a) found signs of elevated disturbance on the edges and in the interiors of two rainforest fragments surrounding Lake Barrine and Lake Eacham, more than 80 years after the isolation of these two remnants. Fragment edges and interiors had more open canopies, greater abundances of rattans and lianas and more broken tree limbs and dense woody debris than the interior of nearby continuous forest. Similar signs of disturbance were found on the edges of continuous forest and it was suggested that the changes in vegetation structure within fragment interiors were due to additive edge effects (Laurance 1997a). This study indicates that elevated wind disturbance may persist on forest edges for more than 80 years after edge creation.

In another study of a 20 ha remnant isolated for more than 60 years, Turton and Freiburger (1997) found that the total abundance of seedlings of dicotyledonous plants decreased within 30 m of the edge. Within this edge zone, soil temperature and vapour pressure deficit were elevated, suggesting that microclimatic edge effects may have had a negative influence on the dicotyledonous seedlings. The canopy of the forest was also more open near the edge (Turton and Freiburger 1997) and greater penetration of sunlight on the east- and west-facing edges of the fragment corresponded to increased seedling abundances on those edges in comparison to edges facing either north or south (Turton and Freiburger 1997). Although the species composition of seedlings was not recorded in this study, the results appear to have an intriguing similarity to those of Benitez-Malvido (2001) who found that the abundance of seedlings of shade-tolerant species decreased with proximity to the edge in BDFFP rainforest fragments.

Investigations of species composition of seedlings at the edges of older rainforest fragments would assist in determining whether there are likely to be longterm changes in the species composition of vegetation near rainforest edges. Neither study (Laurance 1997a; Turton and Freiburger 1997) specifically examined whether species composition of either seedlings or adult trees changed with proximity to the fragment edge. However, the long-term persistence of increased soil temperature, vapour pressure deficit and wind disturbance near forest edges (Laurance 1997a; Turton and Freiburger 1997) suggest that long-term changes in species composition near forest edges are not impossible. Further effort is required to determine whether such long-term alterations in vegetation composition and dynamics occur and, if so, the effect these may have on the future persistence of different species within fragmented landscapes.

2.2.1.3 Indirect Biotic Edge Effects (Higher order edge effects)

In addition to changes in the abiotic environment and the direct responses of the biota to these changes, interactions between species may be affected near the forest edge. Such interactions may include herbivory, pollination, seed dispersal, predation and parasitism. For example, insect herbivory on plant seedlings varied with distance from the edge in temperate forest in North America, affecting seedling survival and germination (Meiners *et al.* 2000). Similarly, seedling herbivory by Red-necked Pademelons (*Thylogale thetis*) was greater near subtropical rainforest edges than in the forest interior in south-eastern Queensland (Wahungu *et al.* 1999, 2002) and Meadow Vole (*Microtus pennsylvanicus*) predation of tree seedlings is elevated near deciduous forest edges in the United States although White-tailed Deer (*Odocoileus virginianus*) seedling predation is lower near forest edges (Cadenasso and Pickett 2000).

In contrast, there was no difference in the rate of herbivory on shade-tolerant seedlings with distance from the edges of 100 ha fragments of tropical Amazonian rainforest at the BDFFP in Brazil (Benitez-Malvido 2001) or between edges and the forest interior of tropical lowland rainforest in Chiapas, Mexico although incidence of leaf fungal infection was higher near the forest edge (Benitez-Malvido and Lemus-Albor 2005). Jules and Rathcke (1999) found increased seed predation and decreased pollination of the understorey herbaceous species *Trillium ovatum*, which combined to cause almost complete recruitment failure of this species within 65 m of the edge in a western North American conifer forest. Rodent seed predation decreased near the edges of artificial islands isolated by inundation for a large dam in rainforest in French Guiana (Chauvet and Forget 2005) and decreased slightly near upland rainforest edges in northeastern Queensland (Osunkoya 1994). Kollman and Buschor (2003) found that seed predation by rodents on the woody seeds of Prunus avium and Viburnum lantana in temperate deciduous forest in Switzerland increased near the forest edge when a dense shrub layer was present at the edge but did not increase when the shrub layer was removed. Shrub cover increased with proximity to the edge and it was this feature of the altered structure of the vegetation at the edge that led to the increase in seed predation (Kollmen and Buschor 2003).

Termites have also been found to respond to changes in vegetation structure at the forest edge (Davies 2002). In a series of four-year-old artificial islands formed by inundation from a hydroelectric reservoir in tropical rainforest in French Guiana, the abundance and species richness of wood and leaf feeding termites increased while abundance of soil feeding termites decreased in response to increased mortality of the vegetation near the edges of the islands (Davies 2002).

Edges may also interrupt mutualisms between plants and insects. In tropical Atlantic rainforest in Brazil, seeds of the native tree species *Cupania vernalis* are covered with an aril, which acts as an attractant for ants and which must be removed before the seeds can germinate (Guimaraes and Cogni 2002). In a rainforest fragment, however, fewer seeds had their arils removed by ants and more seeds were lost to predation near the fragment edge than in the fragment interior (Guimaraes and Cogni 2002). Similarly, in mesic deciduous forest in Georgia, USA, ants near forest edges preferentially dispersed seeds of the perennial herb *Sanguinaria canadensis* towards the forest interior rather than towards the edge or matrix although dispersal distance was not affected by proximity to the forest edge (Ness 2004). This dispersal bias reduced *S. canadensis* recruitment at the forest edge (Ness 2004).

Predation and parasitism may also be affected by the forest edge. Predation on birds' nests can be elevated near forest edges. Hartley and Hunt (1998) found that, in temperate forests in America, experimental nest predation on medium and large eggs was higher at forest edges in landscapes with less than 50 % remaining forest cover but such edge effects were less frequently observed in landscapes with more than 50 % remaining forest cover. In addition, Gates and Evans (1998) found that brown-headed cowbirds, a species which brood-parasitises other birds and has greatly increased in abundance since European settlement of America, is strongly associated with forest edges. Ectoparasitism of lizards in fragments of tropical rainforest near Las Cruces, Costa Rica was also affected by proximity to the forest edge; parasitism rates for one common lizard species were lower near the edge than in the rainforest interior (Schlaepfer and Gavin 2001). Elevated predation rates near the edge can affect the behaviour of vulnerable animals (Anderson and Boutin 2002). Juvenile red squirrels (Tamiasciurus hudsonicus) in temperate forests in Kluane, Yukon, spent less time travelling and foraging and had slightly higher survival rates prior to weaning near the forest edge than in the forest interior (Anderson and Boutin 2002). Considering the interconnected nature of species within an ecosystem, it is highly likely that changes in

some species near a forest edge will flow on to others and that highly complex effects may cascade throughout the ecosystem at the edges of both temperate and tropical forests (Laurance *et al.* 2002).

2.2.2 Isolation of Populations

Remnant populations of floristic species in forest fragments scattered across a landscape are vulnerable to a variety of threats to their long-term persistence. These threats include the direct impacts of altered abiotic conditions within fragments, loss of connectivity between populations and threats associated with small population size (eg stochastic population decline, environmental catastrophes and inbreeding depression). Some of these processes and their potential impacts on plant species in forest fragments are outlined below.

Changes in the abiotic environment within fragments may differentially affect the survival and persistence of different species within those fragments. Effects on species may be positive, negative or negligible. For example, in tropical rainforest fragments in the BDFFP in Brazil which had been isolated for over 15 years, the understorey herbaceous perennial Heliconia acuminata, a common species in central Amazonia, showed reduced seed germination and more variable seedling survival in 10 ha and 1 ha forest fragments than in continuous forest. These differences were thought to be due to higher leaf litter accumulation and the hotter and drier microclimate within forest fragments (Bruna 2002). Seedling recruitment in *H. acuminata* populations was also positively correlated with the number of flowering plants and the total plant density within each population with populations in fragments being smaller with fewer flowering plants than populations in continuous forest (Bruna 2002). The smaller number of reproductive plants in fragment populations was at least partially due to reduced (or even negative) growth rates of adult H. acuminata plants due to more hostile abiotic conditions (Bruna et al. 2002). As there is a strong, positive relationship between plant size and reproduction for this species, reduced growth rates in fragments have resulted in fragment populations becoming skewed towards smaller plant sizes than populations in continuous forest, thus exacerbating the reduction in seedling recruitment within fragment populations (Bruna et al. 2002). Similarly, the mean density of seedlings of shade-tolerant tree species in the BDFFP was lower in fragments than in continuous forest and this reduction was greater for smaller fragments although the impact on individual species within this group is not known (BenitezMalvido 1998, 2001). In Hokkaido, Japan, small populations of the common understorey perennial species *Trillium camschatcense* in forest fragments had fewer seedlings than larger populations in continuous forest, possibly due to reduced seedling survival in the altered abiotic environments within fragments (Tomimatsu and Ohara 2002). In contrast, the pollination and seed set of the New Zealand mistletoe species *Peraxilla tetrapetala* were increased by limited amounts of forest fragmentation; these responses appear to have been driven by the creation of more favourable abiotic conditions for the pollinators of this species at forest edges (Kelly *et al.* 2000).

As all negative environmental responses listed above were more severe in smaller fragments, it is likely that edge effects within fragments play a significant role in alterations to abiotic conditions to which populations of these species were responding (Benitez-Malvido 1998; Bruna 2002; Tomimatsu and Ohara 2002). Such direct, negative impacts of the abiotic environment upon the regeneration of species may result in fragments becoming unsuitable for long-term survival of these species, further increasing the loss of habitat above that already lost to fragmentation.

Even if alterations in environmental conditions within forest fragments are not sufficiently severe to directly eliminate populations of a species, small fragments may not be able to support populations large enough to survive over the long term. Small populations face a number of threats which are the subject of much concern in conservation biology (eg Primack 1993 and references therein). Small populations may be eliminated through random fluctuations in the environment or in the dynamics of the population itself (Holsinger 2000). Theoretically, isolated populations may decline to extinction if the variance in their growth rates is more than twice the average growth rate (Holsinger 2000). This variance may be due to random fluctuations in recruitment and mortality rates which normally occur in populations (demographic stochasticity) or to random fluctuations in factors external to the population that may affect mortality rates (environmental stochasticity). Small populations may be particularly vulnerable to these effects (Holsinger 2000). However, although accelerated dynamics have been observed in fragment populations for some species (Leigh et al. 1993; Laurance et al. 2002), fragment populations are not necessarily always more variable than populations in continuous habitat (Davies et al. 2001; Zartman and Shaw 2006).

In addition, animal- or insect-pollinated plants in smaller populations may be unable to attract pollinators or support pollinator populations of sufficient size to provide adequate pollination, leading to reduced seed set and thus reduced population fecundity. For example, small, isolated populations of Trillium camschatcense in Hokkaido, Japan, suffered reduced seed set due to pollen limitation, possibly caused by changes in pollinator species composition in small fragments (Tomimatsu and Ohara 2002, 2003). Similarly, lower pollination rates led to reduced seed set in the shrubs Acacia brachybotrya and Eremophila glabra in small fragments of mallee woodland in central New South Wales, Australia (Cunningham 2000a, b) and in the forest shrub *Cestrum parqui* in small fragments (< 5 ha) in the Chaco Serrano region of central Argentina (Aguilar and Galetto 2004). In isolated plant populations, where neither pollinators nor seed-dispersers are able to cross the matrix between fragments, plants within fragments will only be able to reproduce with other plants from within the same population and, over a number of generations, this may lead to the population becoming inbred (Young et al. 1996; Dudash and Fenster 2000). In some species, this results in a reduction of fitness (known as 'inbreeding depression'), which further reduces the ability of the population to survive within that fragment (Young et al. 1996; Dudash and Fenster 2000). For example, inbreeding dramatically reduced seed germination in the dioecious perennial Silene alba (Richards 2000).

The level of connectivity between fragment populations will determine the rate of gene flow between populations and thus affect the rate of loss of genetic variation within populations through inbreeding. Completely isolated populations of *Grevillea caleyi* in New South Wales have developed a high level of genetic differentiation between populations (Whelan *et al.* 2000). In contrast, pollinators of the neotropical tree species *Swietenia humilis* are able to cross the matrix in fragmented dry forest in central America and, consequently, this species has not suffered reduced genetic diversity following forest fragmentation (White and Boshier 2000). Similarly, genetic connectedness has been maintained between island and mainland populations of the epiphytic orchid *Catasetum viridiflavum* in the man-made Gatun Lake (Panama Canal, Panama) because the main pollinators (euglossine bees) are able to cross the lake to reach the island orchid populations although fruit set in these populations is lower than on the mainland (Murren 2002, 2003). Additionally, once gene flow between previously isolated populations of *Silene alba* was restored, inbreeding depression within populations was reduced (Richards 2000).

Genetic variation within a population may also be buffered, for a time, by a genetically diverse, long-lived seed bank (eg *Grevillea macleayana*) (Whelan *et al.* 2000). As the seeds of trees in tropical rainforests tend to be short-lived, however, it is

unlikely that this mechanism would be applicable in tropical rainforests although it is conceivable that the understorey seedling pool might perform a similar function (Bruna 2002). It is unlikely, however, that either seed banks or seedling pools could buffer isolated populations against the loss of genetic diversity and effects of inbreeding depression indefinitely. Without a restoration of gene flow between populations, the processes described above would eventually lead to erosion of genetic diversity, albeit much more slowly (Whelan *et al.* 2000).

The degree of population isolation between fragments also influences the rate of fragment colonisation and thus the long-term metapopulation dynamics of species within fragmented landscapes (Gonzalez and Chaneton 2002). The species richness of a fragment may be buffered, at least for a time, by recolonisation of extirpated species from elsewhere in the landscape (Tilman et al. 1994). However, the ability of different species to cross the matrix will depend on the mobility of the species and the characteristics of the matrix itself (Tilman et al. 1994; Jacquemyn et al. 2001; Kupfer et al. 2006). For example, mammal species that were more tolerant of matrix conditions were more likely to persist in fragments of upland rainforest in north-eastern Queensland (Laurance 1997b), in rainforest fragments in the southern Brazilian Amazon (Michalski and Peres 2005) and in rainforest fragments in central Amazonia (the BDFFP, Gascon et al. 1999). Additionally, matrix conditions that present a lesser contrast to interior habitat conditions may allow a greater number of species to persist (Kupfer et al. 2006). Even if the matrix does allow some degree of population connectivity between fragments, species will still be lost from fragments and potentially from the entire landscape (Brook et al. 2003; Ferraz et al. 2003). For example, the number of tropical forest interior bird species declines rapidly after forest fragmentation with declines more pronounced and more rapid with decreasing fragment size (Brooks et al. 1999; Ferraz et al. 2003). Moreover, some species are consistently more vulnerable to extinction than others (Beuer et al. 2002 Ferraz et al. 2003); very large forest reserves may be required to preserve viable populations of these species (Ferraz et al. 2003).

Processes which affect individual species may eventually alter species composition of forest fragments. Some species decline or are eliminated, some increase in abundance, some invade from the matrix and others remain unaffected. For example, in palm tree communities of rainforest fragments with 'closed edges' in the BDFFP in Brazil, five species from the matrix that do not occur in continuous forest have invaded forest fragments. The species richness of closed-forest palm species is declining in 1 ha and 10 ha fragments and the community composition of palm seedlings (though not yet of adults) is starting to diverge between continuous forest and smaller fragments (Scariot 2001). As these palms may live for over 50 years, any changes in species composition due to fragmentation may take many years to be fully realised but could eventually be quite marked (Scariot 2001). Indeed, in Gatun Lake in Panama, small islands of rainforest that were isolated by inundation for the Panama Canal approximately 70 years previously had an extremely restricted subset of tree species compared to larger islands or mainland areas (Leigh *et al.* 1993).

Common species are not immune to the effects of forest fragmentation and rare species may be even more vulnerable (Bruna 2002). This may be particularly alarming for tropical rainforests which typically have a substantial proportion of species that occur at very low densities (< 1 individual ha⁻¹) (Laurance 2001). Indeed, metapopulation modelling indicates that, if widespread trade-offs exist between competitive ability and dispersal ability, competitive species with poor dispersal ability will be particularly vulnerable to population extinction in fragmented landscapes and thus species which were previously common may be among the first to decline to extinction after forest fragmentation (Tilman et al. 1994). The shade-tolerance spectrum of tropical rainforest tree species between pioneer species with large numbers of small fruit and shade-tolerant climax species with larger fruit that provide greater reserves for seedlings to persist in low light and recover from damage (Osunkoya 1996; Turner 2001; Moles and Westoby 2004, 2006; Murray et al. 2005) may be an example of one such trade-off in ability to compete compared with ability to disperse. Reductions in recruitment of tree species with animal-dispersed diaspores in small forest fragments in the East Usambara Mountains, Tanzania (Cordeiro and Howe 2001) and in the abundance of herbaceous species with low numbers of large diaspores lacking specialised dispersal structures in temperate deciduous forest in Germany (Kolb and Diekmann 2005) provide some support for this hypothesis. The species composition of forest fragments may eventually become vastly altered with higher numbers of invasive or exotic species (Fox et al. 1997) and fewer species of the original forest remaining (Tabarelli et al. 1999; Brook et al. 2003; Lovei et al. 2006).

Other interactions between plants and animals may also be altered within forest fragments and these changes may further exacerbate processes of species loss. For example, the loss of predators on islands in artificial lakes can lead to increased

population densities of remaining herbivorous species, which can, in turn, affect the structure and composition of plant communities (Asquith and Mejia-Chang 2005; Terborgh et al. 2006). Small and medium-sized islands (< 12 ha) in Lago Guri, an artificial lake in semideciduous tropical dry forest in Bolivar, Venezuela, lost over three quarters of their original vertebrate species within a decade of inundation, including all large carnivore species and almost all frugivorous species (Terborgh et al. 2001). Reduced predation led to a dramatic increase in the densities of herbivorous species (Rao et al. 2001; Terborgh et al. 2001; Aponte et al. 2003), which in turn led to a reduction in seedling survival and sapling recruitment and a shift in vegetation composition towards species less preferred by herbivores (Rao et al. 2001; Terborgh et al. 2001, 2006). Indeed, on the smallest islands, there has been complete recruitment failure for canopy tree species and, in some instances, as the forest canopy has died off, the original vegetation has been replaced by dense thickets of lianas (Terborgh et al. 2006). Reduced recruitment on other small and medium islands suggests that the same processes are underway on these islands although at a slower rate (Terborgh et al. 2006).

Similarly, in Gatun Lake, an artificial lake in rainforest in Panama, most of the original mammal community has been lost from small (< 2.2 ha) islands whilst larger mammals have been lost from medium-sized (< 17 ha) islands (Asquith and Mejia-Chang 2005). On small Gatun Lake islands, a combination of desiccating dry season winds, storm damage and altered plant - animal interactions have dramatically reduced tree diversity (Leigh et al. 1993; Asquith and Mejia-Chang 2005). Seed predation and seedling herbivory are higher on small and medium islands than on larger islands or mainland sites and exposure to dry season winds leads to reduced seedling survival on small and less-protected islands (Asquith et al. 1997; Asquith and Mejia-Chang 2005). In contrast, exposure to prevailing winds did not affect sapling recruitment on Lago Guri islands (Terborgh et al. 2001). The dominant tree species on small Gatun Lake islands tended to be either favoured by disturbance or species of secondary forests (Leigh et al. 1993; Asquith and Mejia-Chang 2005). Similar alterations in plant herbivore interactions have been observed in temperate conifer forest in the Siskiyou Mountains of south-western Oregon, USA, where the abundance of Deer Mice (*Peromyscus maniculatus*) increased in forest fragments (< 4 ha) leading to an increase in the rate of seed predation for the herb Trillium ovatum which may increase the risk of T. ovatum population extinctions within forest fragments (Tallman et al. 2003).

Changes in plant – animal interactions in fragments may also affect plant species diversity by altering spatial patterns of seed dispersal and seedling recruitment within fragments. For example, on small islands in Gatun Lake, Panama, as well as in nearby mainland areas subject to human hunting pressure, loss of rodent seed predators has altered the spatial distribution of seedlings of the canopy palm Attalea butyraceae, increasing the abundance of seedlings close to parent trees, decreasing the overall rate of seed predation and thus increasing overall seedling recruitment (Wright and Duber 2001). As increased seed and/or seedling mortality near parent trees is one mechanism considered to be important in maintaining overall tree species diversity in tropical rainforests by preventing the formation of monospecific stands (Janzen 1970; Connell 1971), the formation of such monospecific stands on small Gatun Lake islands is suggested to be at least partly responsible for the increased abundance of Attalea and decreased overall tree diversity on these islands (Wright and Duber 2001). In contrast, in rainforest fragments in the East Usambara Mountains of Tanzania, altered patterns of seedling recruitment have led to a decline in overall recruitment rates for the tree species Leptonychia usambarensis (Cordeiro and Howe 2003). In this instance, reduced abundances of frugivorous birds in forest fragments led to a reduction in the rate of seed dispersal away from parent trees but the rate of seedling survival remained lower within 10 m of parent trees than further away and thus the overall sapling recruitment rate for L. usambarensis has declined in forest fragments (Cordeiro and Howe 2003). Thus, alterations in the interactions between species may cause dramatic changes in the ecology of fragmented forests although the nature of such changes may vary between regions.

2.2.3 Internal Fragmentation

Internal fragmentation of forests by artificial linear canopy openings (eg roads, highways, powerline clearings and railway tracks) is widespread throughout much of the world with many areas having extensive networks of highways, secondary and tertiary roads, forestry roads, powerline clearings and other infrastructure corridors (Goosem 1997; Goosem and Marsh 1997; Forman and Alexander 1998; Goosem 2004). Such networks may have effects reaching far beyond the areal extent of loss of habitat due to the clearing network itself. For example, in an area of forest fragmented by roads, 55 % of the remaining natural habitat had a lowered probability of occupation by

Moor Frogs (*Rana arvalis*) due to population isolation by roads (Vos and Chardon 1998).

Internal fragmentation may also lead to significant edge effects within the forest and can pose barriers to the movement of numerous native animal taxa. These barrier effects may result in populations of animals becoming fragmented and genetically isolated with potentially serious consequences for plant taxa which rely on animals for pollination or seed dispersal (Goosem 1997; Goosem and Marsh 1997; Harrington *et al.* 1997). Roads and powerlines also often facilitate the movement of native and exotic species from other habitats into the forest (Goosem 1997; Goosem and Marsh 1997). I will briefly review the edge and isolation effects of artificial linear canopy openings on plants and animals within forest ecosystems.

2.2.3.1 Edge Effects

Artificial linear canopy openings such as roads and powerlines may alter the physical and biological properties of the adjacent forest greatly increasing the area of altered forest habitat. As occurs with larger clearings (such as those for agriculture or silviculture), the edge effects caused by linear clearings may affect the abiotic environment, directly alter the distribution and abundance of species and/or indirectly affect species near the edge (Murcia 1995; Forman and Alexander 1998; Siegenthaler 1999).

Alterations in the abiotic environment near edges of roads and powerline clearings may include an increase in pollution levels, alterations of the natural overland flow and increases in erosion rates, increased noise levels (particularly for heavily-used roads and highways) and changes in microclimate (Forman and Alexander 1998; Siegenthaler 1999). The extent and severity of microclimatic edge effects may be influenced by the width of the linear clearing and hence the degree of canopy closure above the linear feature (Siegenthaler 1999; Siegenthaler and Turton 2000).

In tropical upland rainforest in the Palmerston area of north-east Queensland, microclimatic edge effects were more intense for a powerline clearing that was 60 m wide and covered with exotic grass and weed species than for a 12 m wide clearing for a forestry road with grassy verges and an open tree canopy above the road, the effects of which were, in turn, more intense than those associated with a 10 m wide clearing for a small forestry road with a closed tree canopy above the road and no grassy or weedy verges (Siegenthaler 1999; Siegenthaler and Turton 2000). Light intensity was elevated within 7 m of the powerline edge and the wider road edge and within 3 m of the smaller road edge and this increase in light intensity was more severe in the dry season than in the wet season (Siegenthaler 1999; Siegenthaler and Turton 2000). These increases in light intensity led to a number of changes in soil temperature, air temperature, vapour pressure deficit and wind speed (Table 2.1). These microclimatic edge effects generally extended further from powerline edges than road edges and were more severe in the dry season than in the wet season. Diurnal changes in temperature were greater in the forest near the powerline than in the forest near either of the roads and the diurnal variation in temperature increased with proximity to the powerline edge (Siegenthaler 1999).

Parameter	Edge Distance		
	Powerline	Road, open canopy	Road, closed canopy
Light intensity	↑ 7 m	↑ 7 m	↑ 3 m
Red:far red ratio	↑ 7 m	↑ 7 m	↑ 3 m
Air temperature _{150cm}	↑ 3 – 7 m	↑ 3 – 7 m	↑ 3 m
Air temperature _{20cm}	↑ 3 m	↑ 3 m	↑ 3 m
Vapour pressure deficit _{150cm}	↑ 3 – 20 m	↑ 11 – 20 m	↑ 20 m
Vapour pressure deficit _{20cm}	↑ 25 m	↑ 11 m	↑ 11 m
Soil temperature _{0cm}	↑ 11 m	↑ 7 m	↑ 3 m
Soil temperature _{10cm}	↑ 3 m	↑ 3 m	_
Wind speed	↑ 11 m	_	_

Table 2.1. Edge distances observed for microclimatic edge effects near powerlines and unpaved roads in northeastern Queensland (Siegenthaler 1999; Siegenthaler and Turton 2000). Arrows indicate the direction of the change in each parameter near the edge (↑ increase near the edge, ↓ decrease near the edge).

Some of these microclimatic edge effects were comparable in extent with those measured for agricultural edges in neotropical forests in Panama (Williams-Linera 1990a) and the extent of the elevated vapour pressure deficit was comparable to those observed on older edges in the BDFFP in Brazil (Kapos *et al.* 1997). Other microclimatic changes, however, were restricted to within 3 - 7 m of the forest edge (Table 2.1). Variation in extent and severity of microclimatic edge effects between wet and dry seasons could have implications for germination and survival of different plant species as well as distributions of invertebrates and other taxa and the rates of nutrient cycling near the forest edge (Vitousek 1984; Osunkoya 1996; Whitmore 1996; Davies

2002). The extent and severity of penetration of wind into the forest could also have important consequences for the dynamics of tree and seedling communities (eg Laurance 2001). Although the extent of relatively mild increases in wind speed in the understorey appeared to be limited to within 7 m of the edge, there may be greater changes towards the canopy of the forest (Siegenthaler 1999) and possible effects of artificial linear canopy openings on the susceptibility of forest near the edge to wind and storm damage caused during tropical cyclones are not known.

Microclimatic edge gradients have also been detected near roads in temperate forest. Elevated light levels have been detected near paved and unpaved roads in temperate forest in the USA (Haskell 2000; Parendes and Jones 2000; Watkins *et al.* 2003) and elsewhere (Trombulak and Frissell 2000) although some studies of narrower roads have not found any microclimatic edge effects (King and DeGraaf 2002; Ortega and Capen 2002). Air temperature and vapour pressure deficit may also be elevated near road edges in temperate forest (Watkins *et al.* 2003) although reported edge patterns in soil moisture near linear canopy openings have been inconsistent (Marsh and Beckman 2004). Edge gradients in wind speed do not appear to have been investigated near linear canopy openings in temperate forest.

Changes in the abiotic environment near edges of artificial linear clearings may also affect biotic characteristics of forest near the edge. Vegetation structure and composition may be altered near the edges of roads and powerlines. Near edges of wider linear clearings (powerline corridors, highways and forestry roads with open canopies) in temperate deciduous forest in Maryland, there are more seedlings and saplings, fewer small trees (7.5 - 30 cm dbh), fewer small dead trees (7.5 - 22.5 cm)dbh) and more large dead trees (> 22.5 cm dbh). A greater volume of space is occupied by vegetation beneath the canopy but the overstorey canopy is more open than for forest near narrow linear clearings (small forestry roads with closed tree canopies) or within the forest interior (Evans and Gates 1997; Gates and Evans 1998). In this study, vegetation structure was recorded to characterise animal habitat with further research needed to determine the significance for plant community dynamics; however, it appears possible that increased recruitment rates and tree mortality similar to those observed near agricultural edges (eg Williams-Linera 1990a) may occur near the edges of powerlines and roads with open tree canopies. Similar changes in vegetation structure have been observed near road edges in subalpine coniferous forest in Japan (Nagaike 2003) and tropical rainforest in Africa (Malcolm and Ray 2000). In Japanese subalpine

forest, there were a greater number of saplings and dead trees near road edges and the living trees near the road edge had smaller diameters than the dead trees (Nagaike 2003). There was a similar shift towards smaller tree diameters near road edges in the African tropical rainforest although in that study sapling density declined near roads (Malcolm and Ray 2000). These shifts towards smaller tree sizes, and the larger diameters of dead trees near road edges in Japan, suggest that increased mortality of large trees and increased recruitment of smaller trees similar to observations near edges of neotropical rainforest fragments (Williams-Linera 1990a; Laurance *et al.* 2002) and temperate fragment edges (Harper and Macdonald 2002) may occur near road edges.

Additionally, in a study of edge effects on seedling communities near roads and powerlines in tropical rainforest in north-east Queensland, Siegenthaler (1999) found that, compared to the forest interior, the forest canopy was more open within 7 m of the edges of a powerline and a road with an open canopy overhead and at the very edge of a road with a closed overhead canopy. Seigenthaler (1999) also found that there were fewer small (≤ 20 cm tall) and large (20 - 150 cm tall) seedlings within 3 m of the edges of the powerline, the open-canopy road with grassy verges and the closed-canopy road compared with the forest interior. The abundance of small seedlings was negatively correlated with light intensity suggesting that these seedlings may have been negatively affected by microclimatic changes driven by increased light penetration into the understorey (eg increased temperature and decreased vapour pressure deficit) (Siegenthaler 1999; Siegenthaler and Turton 2000). The overall species composition of seedlings was also influenced by edge proximity and edge type. Abundance of seedlings of rainforest interior species was positively correlated with distance from the edge and this effect was strongest for the powerline edge. Abundance of vines was elevated within 25 m of the edge of the powerline. In contrast, abundance of seedlings of pioneer species was not correlated with distance from the edge (Siegenthaler 1999; Siegenthaler and Turton 2000). The decrease in abundance of seedlings of rainforest interior species near the edges of powerlines and roads may be similar to the decrease observed in the abundance of shade-tolerant seedlings near the edges of forest fragments in the BDFFP in Brazil (Benitez-Malvido 2001). These changes suggest that some of the alterations in vegetation structure and dynamics observed in neotropical forest fragments (eg Williams-Linera 1990a; Benitez-Malvido 1998) may occur at the edges of powerline clearings and roads although further research is required to determine if this is in fact the case.

Similar alterations in composition of native animal communities near linear canopy openings have been observed (Goldingay and Whelan 1997; Goosem and Marsh 1997; Ortega and Capen 2000; Goosem 2001) while such clearings may also facilitate the spread of invasive species into the forest (Goosem and Marsh 1997; Forman and Alexander 1998; Delgado et al. 2001) and further alter the composition of plant and animal communities at the forest edge. For example, Siegenthaler (1999) found that exotic weeds were present at the edges of powerlines and forestry roads in tropical rainforest, but that weeds did not penetrate further than 3 m into the forest. In temperate forest, weeds were common within 15 m of road edges in Wisconsin, USA (Watkins et al. 2003) and within 10 m of road and railway edges in the Canadian Rocky Mountains (Hansen and Clevenger 2005) but almost absent from the forest interior. Goosem and Marsh (1997) found that the grassland specialist small mammal species Melomys burtoni and Rattus sordidus were able to utilise a grassy powerline clearing and perhaps competitively exclude native small mammals but were unable to penetrate into the rainforest. In addition, Delgado et al. (2001) found that the introduced Ship Rat (Rattus *rattus*) utilised forest within 60 m of paved road edges on Tenerife, in the Canary Islands. In contrast, Goldingay and Whelan (1997) found that introduced cats and dogs did not utilise powerline corridors in eucalypt forests in New South Wales but were present between 50 and 200 m of the powerline edge.

Some indirect biotic edge effects may also be observed near the edges of linear canopy clearings. For example, nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) in temperate deciduous forests in Maryland, USA, was higher near agricultural, powerline and road edges than in interior forest (Evans and Gates 1997; Gates and Evans 1998). The abundance and species richness of host bird species were higher near such edges than in the forest interior and female cowbirds aligned their breeding and roosting ranges along forest edges (Evans and Gates 1997; Gates and Evans 1998). In contrast to these results, however, Ortega and Capen (2002) found no relationship between nest predation and distance from the edge of an unpaved road. Further research is required to determine whether any general patterns exist in predation and parasitism with relation to the edges of artificial linear canopy openings.

Plant species may also be affected by indirect biotic changes at the edges of artificial linear canopy openings. Seed detection and removal by introduced ship rats in the Canary Islands occurred at higher rates within 60 m of unpaved road edges in laurel forest and 20 m of unpaved roads in pine forests (Delgado *et al.* 2001). Changes in

distribution and abundance of native and introduced species near the edges of artificial linear canopy openings could have important implications for the population dynamics of plant species with seeds that are dispersed or preyed upon by such animals. For example, in tropical rainforest in north-east Queensland, there are many native tree species that have large fruits that are preyed upon by small mammals or which rely upon small mammals, birds or fruit bats for their dispersal (Harrington *et al.* 1997). Further research into the effects of artificial linear canopy openings on such plant-animal interactions will be required to fully elucidate the nature of such indirect edge effects upon forest ecosystems.

In summary, although much research has been done on edge effects experienced within tropical forest fragments, relatively few studies have examined edge patterns generated by internal linear clearings in tropical rainforest. Where they exist, such edge gradients have the potential to substantially reduce the area of intact interior forest even within protected areas (Goosem 1997). In particular, very few studies have examined microclimatic edge gradients near roads or powerlines and the majority of these studies have been undertaken in temperate forests (Haskell 2000; Parendes and Jones 2000; Trombulak and Frissell 2000; King and DeGraaf 2002; Ortega and Capen 2002; Watkins et al. 2003; Marsh and Beckman 2004). Additionally, only one study (Siegenthaler 1999) has examined alterations in wind speed near linear clearings. Biotic edge gradients near linear clearings have also received less attention than those near fragment edges. Although measurements of vegetation structure and seedling density (Evans and Gates 1997; Gates and Evans 1998; Siegenthaler 1999; Malcolm and Ray 2000; Nagaike 2003) suggest that similar processes of elevated tree mortality and reduced recruitment of interior forest plant species may occur near linear clearings as those observed near fragment edges (eg Laurance et al. 2002), no studies have specifically tested whether this is the case and no systematic comparisons of species composition between the edge and the forest interior have been conducted near linear features in tropical rainforest. Additionally, very little attention has been given to potential alterations in species interactions near the edges of linear clearings although changes in the abundance and distribution of numerous mammal species (Goosem 2004), many of which are known to be seed predators, seed dispersers or herbivores (Lott et al. 1995; Vernes et al. 1995; Harrington et al. 1997; Theimer 2001; Dennis 2003), suggest that such changes may occur.

In this thesis, I will investigate microclimatic edge gradients associated with linear features in tropical rainforest using both instantaneous and diurnal measurements (Chapter 4). Measures of light availability, desiccation stress (eg air temperature, vapour pressure deficit, soil temperature and soil moisture) and wind speed will be examined (Chapter 4). I will also investigate whether linear features are associated with edge gradients in vegetation structure and species composition (Chapter 5) or with elevated levels of physical disturbance (Chapter 6). In addition, I will briefly examine whether species interactions are altered near the edges of linear features through 1) a seedling experiment designed to measure changes in herbivory by vertebrate species on tree seedlings (Chapter 7) and 2) indirect measurements of possible seed dispersal limitation near the forest edge using an examination of the relative abundance of seedlings with large, vertebrate-dispersed diaspores near the forest edge as compared with the forest interior (Chapter 5).

2.2.3.2 Isolation

Artificial linear openings in the forest canopy may form barriers to the dispersal of individuals and, where such barriers divide existing populations or meta-populations, the resulting, smaller populations may become isolated. Such isolation may be further exacerbated if the mortality of individuals which do attempt to cross such barriers is increased (Goosem 1997; Forman and Alexander 1998).

In tropical rainforest in the Wet Tropics of north-east Queensland, the movements of small mammals such as *Melomys cervinipes*, *Rattus fuscipes* and *Rattus* sp. are inhibited by the presence of small paved and unpaved roads (Burnett 1992; Goosem 2002) and this inhibition may occur independently of the volume of traffic (Goosem 2002). These small mammal species are all capable of travelling distances greater than the width of such roads (Burnett 1992; Goosem and Marsh 1997) but may avoid roads or align their territories or home ranges with the edge of the road so that only dispersing individuals are likely to cross small roads (Burnett 1992). In contrast, the movements of the larger and more mobile *Uromys caudimaculatus* are not inhibited by the presence of such small roads (Burnett 1992; Goosem 2002). *U. caudimaculatus*, *M. cervinipes* and *Rattus* sp., however, were unable to cross a 60 m-wide, grassy powerline clearing in rainforest in the Palmerston region (Goosem and Marsh 1997). These forest specialists may have been excluded from the grassy powerline corridor through interspecific competition with the grassland species occupying the corridor and

through differences in habitat quality between the rainforest and the powerline clearing (Goosem and Marsh 1997). These rainforest mammals were only able to cross the powerline corridor in areas of rainforest regrowth within the corridor (Goosem and Marsh 1997). Such restrictions of movement may lead to increased isolation of populations of the smaller mammals and may also increase the isolation of populations of plant species that rely on small mammals for seed dispersal (Goosem 1997; Harrington *et al.* 1997).

Gene flow between plant populations may also be reduced for insect- and animal-pollinated species if the movements of pollinators are inhibited by the presence of artificial linear clearings. For example, bumblebees (worker bees of the species *Bombus impatiens* and *B. affinis*) in a temperate conservation area in Boston, Massachusetts, very rarely cross a railroad and small road that subdivide the area (Bhattacharya *et al.* 2003). Although the bumblebees are capable of crossing these barriers, they align their feeding ranges with plant populations on one side of the road or railroad only and show a high site fidelity to these populations (Bhattacharya *et al.* 2003). As bumblebees use such features as landmarks, if roads and powerlines are built through the middle of an existing plant population, bumblebees may see the population as two separate populations and gene flow between plants on opposite sides of the road may be dramatically reduced (Bhattacharya *et al.* 2003). Further research is required to determine how widespread such effects may be on plant pollination in both temperate and tropical ecosystems.

Animal populations may also be directly affected by increased isolation due to roads and other artificial linear features. For example, the Moor Frog, *Rana arvalis*, is negatively affected in the province of Drenthe in the Netherlands (Vos and Chardon 1998). Increases in road density increase isolation between suitable habitat patches (and are also correlated with reduced habitat quality) and increase mortality of dispersing individuals leading to a reduced probability of site occupancy in 55 % of the region and less than 30 % occupation probability in areas close to a major motorway (Vos and Chardon 1998). Similarly, populations of Desert Bighorn Sheep (*Ovis canadensis nelsoni*) in the Mojave and Sonoran Deserts of California, USA, that were isolated by road networks suffered a 15% decline in nuclear genetic diversity within 40 years of road construction (Epps *et al.* 2005). Linear infrastructure networks thus may potentially have severe negative consequences for the survival of species in fragmented habitats.

2.2.3.3 Natural linear canopy openings

Natural linear canopy openings such as streams, creeks and rivers provide a source of natural environmental heterogeneity within forests. In temperate forests in North America and Europe, rivers and larger streams can influence the community composition of the nearby vegetation creating a distinctive riparian zone within the forest (Gregory *et al.* 1991; Bendix and Hupp 2000; Nilsson and Svedmark 2002; Van Pelt *et al.* 2006). The composition of this riparian zone is determined by the frequency, intensity and duration of floods and the variability of flow (Gregory *et al.* 1991; Bendix and Hupp 2000; Nilsson and Svedmark 2002; Van Pelt *et al.* 2006). This son and Svedmark 2002; Van Pelt *et al.* 2006). Floods can destroy existing vegetation and deposit alluvial soil and debris creating surfaces for the establishment of seedlings. Thus, the frequency of flooding and the variability of other flows can determine which species are able to survive and reach maturity in different locations within the riparian zone (Robertson and Augspurger 1999; Van Pelt *et al.* 2006).

These factors are influenced by the height of the vegetation above the channel as vegetation closer to the channel will be exposed to more frequent, more intense and a greater duration of flooding than vegetation further upslope. The vegetation within the riparian zone is also influenced by the degree of constraint on the flow of the channel; rivers in narrow, constrained valleys will have steeper slopes and more abrupt alterations in the vegetation community than rivers in wider, less constrained valleys (Gregory et al. 1991; Bendix and Hupp 2000; Nilsson and Svedmark 2002; Van Pelt et al. 2006). River channels that are free to meander and shift the course of their channels may produce complex patterns of riparian vegetation at different successional stages. The destruction of existing vegetation by floods generally leads to riparian zones of younger, earlier-successional plant communities within the forest and the complex environmental variability near river channels can often result in greater species diversity in the riparian zone than in the surrounding forest (Gregory et al. 1991; Bendix and Hupp 2000; Nilsson and Svedmark 2002; Van Pelt et al. 2006) although, in a recent review, Sabo et al. (2005) found that rivers increase regional species diversity through sheltering distinct riparian communities rather than a greater number of species.

Smaller streams and watercourses in temperate forests can also influence the forest microclimate and the composition of the nearby vegetation. In temperate forest in western Washington, USA, air temperature, soil temperature and ground surface temperature were lower and relative humidity was greater within 30 - 50 m of the edges

of small (2 - 4 m wide) streams than in the forest interior although there were no detectable gradients in solar radiation or wind speed (Brosofske *et al.* 1997). In mixed conifer forests in northern Sierra Nevada in California, fire frequency decreased, canopy cover decreased and the abundance of hardwoods increased with proximity to a small watercourse (Russell and McBride 2001). As the abundance of hardwoods declined with time since fire, it is likely that frequent disturbance associated with floods and other strong flows was a significant contributing factor to the increased abundance of hardwood tree species near the watercourse indicating that even small streams can exert a significant influence on the composition of nearby vegetation (Russell and McBride 2001).

Similarly, the distribution of different vegetation types and tree species was subtly influenced by microhabitat differences within 50 m of small streams (~5 m wide) in the Oregon Coast Range in North America (Hibbs and Bower 2001). Although the different vegetation types had overlapping habitat preferences, pure conifer stands were found towards the base of steeper, northerly slopes, close to streams but were excluded from flat surfaces near streams by competition with shrubs (Hibbs and Bower 2002). In temperate deciduous forests in Maryland, forest near stream edges had a greater number of seedlings and saplings and large dead trees (>22.5 cm dbh), fewer small (7.5 – 30 cm dbh) live trees and small (7.5 – 22.5 cm dbh) dead trees and a greater volume of space beneath the canopy occupied by vegetation than the forest interior (Evans and Gates 1997; Gates and Evans 1998). Such stream edges were utilised by edge-preferring bird species in a similar manner to powerline and road edges (Evans and Gates 1997; Gates and Evans 1998).

Relatively less research has examined the potential influence of watercourses on the structure and composition of vegetation in tropical forests. Climatic data suggest that the Amazon River may exert an influence on local rainfall regimes in the Amazon rainforest through a "river breeze" that can alter the diurnal pattern of rainfall near the river (Cutrim *et al.* 2000). Such climatic effects, however, may not occur for smaller rivers and watercourses. In small (< 5 ha) gallery rainforest patches occurring along watercourses in tropical savannah in Belize, tree species composition and recruitment were affected by proximity to the rainforest-savannah edge but not distance to the stream (Kellman *et al.* 1998). Immigrating and fire-intolerant species, however, were concentrated closer to the stream suggesting that proximity to the watercourse may have provided some protection from fire and some degree of connectivity with other

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rainforest patches (Kellman *et al.* 1998). Additionally, it has been suggested (Putz 1984) that greater numbers of smaller trees and other supports that provide lianas with access to the canopy in tropical forest gaps may also occur along stream and river edges in continuous tracts of tropical rainforest leading to an increased abundance of lianas along watercourses although studies to test this hypothesis have not been undertaken.

Watercourses may also be important corridors for plant and animal dispersal. Some animals are known to use creek lines and watercourses as dispersal routes within forests (Gregory et al. 1991; Lindenmayer and Peakall 2000). Floodwaters may carry seeds for long distances downstream of their parent trees and may eventually deposit seeds among alluvial debris on surfaces scoured of other vegetation thus placing seeds in a suitable location for germination and seedling establishment (Gregory et al. 1991; Bendix and Hupp 2000; Nilsson and Svedmark 2002; Jansson et al. 2005). Floodwaters may also deposit seeds higher up the slope from the stream in locations that may be subject to less frequent flooding and thus provide seeds with a greater chance of surviving to reach maturity (Pettit and Froend 2001). Such downstream dispersal of seeds may be important in maintaining connectivity within and between plant populations (Kellman et al. 1998; Honnay et al. 2001) and some plant species in temperate and tropical river systems in Australia have adapted their flowering and fruiting phenology and evolved seed and fruit morphologies to take advantage of floods for the dispersal of their seeds (Pettit and Froend 2001). The seeds of non-riparian species may also be deposited alive, in flood debris, as a result of being carried to watercourses in overland flow (Pettit and Froend 2001). As large overland flows are a frequent occurrence in undisturbed rainforest in north-east Queensland (Bonell et al. 1983), it is possible that the seeds of rainforest plants may also be dispersed in this manner.

In this thesis, I will examine whether streams are associated with edge gradients in understorey microclimate, vegetation structure and plant species composition in tropical rainforest. Although the influence of rivers in tropical rainforest (eg Salo *et al.* 1986) and rivers and streams in temperate forest (eg Gregory *et al.* 1991; Brosofske *et al.* 1997; Bendix and Hupp 2000; Hibbs and Bower 2001; Russell and McBride 2001; Nilsson and Svedmark 2002; Van Pelt *et al.* 2006) on the vegetation community have been studied, the influence of smaller streams on tropical rainforest vegetation and microclimate has not received much attention (eg Kellman *et al.* 1998). I will compare the influence of these widespread, natural linear features with that of artificial linear features (powerline and highway clearings) within tropical rainforest in north-eastern Australia.

2.3 Conclusion

Forest fragmentation due to clearing for agriculture, silviculture, infrastructure corridors and other human activities is rapidly altering the nature and extent of the earth's forest ecosystems (Whitmore 1997). Understanding the long-term consequences of these changes for the survival and interactions of different species is imperative if many forest species are not to be lost.

Fragmentation has been observed to have a number of negative effects on forest biota including alteration of the abiotic and biological characteristics of fragment edges, increased invasion of exotic species and increased isolation of populations of species restricted to scattered remnants of forest. Over time, such changes may result in fragments of forest that bear little resemblance to the original forest in either their structure, species composition, ecosystem processes or biodiversity.

The effects of internal fragmentation by linear clearings within otherwise intact areas of forest have received relatively less attention than the effects of broad-scale habitat destruction and fragmentation. It is apparent, however, that such internal forest fragmentation may generate edge gradients in the abiotic environment as well as the distribution and abundance of, and interactions between, different species. Most studies of the effects of infrastructure clearings have been conducted in temperate regions and research on the effects of these clearings on tropical forest communities is sparse. Moreover, very few such studies have compared the effects of artificial linear clearings for human infrastructure with the effects of natural linear canopy openings such as streams and rivers which have a long evolutionary history and provide a widespread source of natural environmental heterogeneity within forests.

In this thesis, I will explore the effects of two widespread types of linear clearings (powerlines and highways) on the understorey microclimate, vegetation structure, plant species composition and levels of physical disturbance in surrounding forest and compare these edge gradients with those associated with perennial streams in tropical rainforest in north-eastern Queensland, Australia.

Chapter Three: General Methodology

3.1 Introduction

In this chapter, I will provide an introduction to my overall research design and research questions. More specific details of the designs, materials and analyses used in individual experiments and surveys will be provided in the chapters devoted to individual sections of the project. My overall research questions were:

- 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?

3.2 Research Design

I investigated the nature of edge effects associated with one natural (watercourse) and two artificial (powerline and highway) types of linear canopy opening. My study took place in rainforest in north-eastern Australia, an area with an extensive network of clearings for linear infrastructure (Trott *et al.* 1996; Goosem 1997; Weston and Goosem 2004). I included watercourses in the study, as a widespread natural type of linear canopy opening with a long evolutionary history in tropical rainforests, allowing a comparison of the effects of anthropogenic (relatively recent) and natural internal fragmentation on the nearby rainforest.

3.2.1 Study Sites

Field work was conducted in Wooroonooran National Park and South Johnstone State Forest (State Forest 756), in the region around 17° 36' S, 145° 45' E in the Wet Tropics World Heritage Area of north-eastern Queensland, Australia. Sites were located at elevations between 350 and 720 m above sea level (Figure 3.1) on fertile soils derived from basalt. The forest in this area is complex mesophyll vine forest (Type 1a, *sensu* Tracey 1982). This area falls between the 3000 and 4000 mm annual precipitation isohyets (Siegenthaler and Turton 2000) and the nearest weather station, the South Johnstone Experimental Station (17° 36' 20.16" S, 145° 59' 48.84" E, 18.3m asl) receives an average annual rainfall of 3307mm, an average daily maximum temperature of 28.1°C and an average daily minimum temperature of 19.1°C (Bureau of Meteorology <u>www.bom.gov.au</u>). The area experiences a wet season between December and May, with a peak of rainfall between January and March. Forest in this area has been disturbed by selective logging prior to the 1950s and scattered small-scale mining activities prior to the 1990s (Siegenthaler and Turton 2000).

Three types of linear canopy opening were investigated: powerlines, highways and creeks, representing some of the most widespread linear canopy openings in the region (Trott et al. 1996; Goosem 1997; Weston and Goosem 2004). Powerline sites were established on the 50-year old Kareeya to Innisfail powerline corridor (Plate 3.1a), at locations where the clearing was approximately 60 m wide and dominated by exotic grasses [eg Urochloa maxima (guinea grass) and Melinus minutiflora (molasses grass)], with dense patches of the exotic shrubs Lantana camara (lantana) and Rubus alceifolius (wild raspberry) near the edge of the forest. Prior to the 1990s, transmission lines in the Palmerston area were managed through lighting fires on the easement and cutting back vegetation with brush hooks. After this time, selective use of herbicides on tallergrowing species was adopted as the preferred method of control of vegetation along the easements. Slashing occurs around electricity transmission towers and along 4 m-wide centrally-positioned access tracks to allow safe access to transmission assets, leaving the rainforest edge untouched; the current edge has not been disturbed for about 15 years. Currently vegetation and access programs happen on a 2 yearly cycle in this area in consultation with QPWS and the Wet Tropics Management Authority (S. Martin, Powerlink, pers. comm.).

Highway sites were established along the Palmerston Highway (Plate 3.1 b), which runs between the towns of Ravenshoe and Innisfail with a clearing width of 14 to 22 m. The highway was widened in the late 1980s, making the current edge approximately 15 years old. The 2 m-wide highway verges are dominated by exotic grasses (eg *U. maxima*) and the exotic shrubs *L. camara* and *R. alceifolius*. The highway verges are periodically slashed and fallen trees are removed but weeds closer to the rainforest edge are generally left unmanaged.

Creek sites were established along Henrietta Creek (Plate 3.1 c and d), a third order stream in the North Johnstone River catchment. At the study sites, the creek was between 16 and 30 m wide and without overhead canopy cover. All sites were established on relatively level terrain. The creek edge experiences minor flooding in most years during the wet season (with the frequency of flooding depending on the amount of rain-fall during the wet season) and substantial flooding after heavy rain-fall events in the catchment area (> 200 mm within approximately 24 - 72 hours), at irregular intervals separated by less than 5 to 10 years (Richard Carrigan, National Parks Ranger, *pers. comm.*).

Two sites separated by at least 3 km were established per edge type (powerline, highway or creek). Two transects, each running for 100 m adjacent to the forest edge (Figure 3.2) were established on opposite sides of the linear canopy opening at each site (Figure 3.1). Due to terrain limitations, it was not possible to place transects exactly opposite each other at each site and in some cases transects were offset by a distance of between 500 m and 3 km. In the case of the second creek site, transects were placed on the same side of the creek but were separated by over 400 m and were established on different orientations (Figure 3.1). Previous studies of rainforests in north-east Queensland have demonstrated that edge gradients in microclimate and vegetation do not extend beyond 25 - 30 m; thus at 100 m from the edge, conditions are considered to be equivalent to the forest interior (Turton and Freiburger 1997; Siegenthaler and Turton 2000). To avoid confounding the effects of edge type with other environmental gradients (eg soil type, forest type, annual precipitation), only one linear feature per canopy opening type (powerline vs. highway vs. creek) was included in the study. However, as the sites covered a range of elevations and were physically separated by several kilometres (Figure 3.1), these data allowed me to assess variation in the nature of the associated edge gradients among the three linear canopy opening types within the study area.



shows the layout of creek site two and highway site two, transect 2. The map was prepared by Ms Tina Lawson with data from Geosciences Australia. Figure 3.1. Study Area in Wooroonooran National Park and South Johnstone State Forest. Inset P1 shows the layout of powerline site one and inset S2

3.2.2 Research Outline

To address my research questions, I have investigated four aspects of rainforest ecology, which will be described in more detail in individual chapters of the thesis; 1) microclimate, 2) vegetation structure and composition, 3) physical disturbance and 4) seedling survival and growth.

3.2.2.1 Microclimatic Variation.

In Chapter Four I will examine the microclimatic edge gradients associated with powerlines, highways and creeks. In particular, I will examine whether the nature of microclimatic edge gradients varies between natural and anthropogenic linear canopy openings, with season (wet *vs*. dry season) or with time of day. I will also examine how the light environment of the rainforest understorey varies with both distance from the forest edge and between the different types of linear canopy openings.

Understorey microclimate, particularly light quality and availability and the degree of moisture stress, significantly influences the germination, survival and growth of many plant species (Osunkoya *et al.* 1992; Osunkoya 1996; Capers and Chazdon 2004). Thus alterations in these parameters near the edges of linear canopy opening have the potential to alter the dynamics and composition of the entire rainforest plant community (Laurance *et al.* 2002).

3.2.2.2 Species Composition and Abundance.

In Chapter 5, I will examine whether vegetation structure and composition are altered near the edges of natural and anthropogenic linear canopy openings. Vegetation surveys will be used to explore alterations in the abundances of different plant functional groups (defined on the basis of growth form, successional status and diaspore size) and individual species for which there is sufficient data. The composition of adult-, saplingand seedling-sized individuals will be compared to determine whether there are any systematic shifts in the successional status of plants between adult and juvenile stages, which might have implications for the future composition of the forest near the edge. Differences between edge types will also be examined.

3.2.2.3 Physical Disturbance.

Physical disturbance affects many aspects of the ecology of tropical forests (Chazdon 2003). Disturbance to the forest canopy is affects rates of tree mortality and turnover,

understorey light availability and thus seedling and sapling growth and is considered to be an important mechanism maintaining tropical forest species diversity (Brokaw 1985; Connell 1978; Martinez-Ramos *et al.* 1988; Uhl *et al.* 1988; Schnitzner and Carson 2001). At a finer scale, physical disturbance due to falling leaf litter and canopy debris is a significant cause of mortality and damage for seedlings and saplings (Aide 1987; Clark and Clark 1989, 1991; Guariguata 1998; Drake and Pratt 2001; Peters *et al.* 2004) and variation in the rate of physical damage within a forest may influence the community composition of the understorey (Gillman *et al.* 2003, 2004; Pauw *et al.* 2004; Peters *et al.* 2004; Gillman and Ogden 2005). In this chapter, I examine whether tree-fall disturbance and small-scale physical disturbance are elevated near the edges of natural and anthropogenic linear canopy openings.

3.2.2.4 Seedling Survival and Growth.

In Chapter 7, I examine how the survival and growth of species with differing successional status (and thus different physiological requirements for regeneration) vary with distance from the forest edge and between natural and anthropogenic linear canopy openings. I will also explore whether vertebrate herbivory pressure is elevated near the forest edge. This will be done using shadehouse-germinated seedlings planted into the forest understorey in a "seedling experiment". Of particular interest is whether any patterns detected in this seedling experiment reflect those observed in the existing vegetation (described in Chapter 5).



Figure 3.2. Transect layout. Measurements were made at various distances from the forest edge. Distances marked in red were only measured on the highway transects and distances marked in beige were only measured on the powerline transects.

3.2.3 Alterations to the Original Design

I had originally planned to include the effects of successional changes within the powerline clearing in the study design. However, budgetary and logistical constraints prevented this and, in any case, all potential additional sites were on steep slopes, which would have irredeemably confounded the effects of distance from the edge, edge type and slope. Thus, this effect was not included in the study. In addition, time and logistical constraints prevented the examination of variation in the soil seed bank and the composition of the seed fall with distance from the edge and between natural and anthropogenic linear canopy openings.



Chapter Four: Microclimatic Variation

4.1 Introduction

At the edges of forest fragments, increases in the penetration of sunlight and wind drive changes in the entire microclimatic regime of the forest understorey (Kapos 1989; Williams-Linera 1990a; Chen et al. 1993; Chen et al. 1995; Murcia 1995; Turton and Freiburger 1997; Laurance 2001; Newmark 2001). These microclimatic changes can lead to further, long-lasting alterations of the biotic community at the forest edge, which may themselves further exacerbate the original abiotic edge effects (eg Kapos 1989; Williams-Linera 1990a; Matlack 1994; Murcia 1995; Fox et al. 1997; Laurance 1997a, 2001b; Laurance et al. 1998a, b, 2002; Benitez-Malvido 1998, 2001; Mourelle et al. 2001; Burton 2002; Harper and Macdonald 2002; Honnay et al. 2002; Rheault et al. 2003; Ries et al. 2004; Harper et al. 2005). In comparison with forest fragments in agricultural landscapes, edge effects associated with linear clearings for roads and powerlines have received relatively little attention (Forman and Alexander 1998; Siegenthaler and Turton 2000). However, given the widespread distribution of linear infrastructure within remaining areas of otherwise intact forest, edge effects from such internal fragmentation have the potential to increase substantially the spatial extent of disturbed areas (Goosem 1997; Forman and Alexander 1998; Olander et al. 1998; Siegenthaler and Turton 2000; Marsh and Beckman 2004) and it is imperative to understand their impacts if these forests are to be preserved and managed successfully.

In this study, I investigated the nature of microclimatic edge gradients associated with one natural (watercourse) and two artificial (powerline and highway) types of linear canopy opening. I included watercourses in the study, as being a widespread natural type of linear canopy opening with a long evolutionary history in tropical rainforests, thus allowing a comparison of the effects of anthropogenic (relatively recent) and natural internal fragmentation. I also examined the effect of seasonality (wet season *vs.* dry season) on microclimatic edge gradients, as seasonality influences microclimatic gradients observed near forest fragment edges in non-Equatorial tropical forests (Turton and Freiburger 1997). I also examined the diurnal variation in the nature and extent of microclimatic edge gradients.

4.1.1 Research Questions

In this chapter, I address the following questions:

- Do linear canopy openings cause microclimatic gradients in the adjacent rainforest understorey?
- 2) Do the extent and severity of any edge effects differ between edge types (powerlines, highways and creeks)?
- 3) How do these edge effects vary between the wet and the dry seasons?
- 4) How do these edge effects vary diurnally?
- 5) Is wind speed elevated near the edge of the forest? Is this as important as changes in light availability?
- 6) How does the understorey light environment differ between the edge and the interior of the forest?

With regard to my second question, I predicted that the width of the linear canopy opening would be the main determinant of the microclimatic edge effects experienced in the rainforest understorey; thus powerlines, as the widest linear clearing type, 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 near creek edges. Also, as the severity (the magnitude of the difference between edge and interior conditions) of edge gradients is influenced by 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)], which is in turn affected by the time 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).

In this section of the project, I examined changes in the microclimate of the rainforest understorey near the edges of powerlines, highways and watercourses. I used three methods to investigate the nature of the relationship between microclimate and distance from the edge: traverse measurements were used to assess the extent and severity of edge effects during daylight hours in the wet season and the dry season; data loggers were used to measure diurnal changes in microclimatic edge effects; variation in the understorey light environment was assessed by measuring the ratio of red to far red light. These measurements were performed at the study sites described in Chapter Three

(three edge types * two sites per edge type * two transects per site = 12 transects in total).

4.2 Traverse Measurements

4.2.1 Materials and Methods

The aim of this section of the project was to assess the extent and severity of microclimatic edge effects in the understorey of rainforest adjacent to powerlines, highways and watercourses and to determine how these edge effects vary with season (research questions 1, 2, 3 and 5). The traverse method was used, as it allows the rapid measurement of spatial variation in the forest understorey microclimate (Turton and Freiburger 1997). Measurements began at the outermost point of each transect and continued inwards, towards the forest interior, with a minimum time lapse between start and finish. The distances at which measurements were to be taken were marked with brightly painted wooden stakes. Measurements were made at 0, 2, 4, 8, 12, 16, 20, 25, 30, 50 and 100 m for all transects. Extra measuring points were taken within the linear canopy opening for powerline transects (-10 m) and highway transects (-5 m), to provide an "open" contrast (Figure 4.1). Previous studies in rainforests in north-east Queensland have demonstrated that edge gradients in microclimate do not extend beyond 25 - 30 m; thus at 100 m from the edge, microclimatic conditions are considered to be equivalent to forest interior conditions (Turton and Freiburger 1997; Seigenthaler and Turton 2000).



Figure 4.1. The set-up for the traverse measurements. Microclimate measurements were made at each distance marked with an "X". Distances marked in red were measured only on the highway transects and distances marked in beige were measured only on the powerline transects.

Microclimate measurements were undertaken in clear weather or relatively clear (cloudy or overcast but not raining) weather, between 9:30 am and 3:30 pm in the wet season and between 10:00 am and 3:00 pm in the dry season, to avoid the collapse of edge gradients that occurs at low solar angles (Chen *et al.* 1995; Turton and Freiburger 1997). Transects were measured in a semi-random order (ie for logistical reasons, when transects within sites were close together, they were measured consecutively; eg powerline site one, highway site one), in the wet season (between the 10^{th} of March and the 4^{th} of April 2004 and February 11 - 13, 2005) and remeasured in the dry season (between the 19^{th} and 24^{th} of September 2004), to encompass variation in cloud cover and time of day for each clearing type. Logistical and weather constraints prevented a complete wet season data collection in 2004 but there were no significant natural disturbances to the study area between measurement periods. Therefore measurements were taken once in each season. While it would have been preferable to take more than one set of traverse measurements per transect per season, this was prevented by a shortage of suitably clear weather in the wet season.

Parameters measured included photosynthetically active radiation (PAR), air temperature and relative humidity, air speed, canopy temperature, ground surface temperature, soil temperature and soil moisture. Photosynthetically active radiation (PAR) (electromagnetic radiation between 400 and 700 nm in wavelength) was measured at a height of 165cm, using a LiCor quantum sensor (LI-190SA) and meter (LiCor Light Meter, LI-250, Li-COR, Lincoln, Nebraska, USA), which measured the average value of PAR (μ mol m⁻² s⁻¹) at each point over 15 seconds. Air temperature, relative humidity and air speed were measured at heights of 165 cm and 30 cm, using a VelociCalc Portable Air Velocity Meter (Model 8347-M-GB, TSI Incorporated, Shoreview, MN, USA). This instrument uses a hot-wire probe to measure air speed (m s⁻¹), which must then be allowed to cool for a minimum of 30 seconds before measurements of air temperature and relative humidity are taken (T.S.I. Incorporated 2002). Vapour pressure deficit (VPD) was calculated (in Pascals) from the temperature and humidity data for both heights (Jones 1992). PAR and air speed were measured within simultaneous "open" controls because I was not attempting to measure canopy transmittance in either parameter; I was interested instead in the mean edge gradients in light level and air speed.

Canopy temperature and ground surface temperature were measured using a TASCO Infrared Thermometer (THI-700, Osaka, Japan), which measures the

temperature of the surface at which it is aimed (the area of measurement is indicated by twin laser beam markers) (TASCO 2001). Ground surface temperature was obtained by aiming the instrument at clear ground that was not in direct sunlight and canopy temperature was obtained by aiming the instrument at the highest part of the forest canopy to which I had a clear line of sight; this resulted in a canopy segment of 1.1 m in diameter (~0.99 m² area) being measured. Soil temperature was measured using a 5 cm soil probe (Testo 106-T1, Testo Inc. Flanders, NJ, USA).

A portable frame of PVC pipe was constructed (Plate 4.1) to allow PAR, air temperature (165 and 30 cm), relative humidity (165 and 30 cm), air speed (165 and 30 cm), canopy temperature, ground surface temperature and soil temperature to be measured together. The quantum sensor (PAR) was attached to the top of the instrument and two "arms" were attached, at 165 cm and 30 cm, to support the hot-wire probe (air temperature, relative humidity and air speed). The infrared thermometer and soil probe were carried separately. It took between 3 and 5 minutes to take all measurements at any one measuring point and between 60 and 90 minutes to complete a full transect.

Soil moisture (mL/g dry soil weight) was measured from samples taken using a bulb planter to extract soil to 10 cm depth. Samples were roughly homogenised and sub-sampled (using 20 ml glass vials), then weighed prior to and after drying in an oven for a minimum of 48 hours at a temperature of 106 °C (until constant weight had been achieved).

4.2.1.1 Statistical Analysis

These data were analysed using multiple analysis of covariance (MANCOVA) with fixed factors edge type (powerline, highway or creek) and season (wet season or dry season). Distance was included as a covariate, as distance is a continuous variable that cannot be broken into discrete treatment levels. Negative distances were not included in the analysis, as no negative distance could be measured for the creek transects and including negative distances for the other two edge types would have unbalanced the design and introduced significant outliers into the data. Means and standard errors (n = 4 per edge type) for the clearing measurements are shown in the results section to allow for visual comparison. Dependent variables were PAR, air temperature_{165cm}, air temperature, soil temperature, VPD_{165cm}, VPD_{30cm}, air speed_{165cm}, air speed_{30cm} and soil moisture. Transects were treated as replicates (Mike Steele, *pers. comm.*) in the MANCOVA analysis (n = 4

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transects per edge type). Each transect had a different orientation and thus a different interaction with solar angle effects (Turton and Frieburger 1997), with several also separated by some distance (Figure 3.1).

Variations in absolute values of temperature and VPD according to time of day, season and elevation (Chen *et al.* 1995; Turton and Freiburger 1997; Newmark 2001) may obscure edge gradients in these parameters. As the edge gradients are the main focus of interest in this study, this variation was accounted for by transforming the temperature and VPD parameters before analysis. Relative values of air temperature_{160cm}, air temperature_{30cm}, canopy temperature, ground surface temperature, soil temperature, VPD_{160cm} and VPD_{30cm} were calculated using the following formula:

Relative $Value_{(i)} = Absolute Value_{(i)} - Absolute Value_{(100m)}$ for each distance *i*.

Thus, the value for each of these parameters at the distance of 100 m was always 0.

PAR was log₁₀ transformed to approximate normality, resulting in no obvious outliers (MANCOVA is more sensitive to the effects of outliers than non-normality; Mike Steele *pers. comm*). No other transformations were required as all other parameters were normally distributed or approximated normality. All statistical analyses were performed using SPSS version 11.0 for Windows.



Plate 4.1. The instruments used for the traverse measurements were supported on a PVC frame. The quantum sensor was attached to the top of the frame (on a leveling mount). Two "arms" were placed at heights of 165cm and 30cm, with supports, to hold the hot-wire probe. As the hot-wire probe was sensitive to very slight movements, the entire frame was slotted into a second, supporting frame that was clamped to a star picket which was hammered into the ground at each measuring point. This allowed the frame to be free-standing and avoided confounding measurements of air speed with inadvertent hand movements from a person holding the frame. The person pictured is Stephen Pohlman, who is holding the display meter for the hot-wire probe. Photo by author.
4.2.2 Results

Rainforest understorey microclimate was significantly altered near the edges of linear canopy openings (MANCOVA, Pillai's Trace = 0.117, F = 2.946, df = 11.000, p = 0.001) and these edge effects varied with both edge type and season (edge type * season interaction, Pillai's Trace = 0.317, F = 4.207, df = 22.000, p < 0.001). The MANCOVA between-subject effects tests revealed significant edge gradients for four of the eleven microclimatic parameters measured (Table 4.1).

PAR was elevated near the forest edge but this effect was more pronounced near creek edges than powerline or highway edges (Figure 4.2 a, b, c; ANOVA Bonferroni *post hoc* test p < 0.01). Edge gradients in PAR did not vary significantly with season (Table 4.1). Relative air temperature_{30cm} was elevated near powerline edges in the dry season and near highway edges in both wet and dry seasons but was not elevated near creek edges in either season (Figure 4.2 g, h, i; Table 4.1). The patterns in relative air temperature_{165cm} closely mirrored those observed at 30 cm (Figure 4.2 d, e, f), but the effect of distance was not significant (Table 4.1). Similarly, relative VPD_{30cm} was significantly elevated near the powerline edges in either season (Figure 4.2 v, w, x; Table 4.1) and, again, patterns in relative VPD_{165cm} closely mimicked those observed at 30 cm, but the effect of distance was not significant (Figure 4.2 s, t, u; Table 4.1).

Relative canopy temperature varied with distance from the edge of the forest but the nature of the edge gradient was not consistent between edge types or seasons (Figure 4.2 j, k, l; Table 4.1). Edge gradients appeared to be relatively flat for all three edge types in the dry season; in the wet season, however, relative canopy temperature appeared to be lowered near the edges of powerlines and creeks but elevated near highway edges.

Neither air speed_{165cm} nor air speed_{30cm} were significantly related to distance from the edge, although both were higher in the dry season than the wet season (Figure 4.2 y, z, aa and ab, ac, ad; Table 4.1) and air speed_{30cm} was lower near creeks than near powerlines and highways (ANOVA Bonferroni *post hoc* test p < 0.05). Neither relative ground surface temperature nor relative soil temperature was significantly related to distance from the forest edge, although there did appear to be a very slight tendency for both parameters to increase near the very edge (≤ 4 m) of highways and to decrease near the very edge (≤ 4 m) of powerlines (Figure 4.2 m, n, o and p, q, r; Table 4.1).

Table 4.1. Effects of distance from the edge, edge type (powerline, highway or creek)and season (wet or dry) on microclimate variables. Significant MANCOVA tests ofbetween-subject effects are highlighted in bold.

Effect	Parameter	F	df	<i>p</i> -value
Distance	$LogPAR \pmod{m^{-2} s^{-1}}$	16.561	1	<0.001
	Relative Air Temperature _{165cm} (°C)	1.515	1	0.219
	Relative Air Temperature _{30cm} (°C)	3.732	1	0.054
	Relative Canopy Temperature (°C)	5.387	1	0.021
	Relative Surface Temperature (°C)	1.836	1	0.177
	Relative Soil Temperature (°C)	1.644	1	0.201
	Relative VPD _{165cm} (kPa)	2.425	1	0.121
	Relative VPD _{30cm} (kPa)	6.383	1	0.012
	Air Speed _{165cm} (m s ⁻¹)	1.679	1	0.196
	Air Speed _{30cm} (m s ⁻¹)	0.441	1	0.507
	Soil Moisture (g H ₂ O per g soil)	2.496	1	0.115
Edge Type	$LogPAR \pmod{m^{-2} s^{-1}}$	16.787	2	<0.001
	Relative Air Temperature _{165cm} (°C)	13.868	2	<0.001
	Relative Air Temperature _{30cm} (°C)	14.126	2	<0.001
	Relative Canopy Temperature (°C)	6.545	2	0.002
	Relative Surface Temperature (°C)	0.963	2	0.383
	Relative Soil Temperature (°C)	10.349	2	<0.001
	Relative VPD _{165cm} (kPa)	7.486	2	0.001
	Relative VPD _{30cm} (kPa)	8.217	2	<0.001
	Air Speed _{165cm} (m s ⁻¹)	0.659	2	0.518
	Air Speed _{30cm} (m s ⁻¹)	4.452	2	0.013
	Soil Moisture (g H ₂ O per g soil)	22.433	2	<0.001
Season	$LogPAR (mol m^{-2} s^{-1})$	1.995	1	0.159
	Relative Air Temperature _{165cm} (°C)	31.689	1	<0.001
	Relative Air Temperature _{30cm} (°C)	18.796	1	<0.001
	Relative Canopy Temperature (°C)	1.898	1	0.170
	Relative Surface Temperature (°C)	3.405	1	0.066
	Relative Soil Temperature (°C)	2.501	1	0.115
	Relative VPD _{165cm} (kPa)	13.795	1	<0.001

Effect	Parameter	F	df	<i>p</i> -value
Season (Cont.)	Relative VPD _{30cm} (kPa)	7.423	1	0.007
	Air Speed _{165cm} (m s ⁻¹)	16.290	1	<0.001
	Air Speed _{30cm} (m s ⁻¹)	5.154	1	0.024
	Soil Moisture (g H ₂ O per g soil)	54.513	1	<0.001
Edge Type * Season	$LogPAR \pmod{m^{-2} s^{-1}}$	2.330	2	0.099
	Relative Air Temperature _{165cm} (°C)	13.214	2	<0.001
	Relative Air Temperature _{30cm} (°C)	16.368	2	<0.001
	Relative Canopy Temperature (°C)	16.924	2	<0.001
	Relative Surface Temperature (°C)	4.678	2	0.010
	Relative Soil Temperature (°C)	1.993	2	0.138
	Relative VPD _{165cm} (kPa)	7.048	2	0.001
	Relative VPD _{30cm} (kPa)	7.247	2	0.001
	Air Speed _{165cm} (m s ⁻¹)	1.028	2	0.359
	Air Speed _{30cm} (m s ⁻¹)	2.403	2	0.092
	Soil Moisture (g H ₂ O per g soil)	1.547	2	0.215







Figure 4.2. Variation in microclimatic parameters with distance from the forest edge. Values represent averages for each distance and error bars represent ±1se. Results for powerline edges are shown in panels on the left-hand side of the figure, highway results are shown in the panels in the centre of the figure and creek results are shown in the right-hand panels. Vertical dashed lines indicate the position of the forest edge. Results for PAR (**a**, **b**, **c**), air speed_{165cm} (**y**, **z**, **aa**), air speed_{30cm} (**ab**, **ac**, **ad**) and soil moisture (**ae**, **af**, **ag**) are averages of the absolute values measured, whereas the results for temperature_{165cm} (**d**, **e**, **f**), temperature_{30cm} (**g**, **h**, **i**), canopy temperature (**j**, **k**, **l**), surface temperature (**m**, **n**, **o**), surface temperature (**p**, **q**, **r**), VPD_{165cm} (**s**, **t**, **u**) and VPD_{30cm} (**v**, **w**, **x**) are averages of the relative values (see Methods). For ease of comparison, for relative values, a horizontal dashed line has been added (at 0 on the y-axis) to indicate the relative position of values measured in the forest interior (100 m).

There was a trend towards decreased soil moisture near the forest edge but this trend was not statistically significant (Figure 4.2 ae, af, ag; Table 4.1). In addition, soil moisture was lower in the dry season than the wet season and lower near creeks than near powerlines or highways (ANOVA Bonferroni *post hoc* test p < 0.001). MANCOVA, however, makes the assumption that parameters are linearly related to covariates (ie distance) and it is possible that a non-linear relationship may exist between soil moisture and distance from the forest edge, particularly for creek and highway edges, that was not detected using this procedure. Individual ANOVAs of soil moisture for each edge type indicated that soil moisture was significantly lower near creek edges (F = 15.029, df = 1, p < 0.001) and significantly (though only minimally) higher near powerline edges (F = 4.955, df = 1, p = 0.029) but unrelated to distance from highway edges (F = 0.019, df = 1, p = 0.892).

4.2.3 Discussion

Internal fragmentation was associated with alterations in understorey microclimate near the rainforest edge, with variations between anthropogenic and natural edges. However, contrary to my initial expectations, powerline edges did not experience the strongest microclimatic edge effects. The understorey near powerline edges was warmer and drier (elevated air temperature and VPD) than the forest interior in the dry season, light intensity (PAR) was elevated in both seasons and the temperature of the forest canopy was lowered near the powerline edge in the wet season. Similar elevations in light intensity were seen during both the wet and dry seasons at the highway edge. However, in contrast to the powerline edge, the forest understorey near highway edges was warmer and drier in both wet and dry seasons and the temperature of the forest canopy was elevated in the wet season. Microclimatic edge effects dissipated within approximately 20 - 25 m of both powerline and highway edges. In contrast to the anthropogenic edges, light intensity was most strongly elevated near the natural creek edges (and this edge effect extended approximately 50 m into the forest). However, the forest understorey near creek edges was not warmer or drier than the forest interior in either the wet or the dry season. The wet season collapse of temperature gradients near the powerline edge is not unprecedented (Siegenthaler and Turton 2000) but the maintenance of temperature and VPD gradients near the highway in both wet and dry seasons and the lack of such gradients near creek edges in either season is surprising.

Microclimatic edge gradients can be reduced or altered through the "sealing" of the forest edge over time (Camargo and Kapos 1995; Harper et al. 2005) and differences in the degree of edge sealing between the powerline, the highway and the creek may be influencing the edge gradients in air temperature and VPD. However, the powerline and highway edges in this study did not differ in either vegetation density (Chapter 5), PAR or red: far red at the forest edge, which indicates that the observed seasonal differences in microclimatic gradients were not due to differences in the degree of edge sealing. This is not surprising, considering the similarity in time elapsed (~ 15 years) since the most recent disturbance of the edge at these sites. In contrast, the forest canopy and subcanopy near creek edges is more open than near either highway or powerline edges (Figure 4.8), which suggests that differences in edge sealing may be influencing differences in the edge gradients between natural and anthropogenic edges. The lowered soil moisture near creek edges is also consistent with this possibility, as it appeared to be associated with an increase in the sand content of soil near creek edges (pers. obs.; see also Nakamura et al. 1997). This suggests that periodic flooding of the creek edge (with the flood waters carrying sand to the soil near creek edges and simultaneously disturbing the tree community; Hupp and Osterkamp 1996; Nakamura et al. 1997; Robertson and Augspurger 1999; Turner et al. 2004; Sabo et al. 2005), may be maintaining a more open forest edge near the creek (for example, in subtropical humid forest in Puerto Rico, tree-falls are more frequent in riparian forest than in upland forest; Scatena and Lugo 1995). However, although this may be responsible for the higher light levels observed near creek edges, it seems unlikely that a more open edge would be responsible for the lack of edge gradients in air temperature or VPD near creek edges. Indeed, without the influence of other factors, greater edge gradients might be expected.

Contrasts in edge gradients in air temperature, VPD and canopy temperature between powerline, highway and creek edges may have been influenced by differences in the nature of the linear canopy openings themselves. For instance, evaporative cooling from flowing water in the creek may have "buffered" creek edges against elevated temperatures and VPD (Nichol 1994). However, the opposing directions of the wet season gradients in canopy temperature near powerline and highway edges (and the lack of such gradients in the dry season) appear to be counterintuitive. Factors known to influence canopy temperature include ambient temperature, vegetation structure (particularly leaf area index [LAI]) and soil moisture (Oke 1987; Kira and Yoda 1989; Nichol 1994; Potter et al. 2001; Cowling 2004); however, none of these differed systematically between powerline and highway edges. It is possible that differences in the nature of highway and powerline clearings were responsible for the opposing wet season canopy temperature gradients. The grassy (and weedy) vegetation in the powerline corridor may have allowed much greater latent heat fluxes (evaporative cooling) than the dark bitumen surface of the highway (Sturman and Tapper 1996). If the highway had a correspondingly greater sensible heat flux, this may have led to elevated canopy temperatures near the highway, particularly in the warmer months of the year (ie the wet season). This explanation would also be consistent with the maintenance of air temperature and VPD gradients near highway edges in the wet season. It is possible to speculate that the lack of edge gradients in canopy temperature near the powerline in the dry season may have been due to the lower latent heat fluxes of grasslands in those months, as compared to the wet season (Sturman and Tapper 1996) and that greater wet season latent heat fluxes (and evaporative cooling) may have also been responsible for the collapse of air temperature and VPD gradients near powerline edges in the wet season. These data, in combination with the "buffering" effect of the creek on temperature and VPD, suggest that the nature of the linear canopy opening may be at least as important as the width (Seigenthaler and Turton 2000) in determining the nature and extent of microclimatic edge effects.

Air speed within the forest understorey was very low, with measured values predominantly less than 1 m s⁻¹, consistent with the majority of microclimate studies in rainforests around the world (eg Oke 1987; Kira and Yoda 1989). In contrast with studies of tropical forest fragment edges, which have detected evidence of increased air mixing between the matrix and the fragment understorey (Kapos *et al.* 1997), increased wind-throw of canopy trees near fragment edges (Laurance *et al.* 2001b, 2002) and increased wind disturbance near fragment edges during severe storms (Laurance 1997a), no significant edge gradients in air speed were detected in our study. This suggests that wind disturbance may not be elevated near the edges of linear clearings under normal conditions. Wind speed, however, is notoriously variable and it is possible that air speed measurements taken at one point in time do not reflect the full range of wind conditions experienced by the rainforest understorey. In addition, the effects of severe winds and cyclones on forest near the edges of linear canopy openings deserve further attention.

Microclimatic edge gradients have received comparatively less attention near linear canopy openings than those near edges of forest fragments in agricultural landscapes. However, elevated light levels have been detected near paved and unpaved roads in temperate forest in the USA (Haskell 2000; Parendes and Jones 2000; Watkins et al. 2003) and elsewhere (Trombulak and Frissell 2000), although some studies of narrower roads have not found any microclimatic edge effects (King and DeGraaf 2002; Ortega and Capen 2002). The penetration distance of alterations in light level, air temperature and VPD observed near roads and powerlines in my study (~20 m) are comparable with those observed in temperate forests (~15 m, Watkins et al. 2003) and near a powerline corridor in tropical rainforest in Queensland (~15 m, Siegenthaler and Turton 2000). However, they are less than those observed near the edges of tropical forest fragments (15 - 100 m) (Kapos 1989; Williams-Linera 1990a; Turton and Freiburger 1997; Newmark 2001). The lack of significant gradients in soil moisture or temperature near highways and powerlines accords with inconsistent results for temperate linear canopy openings (Marsh and Beckman 2004) and the short (3 to 11 m) edge distance of gradients in soil and ground surface temperatures near powerline edges in tropical rainforest in Queensland (Siegenthaler and Turton 2000). All of these linear clearing results contrast with the stronger decreases in soil moisture found near edges of recently formed tropical forest fragments in the Amazon (Kapos et al. 1997). Even the decrease in soil moisture detected near creek edges may not translate to a decrease in soil water availability, as it was associated with an increase in sand content. This suggests that the exposure to desiccation of the forest soil near linear canopy openings is much less than that near the edges of isolated forest fragments.

Although microclimatic edge effects are less severe near linear canopy openings than at the edges of tropical forest fragments, these edge gradients may still have implications for the survival and growth of understorey plant species and for the regeneration of canopy species (Benitez-Malvido 2001; Laurance *et al.* 1998b, 2002). The more desiccating conditions near edges of anthropogenic linear canopy openings, particularly highways, may adversely affect the regeneration of shade-tolerant species dependent on humid, interior forest conditions for seedling survival (Benitez-Malvido 2001) and may also increase the moisture stress experienced by mature individuals near the forest edge (Laurance *et al.* 2002). In addition, temperature and VPD elevations near anthropogenic edges were stronger at 30 cm than 165 cm above the ground, which suggests that small seedlings may be particularly vulnerable to these edge effects. In contrast, the brighter, humid environment near creek edges may be a more benign location for the growth and survival of seedlings and other understorey plants than the more desiccating environments near anthropogenic edges (eg Whitmore 1997; Benitez-Malvido 2001). However, it is uncertain whether this environment would favour interior forest species or more light-demanding species such as pioneers and lianas (Whitmore 1996) or might instead favour the growth of riparian species, particularly if periodic flood disturbance is maintaining a more open forest canopy or influencing the survival and mortality of the plant community near the forest edge (Hupp and Osterkamp 1996; Nakamura 1997; Robertson and Augspurger 1999; Turner *et al.* 2004; Sabo *et al.* 2005).

4.3 Diurnal Variation

4.3.1 Materials and Methods

Data loggers were used to measure diurnal variation in microclimatic edge gradients in the wet season and the dry season (research questions 2, 3, 4 and 5). The microclimatic parameters measured were temperature, relative humidity and wind speed. Vapour pressure deficit was calculated from temperature and relative humidity (Jones 1992). Data loggers were placed at distances of 0 m, 4 m, 12 m, 25 m, 50 m and 100 m from the forest edge (Figure 4.3). For powerline transects, an additional data logger was placed at -10 m from the forest edge (at the request of Powerlink, one of the funding bodies). As my budget allowed me to purchase only sufficient data loggers to monitor one transect at a time, transects were monitored in a semi-random order (ie for logistical reasons, when transects within sites were close together, they were measured consecutively; eg powerline site one, powerline site two, highway site one) for a period of at least four consecutive days in both the wet season and the dry season (Table 4.2).

Air temperature and relative humidity were measured using Tinytag Ultra Temperature and Relative Humidity data loggers (model number TGU-1500) and wind speed was measured using Tinytalk Wind Speed data loggers and cup anemometers (model number TGPR-1201) (Hastings Data Loggers, Port Macquarie, Australia). These instruments were attached to a PVC frame that could be slotted over a wooden stake hammered into the ground (using a spirit level to ensure the stake was placed vertically), in such a way that the TGU-1500 and the cup anemometer of the TGPR-1201 were held at approximately 1.7 m from the ground surface (Plate 4.2). All external cables had to be protected from the attentions of White-tailed Rats (*Uromys caudimaculatus*) and were housed within thick PVC pipe and multiple layers of electrical tape.

Measurements were first attempted in the dry season of 2003 and the wet season of 2004, using TGPR-1201 data loggers to measure wind speed and a combination of three TGU-1500 loggers and four Tinytalk RH+ (9904-0304) loggers with four Tinytalk II Temperature loggers (9904-0020) with external temperature probes to measure temperature and relative humidity. The 9904-0304 and 9904-0020 loggers were purchased for a previous student project several years earlier and suffered repeated malfunctions, rendering all of the 2003 dry season data and approximately half the 2004 wet season data unusable. These older data loggers were replaced mid-way through the

wet season of 2004. Dry season measurements were repeated in 2004 and the corrupted wet season measurements were repeated in the wet season of 2005 (Table 4.2). In addition, owing to the high humidity environment of the rainforest understorey, the relative humidity sensors of the TGU-1500 data loggers needed frequent maintenance (performed in a laboratory at JCU Cairns campus) and occasional repairs (at Hastings Data Loggers in Port Macquarie), which further extended the period of data collection.



Figure 4.3. The set-up for the datalogger measurements. Measurements were made at each distance marked with an "X". Distances marked in beige were measured only on the powerline transects.



Plate 4.2. The instruments used for the data logger measurements were supported on a PVC frame resting on a wooden post. Instruments were attached at a height of 170cm above the ground surface. The person pictured is Stephen Pohlman, who is standing behind and slightly upslope of the apparatus. Photo by author.

4.3.1.1 Statistical Analysis

As there was variation in the length of time data loggers were left at each transect, a subset of 4 days of data were selected from the available data for each transect for each season (Table 4.2). Four days was the time selected, as this was the minimum length of time that any transect was sampled in one season. The raw data were first assessed visually for the presence of diurnal patterns in edge gradients in air temperature, VPD and wind speed, before statistical analyses were performed.

To examine whether diurnal variation in air temperature and vapour pressure deficit (VPD) is greater near the edge of the forest than the interior, I calculated the diurnal range for these parameters for each distance along each transect in each season, by subtracting the overnight minimum value from the following daylight maximum value. This provided a total of three diurnal range values for each distance for each transect, for each season (n = 3 days * 3 edge types * 2 sites * 2 transects per site * 2 seasons = 72) for both air temperature and VPD. As air temperature and VPD were highly correlated with each other (Pearson correlation $r^2 = 0.838$, p < 0.001), I analysed these data using a MANOVA, with the fixed factors of edge type (powerline, highway and creek), distance (0 m, 4 m, 12 m, 25 m, 50 m and 100 m) and season (dry season and wet season). Replication was provided by sites, transects and days. Both air temperature and VPD were normally distributed and did not require transformation prior to analysis. The distance of -10 m measured within the powerline was not included in this analysis, as it would have unbalanced the dataset and introduced significant outliers. Data collected from this point are shown in the results section for comparison only.

As the minimum value for wind speed was 0 km hr⁻¹ in all cases, I used the maximum wind speed measured at each distance for each transect over the four days' data collection period for each season as a substitute for "range" (n = 3 edge types * 2 sites * 2 transects per site * 2 seasons = 24). However, this dataset contained a large number of zero values, which drastically skewed the distribution of the data; I was unable to transform it to achieve a normal distribution, which effectively ruled out the use of parametric statistical tests. The large number of zero values also prevented the use of either chi-square or loglinear analysis of these data. Thus, the relationship between maximum wind speed and distance from the forest edge was examined with Spearman Rank Correlations for each combination of edge type and season. All statistical analyses were performed using SPSS version 11.0 for Windows.

Edge	Site	Transect	Wet Season	Dry Season
Туре				
Powerline	1	1	6 – 10 March 2004 (6 –	1 – 8 October 2004 (3 – 7
			10 Mar)	Oct)
Powerline	1	2	21 February – 5 March	27 September – 1 October
			2005 (21 – 25 Feb)	2004 (27 Sep – 1 Oct)
Powerline	2	1	23 March – 2 April 2005	7 – 20 November 2004 (10
			(24 – 28 Mar)	– 14 Nov)
Powerline	2	2	2 – 11 April 2005 (3 – 7	20 – 28 November 2004
			Apr)	(20 – 24 Nov)
Highway	1	1	2 – 6 March 2004 (2 – 6	23 – 27 September 2004
			Mar)	(23 – 27 Sep)
Highway	1	2	27 February – 2 March	17 – 23 September 2004
			2004 (27 Feb – 2 Mar)	(17 – 21 Sep)
Highway	2	1	23 – 27 February 2004	28 November – 13
			(23 – 27 Feb)	December 2004 (29 Nov -
				3 Dec)
Highway	2	2	16 – 23 March 2005 (19 –	31 October – 5 November
			23 Mar)	2004 (1 – 5 Nov)
Creek	1	1	15 – 21 February 2005	13 – 22 December 2004
			(16 – 20 Feb)	(13 – 17 Dec)
Creek	1	2	5 – 16 March 2005 (5 – 9	12 – 17 September 2004
			Mar)	(12 – 16 Sep)
Creek	2	1	10 – 14 March 2004 (10 –	8 – 17 October 2004 (9 –
			14 Mar)	13 Oct)
Creek	2	2	14 – 26 March 2004 (19 –	17 – 31 October 2004 (26
			23 Mar)	- 30 Oct)

Table 4.2. Dates of data logger measurements for each transect. If more than four days' worth of data were collected for a transect, the subset of data used for analysis is indicated in parentheses.

4.3.2 Results

Visual assessment of the data revealed a number of qualitative differences in the diurnal patterns of air temperature, VPD and wind speed between the edges of powerlines, highways and creeks. In the dry season, positive air temperature and VPD gradients (ie higher temperature and VPD values near the forest edge than in the forest interior) formed a few hours after sunrise near powerline edges and persisted through much of the day, but collapsed back to neutral by mid to late afternoon, before becoming negative (ie lower values near the forest edge than in the forest interior) over night (Figure 4.4 b, d). The initial rise in temperature and VPD values after the overnight minimum tended to occur soon after sunrise at the forest edge and progressively later at distances further from the edge, with a delay between the 0 m and 100 m distances of up to 1.5 hours (Figure 4.4 b, d). During the day, positive gradients extended to between 12 and 25 m from the edge for air temperature and VPD, with a maximum edge distance of 100 m recorded for VPD on particularly cold, clear days. At night, negative gradients extended to between 12 and 25 m for air temperature, with a maximum edge distance of 100 m recorded on cold, clear, windless nights. Negative night-time gradients in VPD extended to between 4 and 12 m, with a maximum of 50 m recorded on a cold, clear, windless night; however, on overcast nights, all VPD values dropped to 0 kPa and no edge gradients were recorded.

In the wet season, daytime gradients in air temperature and VPD became slightly weaker or more complex in shape and VPD gradients collapsed altogether on wet days, when all VPD values fell to 0 kPa. When positive gradients were present, these extended to between 4 and 25 m. At night, all VPD values fell to 0 kPa and no gradients were recorded and temperature gradients also tended to be neutral (ie no edge gradient) (Figure 4.4 a, c).

Highway edges experienced similar gradients to those observed near powerline edges. In the dry season, positive daytime gradients in air temperature and VPD extended to between 12 and 25 m, with a maximum of 100m on cold, clear days, although there was a slight tendency for gradients to be more complex in shape at some sites (Figure 4.4 f, h). At night, gradients in VPD were neutral (ie no edge gradient), as values dropped to 0 kPa and gradients in air temperature also tended to be weaker (extending only to 4 to 12 m) or neutral. In the wet season, daytime gradients in air temperature and VPD were strongest on clear days and neutral on overcast and wet days, extending to between 4m and 50m when present. At night, VPD fell to 0 kPa and no gradients were recorded and air temperature gradients were also mostly neutral (Figure 4.4 e, g).

In contrast, daytime air temperature and VPD gradients tended to be mostly neutral near creek edges in both the wet and dry seasons, although some weak positive gradients did form in the middle of clear days in both seasons, extending to between 12 and 25 m (Figure 4.4 i, j, k, l). VPD tended to fall to 0 kPa overnight in both seasons and air temperature gradients also tended to be neutral overnight, regardless of the season.

Wind speed readings above 0 km hr⁻¹ were recorded more frequently in the dry season than the wet season, across all edge types. Positive wind speed readings tended to occur most often during the daytime and wind speeds and edge gradients tended to be highly variable. Positive wind speed readings tended to be confined to between 0 and 4 m from powerline and highway edges in the dry season and to 0 m in the wet season for powerline edges (and 0 to 4 m from highway edges), although some wind gusts extended up to 25 m from the forest edge in the dry season. In contrast, creeks experienced elevated wind speed readings up to 25 m from the forest edge in the dry season.







different scales on the y-axes for the powerline, highway and creek data. transect (a, b, c, d), a highway transect (e, f, g, h) and a creek transect (i, j, k, l) in the wet and the dry season. Note the Figure 4.4. Examples of data logger measurements of air temperature and vapour pressure deficit (VPD) for a powerline

The diurnal ranges of air temperature and VPD varied with both distance and edge type (distance * edge type, MANOVA, Pillai's Trace = 0.092, F = 1.799, df = 20.000, p = 0.017) and between the wet and dry seasons (edge type * season, MANOVA, Pillai's Trace = 0.118, F = 11.752, df = 4.000, p < 0.001). The season * distance and edge type * season * distance interaction terms were not significant. The MANOVA between-subject effects tests revealed that the diurnal ranges of temperature and VPD were generally greater in the dry season than in the wet season (Figure 4.5 a, c; Table 4.3). Diurnal temperature ranges were greater near the very edges (0 m) of powerlines and highways but not creeks (Figure 4.5 b; Table 4.3); diurnal VPD ranges followed a similar pattern, although the edge effects for anthropogenic linear clearings extended to 4 m and VPD ranges had reached interior values by 12 m from the edge (Figure 4.5 d, Table 4.3). For both air temperature and VPD, the diurnal range experienced within the powerline clearing itself (-10 m, Figure 4.5 b, d) was much greater than that experienced at any distance within the forest.

Table 4.3. Results of MANOVA tests of between-subject effects for diurnaltemperature and VPD ranges. Significant effects are highlighted in bold. In cases wherethe edge type * season effect is significant for a parameter, the individual edge type andseason effects for that parameter should be disregarded.

Effect	Parameter	F	df	p-value
Edge Type	Temperature Range (°C)	5.356	2	0.005
	VPD Range (hPa)	2.249	2	0.107
Distance	Temperature Range (°C)	9.916	5	<0.001
	VPD Range (hPa)	8.338	5	<0.001
Season	Temperature Range (°C)	56.326	1	<0.001
	VPD Range (hPa)	86.164	1	<0.001
Edge Type * Distance	Temperature Range (°C)	2.831	10	0.002
	VPD Range (hPa)	1.970	10	0.035
Edge Type * Season	Temperature Range (°C)	9.021	2	<0.001
	VPD Range (hPa)	0.494	2	0.610
Season * Distance	Temperature Range (°C)	0.414	5	0.839
	VPD Range (hPa)	1.007	5	0.413
Edge Type * Distance *	Temperature Range (°C)	0.288	10	0.984
Season	VPD Range (hPa)	0.263	10	0.989



Figure 4.5. Variation in the diurnal range of air temperature (a, b) and vapour pressure deficit (c, d). Edge type by season interactions are shown in panels a and c; edge type by distance interactions are shown in panels b and d. The vertical dashed lines in panels b and d indicate the position of the forest edge; values for the distance of -10 m on powerline transects were not included in the statistical analyses but are shown here to provide an "open" contrast. Values represent expected means and error bars represent ±1 se.

On average, the forest edge appeared to experience greater maximum wind speeds than the forest interior and this effect was particularly pronounced near creek edges (Figure 4.6, Table 4.4). Maximum wind speeds appeared in general to be greater in the dry season than in the wet season for all edge types (Figure 4.6), although the majority of recorded maximum wind speeds were less than 1.5 km hr^{-1} (~0.42 m s⁻¹). For powerline edges, values appeared to reach forest interior levels at 4 m from the edge in the wet season and 50 to 100 m in the dry season (Figure 4.6a). For highway edges, values appeared to reach interior levels at 12 m from the edge in the wet season and 50 m from the edge in the dry season (Figure 4.6b). For both anthropogenic edge types, the shape of the edge effect did not appear to be a simple linear or curvilinear decrease; instead, there appeared to be a decrease in maximum wind speed between 0 and 12 m from the forest edge, followed by a slight increase at 25 m and a further decline at 50 m or 100 m (Figure 4.6 a, b), which could suggest that the structure of the edge vegetation may be slightly denser or more "closed" than the interior vegetation. In contrast, maximum wind speed appeared to decline in a simple, curvilinear way, with distance from the creek edges (Figure 4.6c). Values near creek edges appeared to reach interior levels by 25 to 50 m in both the wet and the dry seasons (Figure 4.6c).

Table 4.4. Spearman Rank Correlations for maximum wind speed and distance from the forest edge for each edge type and season. Significant correlations are highlighted in bold.

Edge Type	Season	Spearman Rank Correlation	<i>p</i> – value
Powerline	Dry	-0.807	<0.001
	Wet	-0.458	0.024
Highway	Dry	-0.856	<0.001
	Wet	-0.428	0.037
Creek	Dry	-0.454	0.029
	Wet	-0.681	<0.001



Figure 4.6. Variation in maximum wind speed measured near **a**) powerline, **b**) highway and **c**) creek edges. The vertical dashed line indicates the position of the forest edge; values for the distance of -10 m on powerline transects were not included in the statistical analyses but are shown here to provide an "open" contrast. Values represent means and error bars represent ± 1 se.

4.3.3 Discussion

Edge gradients in air temperature and vapour pressure deficit varied with time of day, season, prevailing weather conditions and between anthropogenic and natural linear canopy openings. Edge gradients in temperature and VPD tended to be positive during the day, particularly in the dry season, and were strongest on clear, calm days. These gradients weakened or collapsed in wet weather, particularly during the wet season. These gradients were strongest near powerline and highway edges and weak or absent near creek edges. In contrast, overnight gradients in temperature and VPD were either negative or neutral. The strongest negative gradients were experienced during the dry season, particularly on cold, clear, calm nights, near anthropogenic edges (particularly powerline edges). Night time gradients in VPD tended to disappear in overcast or wet weather and were generally absent in the wet season. Overnight gradients in air temperature also tended to disappear during the wet season.

These patterns resulted in greater diurnal ranges of air temperature and vapour pressure deficit within 4 m of powerline and highway edges in both the wet and dry seasons (and greater diurnal ranges across all distances in the dry season than in the wet season for all edge types). In contrast, the diurnal variation in temperature and VPD was not elevated near creek edges in either season. Overall, these results agree with those of other studies, which have also found significant variation in the extent and magnitude of microclimatic edge gradients with time of day, season, ambient conditions and edge aspect in both tropical and temperate forests (Chen *et al.* 1995; Newmark 2001).

In contrast to this pattern of stronger air temperature and vapour pressure deficit gradients near anthropogenic edges, creek edges displayed the strongest wind speed gradients. Both maximum wind speeds and the percentage of non-zero wind speed readings were higher near creek edges than near powerline or highway edges and this effect extended further from the edges of creeks than from the edges of powerlines or highways. In agreement with the air speed results obtained from traverse measurements, wind speed gradients tended to be stronger in the dry season than in the wet season. However, the data logger results directly contradict the traverse measurement results, in that the data logger results show stronger wind speed effects for creek edges than for anthropogenic edges. The higher dry season wind speeds are most likely due to the influence of the south-easterly trade winds which predominate in the dry season in the study region. The greater edge extent for wind penetration near creek edges may be due to a lower degree of sealing of creek edges, as compared to anthropogenic edges (lower sapling and small tree density, Chapter 5; lower LAI, as expressed in higher red:far red ratio values, Figure 4.8; see also Section 4.4.2, above). Lower vegetation density at the edge would offer less resistance to the movement of air across the edge, resulting in greater severity and extent of edge effects (Harper *et al.* 2005). The discrepancy between these results and those obtained using the traverse method emphasises the importance of measuring highly variable parameters such as wind speed over a longer period of time, rather than relying purely on instantaneous measurements.

4.4 Variation in the Understorey Light Environment

4.4.1 Materials and Methods

Variation in the light environment of the rainforest understorey (research question 6) was assessed using the ratio of red light (~ 660 nm wavelength) to far red light (~730 nm wavelength). The red:far red ratio is highly correlated with percent canopy transmittance and leaf area index, is usually normally distributed and, unlike canopy transmittance, only requires one sensor to measure (Capers and Chazdon 2004). Changes in the red:far red ratio (and light availability) can influence the germination, survival, growth rate and phenotypic responses of many plant species (Capers and Chazdon 2004) and thus, any variation in the red:far red ratio in response to the rainforest edge may have implications for the dynamics and composition of the rainforest plant community.

The red:far ratio was measured using a Skye 660/730nm Ratio Sensor (SKR 110) and meter (SKR 100) (Skye Instruments Ltd., Llandrindod, Wales). The meter displays only instantaneous readings and is not capable of averaging red:far red values over time. However, at any one point in the rainforest, the red:far red ratio tends to be fairly stable in overcast conditions (*pers. obs.*). The sensor was attached to one end of a flat piece of wood, approximately 55 cm in length, with electrical tape. A spirit level bubble was taped onto the wood, approximately 5 cm from the sensor and the meter was taped to the other end of the piece of wood (Plate 4.3). This device was held at breast height (~130 cm) at a distance far enough away from the body of the operator to avoid shading the sensor. The level bubble was used to keep the sensor horizontal.

Understorey light environment was measured at all of the transects described in Chapter 3. 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 from the forest edge (Figure 4.7). The red:far red ratio was measured every 2.5 m along these lines, giving a total of 11 measuring points per line, 22 measuring points per distance, 132 measuring points per transect and 1584 measuring points overall (12 transects *132 points per transect). As it was not possible to average red:far red readings temporally (eg the 15 second averages used for PAR in section 4.2.1), three instantaneous red:far red readings were taken within 25 cm of the position marker and within 50 cm of each other and the average of these three readings was used. All measurements were made in overcast conditions, when light conditions are uniform and the red:far red ratio correlates most strongly with percent canopy transmittance (Capers and Chazdon 2004). Periods of heavy cloud or rain were avoided, as were early mornings and late afternoons, as the light level tended to fall below the detection limits of the sensor. Measurements were made between 10th June 2004 and 25th June 2005.



Figure 4.7. The field site survey design for the red:far red measurements. Three red:far red ratio measurements are taken within 25 cm of each measuring point and averaged.

25m

4.4.1.1 Statistical Analysis

Initially, an ANOVA with fixed factors of distance (0.5 m, 4 m, 12 m, 25 m, 50 m and 100 m) and edge type (powerline, highway and creek) was performed to determine whether there were overall differences in the red:far red ratio between different edge types with distance from the forest edge. I was also interested to see whether the number of very high readings (associated with canopy gaps) was higher near the forest edge than the forest interior; to this end, I analysed variation in the proportion of red:far red values ≥ 0.70 per 25 m line (Figure 4.3) (the ≥ 0.70 value was chosen arbitrarily, as measurements within this range were always observed to be associated with canopy gaps). I analysed these data using ANOVA, with independent variables of edge type

(powerline, highway or creek) and distance from the forest edge. The dependent variable was the percentage of readings ≥ 0.70 per 25 m line. These data were transformed (with ln(1 + x)) to approximate normality. All statistical analyses were performed using SPSS version 11.0 for Windows.



Plate 4.3. The red:far red sensor and display meter were supported on a flat wooden post. The sensor and a level bubble were placed at the far end of the post, to avoid being shaded by the operator. The instrument was held at chest height (~1.3 m above the ground surface) and measurements were taken only on overcast days with uniform light conditions. The person pictured is June Pohlman. Photo by author.

4.4.2 Results

The red:far red ratio varied significantly with both distance from the forest edge and edge type (ANOVA, edge type * distance interaction F = 5.678, df 10, p < 0.001). On average, the red:far red ratio was greater for creek edges than for powerline or highway edges (Bonferroni *post hoc* test, p < 0.001), particularly at distances ≤ 25 m from the forest edge (Figure 4.8). Additionally, the red:far red ratio was greater at the very edge of the forest (0.5 m) than at other distances (Bonferroni *post hoc* test, p < 0.001), particularly for powerline and highway edges (Figure 4.8). Overall, these results suggest that the rainforest canopy is more open near the edges of creeks than near the edges of powerlines and highways and that this canopy openness extends for a greater distance into the forest.



Figure 4.8. Red:Far Red ratio, means for the edge type by distance interaction. The red:far red value for the powerline at 100 m is hidden behind that of the highway at 100 m. Error bars represent \pm 1 se.

The percentage of red:far red readings ≥ 0.70 was elevated within 12 – 25 m of the forest edge (distance, F = 6.750, df = 5, p < 0.001), for all edge types (Figure 4.9); this did not differ significantly between edge types (edge type, F = 2.340, df = 2, p = 0.100) and there was no significant interaction between edge type and distance from the edge (edge type * distance, F = 0.798, df = 10, p = 0.631).



Figure 4.9. Percentage of red:far red values ≥ 0.70 . Error bars represent ± 1 se. Values that share a letter are not significantly different to each other (ANOVA, Bonferroni *post hoc* test, p < 0.05).

4.4.3 Discussion

The red:far red ratio measurements revealed significant differences in the understorey light environment near the edges of powerlines, highways and creeks. Overall, the red:far red ratio was higher near creek edges than near anthropogenic edges. Elevated red:far red values extended at least 25 m from the edges of creeks and returned to interior values by 50 m. In contrast, average red:far values were only elevated at the very edges of highways and powerlines. As the red:far red ratio is negatively correlated with leaf area index (LAI) and positively correlated with percent canopy transmittance (Capers and Chazdon 2004), these results indicate that the forest canopy of creek edges is more open than that of either powerline or highway edges. This was not due to a difference in the number of canopy gaps (Figure 4.9), which were elevated within 12 m of all edge types, nor to a difference in the number of fallen trees, which were elevated within 25 – 50 m of all edge types (Chapter 6).

Lower light availability, associated with a higher leaf area index, near anthropogenic edges is consistent with greater foliage density observed near the edges of logging roads (Malcolm and Ray 2000) and fragment edges in tropical rainforest (Malcolm 1994; Didham and Lawton 1999) and near fragment edges (Mourelle *et al.* 2001), powerlines, roads and streams in temperate forest (Evans and Gates 1997). This is also consistent with a higher degree of edge sealing near powerlines and highways than near creeks. Current powerline and highway edges are approximately 15 years old, an age which is sufficient for edges to become 'sealed' in other fragmented forests (Laurance et al. 2002; Harper et al. 2005). The lowered average red: far red values between 4 and 25 m of anthropogenic edges indicate an increase in foliage density, consistent with that observed near the edges of isolated fragment in north-eastern Queensland (Harding and Gomez 2006) and sealed forest edges in central Amazonia (Malcolm 1994). The higher light availability near creek edges than anthropogenic edges contrasts with the pattern found in temperate forest, where light availability is higher near anthropogenic features than streams (Evans and Gates 1997; Parendes and Jones 2000). It is possible that the lower density of saplings and small trees along creek transects (Chapter 5) has resulted in a less developed subcanopy layer, which may be responsible for a lower LAI near creek edges than near anthropogenic edges; if this is the case, it seems likely to be the result of periodic flood disturbance damaging or removing smaller trees and saplings (Nakamura et al. 1997). Alternatively, the greater proportion of early-successional tree species near creek edges (Chapter 5) may have altered the degree of light interception by foliage at the creek edge (Turner 2001; Falster and Westoby 2005; Bohlman and O'Brien 2006).

The greater percentage of high light (≥ 0.7) measurements within 12 m of the edges of powerlines, highways and creeks is similar to the higher frequency of gaps found near fragment edges in tropical rainforest (Kapos 1989). The number of tree-falls is also elevated near the edges of linear canopy openings (Chapter 6), and these data together suggest that canopy disturbance is elevated near the edges of linear canopy openings in a manner perhaps similar to that observed near fragment edges (Laurance *et al.* 2002; Harper *et al.* 2005). This will be discussed further in Chapter 6.

4.5 Synthesis: Microclimatic Edge Effects of Linear Canopy Openings

Internal fragmentation was associated with a number of alterations in the understorey microclimate near the rainforest edge. These microclimatic changes differed between powerline, highway and creek edges, between the wet and dry seasons and with the time of day. Creek edges were brighter (PAR and red: far red ratio) than anthropogenic edges and this effect extended at least 25 m from the forest edge, possibly due to a lower degree of edge sealing and a less dense subcanopy layer (Chapter 5), which also allowed wind to penetrate further into forest near creek edges than near anthropogenic edges. Air temperature and vapour pressure deficit, however, were not elevated near creek edges. These edge effects are likely to be direct consequences of the geomorphic influence of the creek itself on the disturbance regime and soil properties of the forest near the creek and to the "buffering" effects of flowing water on air temperature and humidity (Nichol 1994; Hupp and Osterkamp 1996; Nakamura et al. 1997; Robertson and Augspurger 1999; Turner et al. 2004). These results also suggest that the brighter, less desiccating environment near creek edges may be a more benign location for the growth and survival of seedlings and other understorey plants than the more desiccating environments near anthropogenic edges (eg Whitmore 1997; Benitez-Malvido 2001).

Anthropogenic edges were warmer and drier than creek edges, but experienced lower wind penetration and less elevation in light levels than creek edges. The diurnal variability of air temperature and vapour pressure deficit was also greater near powerline and highway edges than near creek edges. In addition, many of these edge effects, for both natural and anthropogenic linear canopy openings, were more pronounced in the dry season than the wet season and on clear days rather than overcast or rainy days. These results agree with those of other studies, on the importance of seasonal variability and external weather conditions for the environment experienced in the understorey near the forest edge (Chen *et al.* 1995; Turton and Freiburger 1997; Newmark 2001). These results also have implications for the survival and growth of interior forest specialists near the edges of powerlines and highways (Benitez-Malvido 2001; Laurance *et al.* 1998b, 2002). This question will be addressed in later chapters.

Contrary to my initial expectations, these data suggest that the nature of the linear canopy opening may be at least as important as the width in determining the nature and extent of microclimatic edge effects. In particular, differences in the magnitude of latent and sensible heat fluxes within clearings for powerlines and

highways, and the "buffering" effect of flowing water in creeks, may all influence the forest edge in different ways. This is analogous to the "matrix effect" (or "edge contrast" effect) observed in traditional fragmentation studies, whereby the nature of the matrix between isolated fragments (or the habitat immediately adjacent to a forest edge) can exert a strong influence on the severity of edge effects experienced in forest fragments (Laurance *et al.* 2002; Ries *et al.* 2004; Harper *et al.* 2005). This suggests that management efforts should perhaps be aimed towards minimising the contrast between the physical properties of the forest and the linear canopy opening, particularly in relation to fluxes of water (eg latent heat, evapotranspiration). Given the widespread distribution of highways and powerlines within the study area (Trott *et al.* 1996; Goosem 1997) and throughout other forested regions (Goosem 1997) and consequent length of edges, these effects could potentially have significant implications for the landscape-scale distributions and conservation of rainforest species (Goosem 1997), together with composition and structure of vegetation and faunal communities.

4.6 Conclusions

This chapter addressed the following questions:

- 1) Do linear canopy openings cause microclimatic gradients in the adjacent rainforest understorey?
- 2) Do the extent and severity of any edge effects differ between edge types (powerlines, highways and creeks)?
- 3) How do these edge effects vary between the wet and the dry seasons?
- 4) How do these edge effects vary diurnally?
- 5) Is wind speed elevated near the edge of the forest? Is this as important as changes in light availability?
- 6) How does the understorey light environment differ between the edge and the interior of the forest?

In response to questions 1 and 2, linear canopy openings were found to cause significant microclimatic edge effects and the nature and extent of these effects differed significantly between powerline, highway and creek edges. Light levels were elevated near all edge types but this effect was greatest and extended furthest near creek edges. In contrast, air temperature and vapour pressure deficit were elevated near powerline edges in the dry season and highway edges in both wet and dry seasons but were not elevated near creek edges in either season. In relation to question 3, many of these edge effects were more pronounced in the dry season than in the wet season and, in relation to question 4, edge gradients in air temperature and vapour pressure deficit tended to be positive during the day and neutral or reversed during the night. In relation to question 5, wind speed was slightly elevated near the edge and this effect was strongest near creek edges. However, measured wind speeds were very low and the predominant wind speed measured was in fact 0 km hr⁻¹.

In relation to question 6, the understorey light environment differed significantly between the edge and the forest interior and between different edge types; creek edges were brighter than either powerline or highway edges, possibly due to a lower understorey density and lower degree of edge sealing (as a result of periodic flood disturbance). Canopy gaps, however, occupied an increased proportion of the forest canopy within 12 m of all edge types.

I recommend the following lines of enquiry for further study:

1) The inferred differences in latent and sensible heat fluxes between powerlines, highways and creeks should be directly examined, perhaps through the use of satellite data. Satellite measurements of these parameters, preferably at a resolution of ≤ 20 m, could determine whether these inferred differences are real and how they vary with time of day, time of year and possibly cloud cover. These measurements could also be extended to explore the effects of different soil and forest types.

2) Canopy temperature could be measured from satellite data, preferably at a resolution of ≤ 20 m, to determine whether the edge gradients detected in this study occur over a broader area and in different forest and soil types (eg ASTER satellite data, with a 15 m resolution and 14 bands, including visible and near infrared to thermal infrared could be used for this purpose; Prof. David Gillieson, *pers. comm.*). If suitable data is available, the effects of the 2002/2003 *El Nino* drought on these edge gradients might also be examined.

3) Modelling of the patterns of wind movement within linear canopy openings could be undertaken. Studies of the patterns of windshear along the edges of forest fragments have helped to illuminate the mechanisms behind increased tree-fall disturbance (eg Somerville 1980, *cited in* D'Angelo *et al.* 2004) and air movement (Kapos *et al.* 1993) at fragment edges and similar studies might assist in understanding the patterns of wind speed and movement at the edges of linear canopy openings.

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:

- 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?
- 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 \geq 5 cm dbh (diameter at breast height; \sim 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 m²) 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 m² plots per distance per transect were pooled so that basal areas were calculated on the basis of cm² per 50 m². 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 latesuccessional 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 (\geq 5 cm dbh, 2 – 5 cm dbh and < 2 cm dbh).

Abundances of understorey and canopy trees were analysed for each size class $(\geq 5 \text{ cm dbh}, 2-5 \text{ cm dbh} \text{ and } < 2 \text{ cm dbh})$ 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 ($\geq 5 \text{ cm dbh}, 2-5 \text{ cm}$ 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 (\geq 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 Longnosed 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 m² plots per distance per transect were pooled such that abundances of stems in the largest size class (\geq 5 cm dbh) were measured on the basis of stems per 50 m², stems in the intermediate size class (2 – 5 cm dbh) were measured on the basis of stems per 25 m² and stems in the smallest size class (< 2 cm dbh) were measured on the basis of stems per 6 m².

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 ≥ 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 ≥ 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 5.2g) 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 5.2g) 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 5.2g) 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 5.2h) 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.

$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Size Class	Effect	Parameter	F	df	<i>p</i> -value
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	> 5 cm dbh	Edge Type	n	0.108	2	0.898
H' 0.278 2 0.758 Distancen 2.573 5 0.037 k 0.818 5 0.542 H' 0.326 5 0.895 Edge Type * Distancen 0.806 10 0.624 k 0.998 10 0.457 H' 1.054 10 0.413 $2 - 5 \mathrm{cm} \mathrm{dbh}$ Edge Typen 6.286 2 0.004 k 7.727 2 0.001 H' 6.489 2 0.003 k 3.413 5 0.003 k 0.692 10 0.728 k 0.817 10 0.614 H' 1.052 10 0.415 < 2 cm dbh			k	0.061	2	0.940
Distancen 2.573 5 0.037 k 0.818 5 0.542 H' 0.326 5 0.895 Edge Type * Distancen 0.806 10 0.624 k 0.998 10 0.457 H' 1.054 10 0.413 $2-5 {\rm cm} {\rm dbh}$ Edge Typen 6.286 2 0.004 k 7.727 2 0.001 H' 6.489 2 0.003 k 3.413 5 0.009 H' 3.112 5 0.003 k 0.817 10 0.614 H' 1.052 10 0.728 k 0.817 10 0.614 H' 1.052 10 0.415 Edge Type * Distancen 0.692 10 $10(1 + n)$ 4.309 2 0.018 k 0.817 10 0.614 H' 1.052 10 0.415 $1n(1 + n)$ 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			H'	0.278	2	0.758
k0.81850.542H'0.32650.895Edge Type * Distancen0.806100.624k0.998100.457H'1.054100.4132 - 5 cm dbhEdge Typen6.28620.004k7.72720.001H'6.48920.003k3.41350.009H'3.11250.015Edge Type * Distancen0.692100.728k0.817100.614H'1.052100.415< 2 cm dbh		Distance	n	2.573	5	0.037
H' 0.326 5 0.895 Edge Type * Distancen 0.806 10 0.624 k 0.998 10 0.457 H' 1.054 10 0.413 $2 - 5 {\rm cm} {\rm dbh}$ Edge Typen 6.286 2 0.004 k 7.727 2 0.001 h' 6.489 2 0.003 bistancen 4.229 5 0.003 k 3.413 5 0.009 H' 3.112 5 0.015 Edge Type * Distancen 0.692 10 0.728 k 0.817 10 0.614 H' 1.052 10 0.415 4.299 2 0.001 Edge Type * Distancen 0.692 10 0.728 k 0.817 10 0.614 H' 1.052 10 0.415 $10^{1}(1 + n)$ 4.309 2 0.061 $10^{1}(1 + n)$ 3.173 5 0.014 k 0.2939 2 0.061 1167 5 0.337 H' 0.909 5 0.482 Edge Type * Distance $ln(1 + n)$ 2.748 10 Edge Type * Distance $ln(1 + n)$ 1.010 0.0447			k	0.818	5	0.542
Edge Type * Distancen0.806100.624k0.998100.457H'1.054100.4132 - 5 cm dbhEdge Typen6.28620.004k7.72720.001H'6.48920.003H'6.48920.003k3.41350.009Distancen4.22950.003k3.11250.015Edge Type * Distancen0.692100.728k0.614H'1.052100.415100.614H'1.052100.415100.415< 2 cm dbh			H'	0.326	5	0.895
k0.998100.457H'1.054100.4132 - 5 cm dbhEdge Typen6.28620.004k7.72720.001H'6.48920.003Distancen4.22950.003k3.41350.009H'3.11250.015Edge Type * Distancen0.692100.728k0.817100.614H'1.052100.415< 2 cm dbh		Edge Type * Distance	n	0.806	10	0.624
$\begin{array}{c c c c c c c c c c c c c c c c c c c $			k	0.998	10	0.457
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$			H'	1.054	10	0.413
k7.72720.001H' 6.489 20.003Distancen 4.229 50.003k 3.413 50.009H' 3.112 50.015Edge Type * Distancen 0.692 100.728k 0.817 100.614H' 1.052 100.415< 2 cm dbh	2-5 cm dbh	Edge Type	n	6.286	2	0.004
H' 6.489 2 0.003 Distancen 4.229 5 0.003 k 3.413 5 0.009 H' 3.112 5 0.015 Edge Type * Distancen 0.692 10 0.728 k 0.817 10 0.614 H' 1.052 10 0.415 < 2 cm dbh Edge Type $h(1 + n)$ 4.309 2 0.018 k 0.283 2 0.754 H' 2.939 2 0.061 Distance $hn(1 + n)$ 3.173 5 0.014 k 1.167 5 0.337 H' 0.909 5 0.482 Edge Type * Distance $hn(1 + n)$ 2.748 10 0.008 k 0.781 10 0.647 H' 1.010 10 0.447			k	7.727	2	0.001
Distancen 4.229 5 0.003 k 3.413 5 0.009 H' 3.112 5 0.015 Edge Type * Distancen 0.692 10 0.728 k 0.817 10 0.614 H' 1.052 10 0.415 < 2 cm dbh			H'	6.489	2	0.003
k 3.413 5 0.009 H' 3.112 5 0.015 Edge Type * Distancen 0.692 10 0.728 k 0.817 10 0.614 H' 1.052 10 0.415 < 2 cm dbh		Distance	n	4.229	5	0.003
H' 3.112 5 0.015 Edge Type * Distancen 0.692 10 0.728 k 0.817 10 0.614 H' 1.052 10 0.415 $< 2 cm dbh$ Edge Type $h(1+n)$ 4.309 2 0.018 k 0.283 2 0.754 H' 2.939 2 0.061 Distance $hn(1+n)$ 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			k	3.413	5	0.009
Edge Type * Distancen 0.692 10 0.728 k 0.817 10 0.614 H' 1.052 10 0.415 < 2 cm dbh			H'	3.112	5	0.015
k 0.817 10 0.614 H' 1.052 10 0.415 < 2 cm dbh		Edge Type * Distance	n	0.692	10	0.728
H' 1.052 10 0.415 $< 2 \text{ cm dbh}$ 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			k	0.817	10	0.614
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			H'	1.052	10	0.415
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	< 2 cm dbh	Edge Type	ln(1 + n)	4.309	2	0.018
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			k	0.283	2	0.754
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			H'	2.939	2	0.061
$\begin{array}{c cccccc} k & 1.167 & 5 & 0.337 \\ H' & 0.909 & 5 & 0.482 \\ \hline \\ \hline \\ Edge Type * Distance & ln(1+n) & 2.748 & 10 & 0.008 \\ k & 0.781 & 10 & 0.647 \\ H' & 1.010 & 10 & 0.447 \\ \hline \end{array}$		Distance	ln(1 + n)	3.173	5	0.014
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			k	1.167	5	0.337
Edge Type * Distance $ln(1 + n)$ 2.748100.008k0.781100.647H'1.010100.447			H'	0.909	5	0.482
k 0.781 10 0.647 H' 1.010 10 0.447		Edge Type * Distance	ln(1 + n)	2.748	10	0.008
H' 1.010 10 0.447			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 ($\geq 30 \text{ cm dbh}$) 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).







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 < creek, p = 0.065; *ln*(tree basal area), F = 3.679, df = 2, p = 0.032, Bonferroni *post hoc* tests, powerline < creek, p = 0.065; *ln*(tree basal area), F = 3.679, df = 2, p = 0.032, Bonferroni *post hoc* tests, 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 = 0.065; *ln*(tree basal area), F = 3.679, df = 2, p = 0.032, Bonferroni *post hoc* tests, powerline < highway, p = 0.072, powerline < creek, p = 0.065; *ln*(tree basal area), F = 3.679, df = 2, p = 0.032, Bonferroni *post hoc* tests, powerline < highway, p = 0.072, powerline < creek, p = 0.065; *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 (cm² per 50m²) of **a**) all stems \ge 5 cm dbh, **b**) all trees \ge 5 cm dbh and **c**) all lianas \ge 5 cm dbh. Note the log scale on the y-axis.



Figure 5.5. Above-ground biomass of trees \geq 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^{\dagger}	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	Shrubs	0.155	-0.174	0.088	0.007
dbh	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 \geq 5 cm (**a**, **b**, **c**), 2 - 5 cm (**d**, **e**, **f**) and < 2 cm (**g**, **h**, **i**). Ferns in the largest size class (dbh \geq 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 (\geq 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- (\geq 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).

Size Class	Effect	Parameter	F	df	<i>p</i> -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
		<i>ln</i> (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
		<i>ln</i> (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
		<i>ln</i> (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
		<i>ln</i> (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
		<i>ln</i> (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

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



Figure 5.9. Liana abundance. The abundance of large woody vines (\mathbf{a} , stems > 5 cm dbh; \mathbf{b} , stems 2 - 5 cm dbh; \mathbf{d} , stems < 2 cm dbh), slender woody vines (\mathbf{c} , stems 2 - 5 cm dbh; \mathbf{e} , stems < 2 cm dbh) and climbing herbs (\mathbf{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	<i>p</i> -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
		<i>ln</i> (1 + Canopy trees)	0.402	5	0.845
	Edge Type * Distance	ln (1 + Understorey trees)	1.562	10	0.143
		<i>ln</i> (1 + Canopy trees)	0.661	10	0.755



Figure 5.10. The abundance of understorey and canopy trees in tree (\geq 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 = 0.006) 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	<i>p</i> -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 *	% early-successional	91.121	53	0.001
Size Class	% 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).



Late

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	<i>p</i> -value
Edge Type	% early-successional	$4.628(\chi^2)$	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 *	% early-successional	84.909 (χ ²)	53	0.004
Size Class	% 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* = 0.092; Table 5.7, Figure 5.13 a, b, c). The

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 \ge 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	<i>p</i> -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	<i>p</i> -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 andc) 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, earlysuccessional 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, midsuccessional 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^{\dagger}	-0.198*	
Creek	0.205*	-0.321***	
Large woody vines			
Overall	0.156***	-0.116*	
Powerline	0.083	-0.057	
Highway	0.161^{\dagger}	-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^{\dagger}	-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^{\dagger}	-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 tr	ees			
Overall	-0.006	0.003		
Powerline	-0.031	0.005		
Highway	0.003	0.081		
Creek	-0.067	-0.077		

Functional Group	tional Group Red:Far Red Ratio Correlation			
Late-successional understo	prey trees			
Overall	-0.208***	0.100*		
Powerline	-0.173*	0.278***		
Highway	-0.248**	0.157^{\dagger}		
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 t	rees			
Overall	-0.032	-0.076		
Powerline	0.050	-0.258**		
Highway	0.040	0.148^{\dagger}		
Creek	-0.045	-0.116		
Late-successional canopy t	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 than in 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 \geq 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 reestablished 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 aboveground biomass of trees \geq 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 (\geq 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 ≥ 5 cm 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 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 convzoides (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 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 midsuccessional 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 earlysuccessional 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 earlysuccessional understorey and canopy tree individuals in younger size classes near anthropogenic edges, suggest that there may have been an initial pulse of earlysuccessional 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 earlysuccessional understorey trees, may have resulted from an increased mortality of shaded understorey trees as they were overtaken by taller-growing individuals whilst earlysuccessional 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 latesuccessional understorey trees near anthropogenic edges, and the increase in midsuccessional 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 \geq 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 latesuccessional 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 largefruited, biotically-dispersed plants was not affected by distance from the edge for stems \geq 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 interspecific 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

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measured in this study would have varied between 1% and ~4 %, relative to light intensity above the forest canopy, with occasional patches up to $\sim 8\%$, 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:

- Is rainforest vegetation structure altered near the edges of linear canopy openings and are there any structural differences among powerline, highway and creek edges?
- 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 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 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:

- 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.
- 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 shadetolerance 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

- Is tree-fall disturbance elevated near the forest edge? Is this affected by edge type?
- 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 (\geq 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 \ge 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 \ge 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 \ge 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 \ge 50 cm) were combined into one category (\ge 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 \geq 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 withinfunctional 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 midsuccessional 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 ($n \ge 2$ 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 ≥ 10 cm 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	<i>F</i> = 3.077, df = 10, <i>p</i> = 0.0001	F = 10.681, df = 1, $p = 0.001$
Diameter > 10 cm	F = 5.303, df = 10, $p < 0.001$	<i>F</i> = 27.498, df = 1, <i>p</i> < 0.001
Diameter > 10 cm and	<i>F</i> = 3.727, df = 10, <i>p</i> < 0.001	<i>F</i> = 31.247, df = 1, <i>p</i> < 0.001
Decay class 1 - 3		



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
> 10 cm 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).



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	В	Wald Statistic	df	Р	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 midsuccessional 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 midsuccessional 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 latesuccessional 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 \geq 50cm tall. The number of seedlings in each functional group is given in parentheses.

Functional Group	Edge Type	Distance	Red:far red ratio	Edge Type *
			(covariate)	Distance
Canopy trees				
<i>Early</i> - <i>successional</i> (21)	n.s.	n.s.	n.s.	n.s.
Mid-successional ^b (66)	<i>F</i> = 2.819, df	n.s.	F = 14.388, df = 1,	n.s.
	= 2, <i>p</i> = 0.068		<i>p</i> < 0.001 ^c	
$Late-successional^{b}$ (223)	F = 4.484, df	n.s.	n.s.	n.s.
	= 2, <i>p</i> = 0.012			
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)	<i>F</i> = 3.929, df	n.s.	n.s.	F = 3.631, df = 4,
	= 2, <i>p</i> = 0.021			p = 0.007
Shrubs				
Early- and mid-	n.s.	F = 3.147,	n.s.	n.s.
$successional^{a}(68)$		df = 2, <i>p</i> =		
		0.05		
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 \geq 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 \pm 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 vo	olckii			
Creek	na	7.47 ±0.87 (3)	7.51 ±0.49 (4)	n.s. (distance)
Endiandra mono	thyra			
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 dealba	<i>ita</i>			n.s. (edge type)
Powerline	14.61 ±1.06 (10)	na	na	
Highway	12.69 ±1.23 (8)	na	na	
Understorey Tre	<u>es</u>			
Aglaia tomentos	a			
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 brachy	stylis			
Highway	8.47 ±0.5 (9)	9.36 ±0.69 (8)	10.41 ±0.41 (6)	Pearson correlation r
				= 0.445, p = 0.033
Brombya platyne	ema			(albunee)
Highway	na	8.96 ±0.80 (6)	10.47 ±0.97 (7)	n.s. (distance)

Species	0m & 4m	12m & 25m	50m & 100m	Significant Effects
Haplostichanti	hus sp. Topaz			
Powerline	5.01 ±0.47 (2)	na	9.57 ±0.55 (3)	<i>t</i> = -5.799, df = 3, <i>p</i> =
				0.01 (distance)
Highway	9.35 ±0.21 (2)	7.77 ±0.74 (6)	7.31 ±0.63 (4)	n.s. (distance)
Ni om on oug nu	mifour			n a (distance and
Niemeyera pru	0.01 ± 2.76	8 80 . 0 87 (0)	10.22 . 0.90 (12)	n.s. (distance and
Powerline	$9.01 \pm 2.76 (2)$	8.89 ±0.87 (9)	$10.33 \pm 0.80 (12)$	edge type)
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 haj	plophylla			
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	<i>t</i> = -2.217, df = 6, <i>p</i> =
				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	
<i>Wilkiea</i> sp. Ba	rong			
Highway	6.50 ±1.51 (3)	6.54 ±0.27 (2)	7.07 ±0.50 (5)	n.s. (distance)
Sharaha				
<u>Snrubs</u>	7 .			
Ardisia brevip	edata			
Powerline	6.18 ±0.76 (6)	na	na	t = -2.408, df = 8,
				p = 0.043 (edge type)
Hıghway	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
Powerline	8.21 ±1.26 (4)	7.73 ±1.01 (9)	10.10 ±0.78 (19)	and highway), $F =$
Highway	7.63 ±1.04 (6)	8.06 ±0.84 (12)	9.78 ±0.82 (14)	3.408, df = 2, <i>p</i> =
				0.04
Creek	na	9.02 ±0.86 (4)	9.55 ±1.32 (5)	n.s. (distance within
_				creek)
<i>Diosyrros</i> sp. N	fillaa 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	ı			n.s. (distance and
Powerline	9.84 ±3.38 (2)	10.72 ±1.38 (3)	8.37 ±0.41 (9)	edge type)
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 vil	llosa			
Highway	8.04 ±1.77 (4)	8.82 ±0.78 (3)	6.67 ±0.99 (3)	n.s. (distance)
<u>Lianas</u>				
Carronia protei	nsa ^a			n.s. (distance and
Powerline	na	11.32 ±1.99 (6)	10.41 ±1.09 (7)	edge type)
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 underrepresented 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; 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, longterm 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.
- 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:

- 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 m³ potting mix) and slow release fertiliser with N:P:K ratio of 16:4:4 (Osmocote ~1 kg per m³ 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.

10" E) and Henrietta Creek (17º 36' 31" S, 145º 46' 26" E) are on the 6 seedlings used in the experiment.	astern edge of Wooroonoorar	1 National Park and K-tree roac	1 (~ 17° 37' 00" S, 145° 45' 00"	E) is a forestr	road in the South Johnstone	State Forest. N = number of	
Species (Family)	Growth Habit	Successional Status	Fruit Type (Size)	Dispersal	Seed Source Mode	Collection Date	z
Omalanthus novo-guineensis (Warb.) Schum (Euphortbiaceae)	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)Edin 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

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' Table 7.1. Study species. Data on growth habit, successional status, fruit type and dispersal mode are taken from Cooper 1994, Tucker and Murphy 1997, Tucker 2001 and Hyland et al. 2003. Fruit size is divided into three

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 -1^{st} 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.

×
sect 100m

"Open" herbivory treatment"Caged" herbivory treatment

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.

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

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

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:

- 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*;
- 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

 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 andc) "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 7.5d). Survival of *Argyrodendron peralatum* seedlings also increased with increasing red:far red ratio (Figure 7.5g) although both of these effects were only marginally significant.

Survival time, rather than overall survival, of seedlings of *Omalanthus novoguineensis, 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	<i>p</i> -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 ($\alpha < 0.05$) are highlighted in bold and marginally significant results ($\alpha < 0.10$) are highlighted in italics.

Species	Variable	В	Wald	df	<i>p</i> -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
$Dysoxylum \ pettigrewianum^{\dagger}$	Red:far red	5.204	7.099	1	0.008
	Edge type ²	-1.147	7.053	1	0.008
Argyrodendron peralatum $^{\sharp}$	Red:far red	4.240	2.792	1	0.095
	Edge type ³	1.215	3.799	1	0.051

¶ Model $\chi^2 = 17.867$, 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.

 \ddagger 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 (\mathbf{a} , \mathbf{d} and \mathbf{g}), with distance from the edges of linear canopy openings (\mathbf{b} , \mathbf{e} and \mathbf{h}), with light availability (red:far red ratio; \mathbf{c} , \mathbf{f} and \mathbf{i}) and between seedlings protected from (filled symbols) and exposed to (open symbols) vertebrate herbivores. Values for \mathbf{a} , \mathbf{b} , \mathbf{d} , \mathbf{e} , \mathbf{g} and \mathbf{h} are means ± 1 S.E. Note the different scale on the y-axes of panels \mathbf{c} , \mathbf{f} and \mathbf{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	<i>p</i> -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 7.71) 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 7.70). 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	В	Wald	df	<i>p</i> -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 e	experienc	ed	na	na

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

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

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

fi Model χ^2 = 9.916, df = 1, *p* = 0.002 and 78.3% classification accuracy.

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

¥ Model χ^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 \sim 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* and *A. lathami* 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 edgepreferring 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 latersuccessional 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 $\sim 1 - 4$ % 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 edgesand 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:

- 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?
- 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:

- 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 (\uparrow), decreases (\downarrow) 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	$\uparrow (0.5 \text{ m}) \downarrow (4 - 50 \text{ m})$	$\uparrow (0.5 \text{ m}) \downarrow (4-50 \text{ m})$	↑ (50 m)
Photosynthetically Active Radiation	↑ (< 20 m)	↑ (< 20 m)	↑ (50 m)
Air Temperature	↑ (20 m, dry season)	↑ (< 20 m)	\downarrow (50 m, wet season)
Vapour Pressure Deficit	↑ (< 20 m, dry	↑ (< 16 m)	\downarrow (4 – 50 m, wet
	season)		season)
Canopy Temperature	\downarrow (~20 m, wet	↑ (< 30 m, wet	—
	season)	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	ſ	1	1
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	_	—	ſ
Mid-successional species	—	—	↑ (some species)
Late-successional species	—	—	1

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 (\geq 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 \geq 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 ($\geq 5 \text{ cm dbh}$) 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 latesuccessional individuals decreased towards the forest edge, particularly along creek transects. Additionally, along creek transects the proportions of late- and earlysuccessional individuals differed among adults, saplings and seedlings such that the proportion of late-successional individuals decreased and the proportion of earlysuccessional 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 latesuccessional 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 midsuccessional 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 (\geq 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 (\geq 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 novoguineensis* 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 lightdemanding, 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 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).

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, earlysuccessional 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.







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 lowgrowing 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 lightdemanding 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).

10. References

- Aide, T.M., 1987, Limbfalls: A Major Cause of Sapling Mortality for Tropical Forest Plants. *Biotropica*, **19**: 284 – 285.
- Aguilar, R. and Galetto, L., 2004, Effects of forest fragmentation on male and female reproductive success in *Cestrum parqui* (Solanaceae). *Oecologia*, **138**: 513 520.
- Agyeman, V.K., Swaine, M.D. and Thompson, J., 1999, Responses of tropical forest tree seedlings to irradiance and the derivation of a light response index. *Journal of Ecology*, **87**: 815 827.
- Andrews, S.B., 1990, *Ferns of Queensland*. Queensland Department of Primary Industries, Brisbane, Australia
- Anderson, E.M. and Boutin, S., 2002, Edge effects on survival and behaviour of juvenile red squirrels (*Tamiasciurus hudsonicus*). *Canadian Journal of Zoology*, 80: 1038 1046.
- Antongiovanni, M. and Metzger, J.P., 2005, Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments. *Biological Conservation*, **122**: 441 – 451.
- Aponte, C., Barreto, G.R. and Terborgh, J., 2003, Consequences of Habitat
 Fragmentation on Age Structure and Life History in a Tortoise Population.
 Biotropica, 35: 550 555.
- Armesto, J.J., Diaz, I., Papic, C. and Willson, M.F., 2001, Seed rain of fleshy and dry propagules in different habitats in the temperate rainforests of Chiloe Island, Chile. *Austral Ecology*, 26: 311 – 320.
- Asquith, N.M. and Mejia-Chang, M., 2005, Mammals, edge effects, and the loss of tropical forest diversity. *Ecology*, **86**: 379 390.
- Asquith, N.M., Wright, S.J. and Clauss, M.J., 1997, Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. *Ecology*, **78**: 941 946.
- Augspurger, C.K., 1984, Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology*, 65: 1705 – 1712.
- Baker, T.R., Swaine, M.D. and Burslem, D,F,R.P., 2003, Variation in tropical forest growth rates: combined effects of functional group composition and resource

availability. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**: 21 – 36.

- Bendix, J. and Hupp, C.R., 2000, Hydrological and geomorphological impacts on riparian plant communities. *Hydrological Processes*, **14**: 2977 2990.
- Benitez-Malvido, J., 1998, Impact of Forest Fragmentation on seedling abundance in a Tropical Rain Forest. *Conservation Biology*, **12**: 380 – 389.
- Benitez-Malvido, J., 2001, Regeneration in Tropical Rainforest Fragments. Chapter 11 in Bierregaard, R.O., Gascon, C., Lovejoy, T.E. and Mesquita, R.C.G., (eds), 2001, Lessons from Amazonia, The Ecology and conservation of a fragmented forest. Yale University Press, New Haven, pages 136 – 145.
- Benitez-Malvido, J. and Lemus-Albor, A., 2005, The Seedling Community of Tropical Rain Forest Edges and Its Interaction with Herbivores and Pathogens. *Biotropica*, **37**: 301 – 313.
- Benitez-Malvido, J. and Martinez-Ramos, M., 2003a, Impact of Forest Fragmentation on Understorey Plant Species Richness in Amazonia. *Conservation Biology*, 17: 389 – 400.
- Benitez-Malvido, J. and Martinez-Ramos, M., 2003b, Influence of Edge Exposure on Tree Seedling Species Recruitment in Tropical Rain Forest Fragments. *Biotropica* 35: 530 – 541.
- Beuer, P., Van Drielen, M. and Kankam, B.O., 2002, Avifaunal Collapse in West African Forest Fragments. *Conservation Biology*, **16**: 1097 – 1111.
- Bhattacharya, M., Primack, R.B. and Gerwein, J., 2003, Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? *Biological Conservation*, **109**: 37 – 45.
- Bohlman, S. and O'Brien, S., 2006, Allometry, adult stature and regeneration requirement of 65 tree species on Barro Colorado Island, Panama. *Journal of Tropical Ecology*, 22: 123 – 136.
- Bonell, M., Gilmour, D.A. and Cassells, D.S., 1983, Runoff generation in tropical rainforests of northeast Queensland, Australia, and the implications for land use management, *in* Keller, R., (ed.), 1983, *Hydrology of Humid Tropical Regions with Particular Reference to the Hydrological Effects of Agriculture and Forestry Practice (Proceedings of the Hamburg Symposium, August 1983).*IAHS, Washington, pages 287 297.

- Brienen, R.J.W. and Zuidema, P.A., 2006, Lifetime growth patterns and ages of
 Bolivarian rain forest trees obtained by tree ring analysis. *Journal of Ecology*,
 94: 481 493.
- Briggs, J.D. and Leigh, J.J., 1995, *Rare or Threatened Australian Plants*. Revised Edition. CSIRO Publishing, Collingwood, Australia.
- Brokaw, N.V.L., 1985, Gap-phase regeneration in a tropical forest. *Ecology*, **66**: 682 687.
- Brokaw, N. and Busing, R.T., 2000, Niche versus chance and tree diversity in forest gaps. *Trends in Ecology and Evolution*, **15**: 183 188.
- Brosofske, K., Chen, J., Naiman, R.J. and Franklin, J.F., 1997, Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. *Ecological Applications*, 7: 1188 – 1200.
- Brook, B.W., Sodhi, N.S. and Ng, P.K.L., 2003, Catastrophic extinctions follow deforestation in Singapore. *Nature*, **424**: 420 423.
- Brooks, T.M., Pimm, S.L. and Oyugi, J.O., 1999, Time Lag between Deforestation and Bird Extinction in Tropical Forest Fragments. *Conservation Biology*, 13: 1140 – 1150.
- Bruna, E.M., 2002, Effects of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia. *Oecologia*, **132**: 235 – 243.
- Bruna, E.M., Nardy, O., Strauss, S.Y. and Harrison, S., 2002, Experimental assessment of *Heliconia acuminata* growth in a fragmented Amazonian landscape. *Journal of Ecology*, **90**: 639 – 649.
- Bunker, D.E. and Carson, W.P., 2005, Drought stress and tropical forest woody seedlings: effect on community structure and composition. *Journal of Ecology*, 93: 794 806.
- Burnett, S.E., 1992, Effects of a Rainforest Road on Movements of Small Mammals: Mechanisms and Implications. *Wildlife Research*, **19**: 95 – 104.
- Burton, P.J., 2002, Effects of clearcut edges on trees in the sub-boreal spruce zone of Northwest-Central British Columbia. *Silva Fennica*, **36**: 329 – 352.
- Cadenasso, M.K. and Pickett, S.T.A., 2000, Linking forest edge structure to edge function: mediation of herbivore damage. *Journal of Ecology*, **88**: 31 44.
- Cadenasso, M.L. and Pickett, S.T.A., 2001, Effect of Edge Structure on the Flux of Species into Forest Interiors, *Conservation Biology*, **15**: 91-97.

- Camargo, J.L.C. and Kapos, V., 1995, Complex edge effects on soil moisture and microclimate in central Amazonian forest. *Journal of Tropical Ecology*, **11**: 205 – 221.
- Capers, R.S. and Chazdon, R.L., 2004, Rapid assessment of understorey light availability in a wet tropical forest. *Agricultural and Forest Meteorology*, **123**: 177 – 185.
- Capers, R.S., Chazdon, R.L., Brenes, A.R. and Alvarado, B.V., 2005, Successional dynamics of woody seedling communities in wet tropical secondary forests. *Journal of Ecology*, 93: 1071 – 1084.
- Cause, M.L., Rudder, E.J. and Kynaston, W.T., 1989, *Queensland Timbers: Their Nomenclature, Density and Lyctid-susceptibility*. Technical pamphlet no. 2, Queensland Department of Forestry, Queensland, Indooroopilly.
- Chauvet, S. and Forget, P., 2005, Edge effects on post-dispersal seed removal in a fragmented rain forest in French Guiana. *Journal of Tropical Ecology*, **21**: 113 – 116.
- Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riera, B. and Yakamura, T., 2005, Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145: 87 99.
- Chazdon, R.L., 2003, Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, 6: 51 71.
- Chazdon, R.L. and Fetcher, N., 1984, Photosynthetic light environments in a lowland rain forest in Costa Rica. *Journal of Ecology*, **72**: 553 564.
- Chen, J., Franklin, J.F. and Spies, T.A., 1993, Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology*, 63: 219 – 237.
- Chen, J., Franklin, J.F. and Spies, T.A., 1995, Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications*, **5**: 74 – 86.
- Christen, D. and Matlack, G., 2006, The Role of Roadsides in Plant Invasions: a Demographic Approach. *Conservation Biology*, **20**: 385 391.
- Clark, D.B. and Clark, D.A., 1989, The role of physical damage in the seedling mortality of a Neotropical rain forest. *Oikos*, **55**: 225 230.
- Clark, D.B. and Clark, D.A., 1991, The impact physical damage on canopy tree regeneration in tropical rain forest. *Journal of Ecology*, **79**: 447 457.
- Clark, D.A. and Clark, D.B., 2001, Getting into the canopy: tree height growth in a Neotropical rain forest. *Ecology*, **82**: 1460 1472.
- Coley, P.D. and Barone, J.A., 1996, Herbivory and plant defences in tropical forests. Annual Review of Ecology and Systematics, **27**: 305 – 335.
- Condit, R., Hubbell, S.P. and Foster, R.B., 1996, Assessing the response of plant functional types to climatic change in tropical forests. *Journal of Vegetation Science*, 7: 405 – 416.
- Connell, J.H., 1971, On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *In* den Boer, P.J. and Gradwell, G.R. (eds), *Dynamics of populations*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, pages 298 313.
- Connell, J.H., 1978, Diversity in Tropical Rain Forests and Coral Reefs. *Science*, **199**: 259 267.
- Connell, J.H., Debski, I., Gehring, C.A., Goldwater, L., Green, P.T., Harms, K.E., Juniper, P. and Theimer, T.C., 2005, Dynamics of Seedling Recruitment in an Australian Tropical Rainforest. Chapter 23 *In* Bermingham, E., Dick, C.W. and Moritz, C., (eds), 2005, *Tropical Rainforests, Past, Present and Future*. The University of Chicago Press, Chicago, U.S.A., pages 486 – 506.
- Connell, J.H., Lowman, M.D. and Noble, I.R., 1997, Subcanopy gaps in temperate and tropical forests. *Australian Journal of Ecology*, **22**: 163 168.
- Coomes, D.A., Duncan, R.P., Allen, R.B. and Truscott, J., 2003, Disturbances prevent stem size-density distributions in natural forests from following scaling relationships. *Ecology Letters*, **6**: 980 989.
- Cooper, W. and Cooper, W.T., 1994, Fruits of the Rain Forest, A Guide to Fruits in Australian tropical Rain Forests. GEO Productions, Chatswood, NSW, Australia.
- Cordeiro, N.J. and Howe, H.F., 2001, Low Recruitment of Trees Dispersed by Animals in African Forest Fragments. *Conservation Biology*, **15**: 1733 1741.

- Cordeiro, N.J. and Howe, H.F., 2003, Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences of the United States of America*, **100**: 14052 – 14056.
- Cowling, S.A., 2004, Tropical forest structure: a missing dimension to Pleistocene landscapes. *Journal of Quaternary Science*, **19**: 733 743.
- Cunningham, S.A., 2000a, Effects of Habitat Fragmentation on the Reproductive
 Ecology of Four Plant Species in Mallee Woodland. *Conservation Biology*, 14: 758 768.
- Cunningham, S.A., 2000b, Depressed pollination in habitat fragments causes low fruit set. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, 267: 1149 – 1152.
- Cutrim, E.M.C., Martin D.W., Butzow, D.G., Silva, I.M. and Yulaeva, E., 2000, Pilot analysis of hourly rainfall in central and eastern Amazonia. *Journal of Climate*, 13: 1326 1334.
- D'Angelo, S.A., Andrade, A.C.S., Laurance, S.G., Laurance, W.F. and Mesquita, R.C.G., 2004, Inferred causes of tree mortality in fragmented and intact Amazonian forests. *Journal of Tropical Ecology*, **20**: 243 – 246.
- Davies, K.F., Melbourne, B.A. and Margules, C.R., 2001, Effects of within- and between-patch processes on community dynamics in a fragmentation experiment. *Ecology*, 82: 1830 – 1846.
- Davies R.G., 2002, Feeding group responses of a Neotropical termite assemblage to rain forest fragmentation. *Oecologia*, **133**: 233 242.
- Davies, S.J., 1998, Photosynthesis of nine pioneer *Macaranga* species from Borneo in relation to life history. *Ecology*, **79**: 2292 2308.
- deFries, R., Hansen, A., Newton, A.C. and Hansen, M.C., 2005, Increasing isolation of protected areas in tropical forest over the past twenty years. *Ecological Applications*, 15: 19 – 26.
- Delgado, J.D., Arevalo, J.R. and Fernandez-Palacios, J.M., 2001, Road and topography effects on invasion: edge effects in rat foraging patterns in two oceanic island forests (Tenerife, Canary Islands). *Ecography*, 24: 539 – 546.
- DeMattia, E.A., Rathcke, B.J., Curran, L.M., Aguilar, R. and Vargas, O., 2006, Effects of Small Rodent and Large Mammal Exclusion on Seedling Recruitment in Costa Rica. *Biotropica*, **38**: 196 – 202.

- Dennis, A.J., 2003, Scatter-hoarding by musky rat kangaroos, *Hypsiprimnodon moschatus*, a tropical rain-forest marsupial from Australia: implications for seed dispersal. *Journal of Tropical Ecology*, **19**: 619 627.
- Denslow, J.S., 1980, Gap Partitioning among Tropical Rainforest Trees. *Biotropica*, **12** (Suppl.): 47 – 55.
- Denslow, J.S., 1995, Disturbance and diversity in tropical rain forests: the density effect. *Ecological Applications*, **5**: 962 968.
- Devlaeminck, R., Bossuyt, B. and Hermy, M., 2005, Inflow of seeds through the forest edge: evidence from seed bank and vegetation patterns. *Plant Ecology*, **176**: 1 17.
- Dewalt, S.J., Schnitzer, S.T. and Denslow, J.S., 2000, Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *Journal of Tropical Ecology*, 16: 1 – 19.
- Didham, R.K., 1998, Altered leaf-litter decomposition rates in tropical forest fragments. *Oecologia*, **116**: 397 – 406.
- Didham, R.K. and Lawton, J.H., 1999, Edge Structure Determines the Magnitude of Changes in Microclimate and Vegetation Structure in Tropical Forest Fragments. *Biotropica*, **31**: 17 – 30.
- Drake, D.R. and Pratt, L.W., 2001, Seedling Mortality in Hawaiian Rain Forest: the Role of Small-Scale Physical Disturbance. *Biotropica*, **33**: 319 323.
- Dudash, M.R. and Fenster, C.B., 2000, Inbreeding and outbreeding depression in fragmented populations. Chapter 3 *in* Young, A.G. and Clarke, G.M., (eds), 2000, *Genetics, Demography and Viability of Fragmented Populations*. Cambridge University Press, Cambridge, pages 35 53.
- Engelbrecht, B.M.J. and Kursar, T.A., 2003, Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia*, **136**: 383 – 393.
- Epps, C.W., Palsboll, P.J., Wehausen, J.D., Roderick, G.K., Ramey, R.R., McCullough, D.R., 2005, Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecology Letters*, 8: 1029 1038.
- Evans, D.R. and Gates, J.E., 1997, Cowbird selection of breeding areas: the role of habitat and bird species abundance. *Wilson Bulletin*, **109**: 470 480.
- Fahrig, L., 2003, Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics, 34: 487 – 515.

- Falster, D.S. and Westoby, M., 2005, Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology*, 93: 521 – 535.
- Ferraz, G., Russell, G.J., Stouffer, P.C., Bierregaard, R.O., Pimm, S.L. and Lovejoy, T.E., 2003, Rates of species loss from Amazonian forest fragments. *Proceedings* of the National Academy of Sciences of the United States of America, 100: 14069 – 14073.
- Ferreira, L.V., 1997, Effects of the duration of flooding on species richness and floristic composition in three hectares in the Jau National Park in floodplain forests in central Amazonia. *Biodiversity and Conservation*, 6: 1353 – 1363.
- Ferreira, L.V. and Stohlgren, T.J., 1999, Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. *Oecologia*, **120**: 582 – 587.
- Fine, P.V.A., 2002, The invasibility of tropical forests by exotic plants. *Journal of Tropical Ecology*, 18: 687 705.
- Floyd, A.G., 1989, *Rainforest Trees of Mainland South-eastern Australia*. Inkata Press, Melbourne.
- Forman, R.T.T. and Alexander, L.E., 1998, Roads and their Major Ecological Effects, Annual Review of Ecology and Systematics, **29**, 207 – 231.
- Fox, B.J., Taylor, J.E., Fox, M.D. and Williams, C.,1997, Vegetation Changes Across Edges of Rainforest Remnants, *Biological Conservation*, 82, 1-13.
- Freidenburg, L.K., 1998, Physical Effects of Habitat Fragmentation, Chapter 4 in Fiedler, P.L. and Kereiva, P.M., (eds), 1998, *Conservation biology for the coming decade* (Second Edition). Chapman and Hall, New York, pages 66 – 79.
- Garcia-Guzman, G. and Dirzo, R., 2001, Patterns of leaf-pathogen infection in the understorey of a Mexican rain forest: incidence, spatiotemporal variation, and mechanisms of infection. *American Journal of Botany*, 88: 634 – 645.
- Gascon, C., Lovejoy, T.E., Bierregaard, R.O., Malcolm, J.R., Stouffer, P.C.,
 Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M. and Borges, S.,
 1999, Matrix habitat and species richness in tropical forest remnants. *Biological Conservation*, 91: 223 – 229.
- Gascon, C., Williamson, G.B. and da Fonseca, G.A.B., 2000, Receding Forest Edges and Vanishing Reserves. *Science*, **288**: 1356 1358.

- Gates, J.E. and Evans, D.R., 1998, Cowbirds breeding in the Central Appalachians: Spatial and temporal patterns and habitat selection. *Ecological Applications*, **8**: 27 – 40.
- Gehlhausen, S. M., Schwartz, M.W. and Augspurger, C.K., 2000, Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecology*, 147: 21 – 35.
- Gentle, C.B. and Duggin, J.A., 1997, Allelopathy as a competitive strategy in persistent thickets of *Lantana camara* L. in three Australian forest communities. *Plant Ecology*, **132**: 85 – 95.
- Giambelluca, T.W., Ziegler, A.D., Nullet, M.A., Truong, D.M. and Tran, L.T., 2003, Transpiration in a small tropical forest patch. *Agricultural and Forest Meteorology*, **117**: 1 – 22.
- Gillman, L.N., Ogden, J., Wright, S.D., Stewart, K.L. and Walsh, D.P., 2004, The influence of macro-litterfall and forest structure on litterfall damage to seedlings. *Austral Ecology*, 29: 305 – 312.
- Gillman, L.N. and Ogden, J., 2005, Microsite heterogeneity in litterfall risk to seedlings. *Austral Ecology*, **30**: 497 – 504.
- Gillman, L.N., Wright, S.D. and Ogden, J., 2002, Use of artificial seedlings to estimate damage of forest seedlings due to litterfall and animals. *Journal of Vegetation Science*, **13**: 635 – 640.
- Gillman, L.N., Wright, S.D. and Ogden, J., 2003, Response of forest tree seedlings to simulated litterfall damage. *Plant Ecology*, **169**: 53 60.
- Goldingay, R.L. and Whelan, R.J., 1997, Powerline Easements: do They Promote Edge Effects in Eucalypt Forest for Small Mammals? *Wildlife Research*, 24: 737 – 744.
- Gonzalez, A. and Chaneton, E.J., 2002, Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. *Journal of Animal Ecology*, **71**: 594 – 602.
- Goosem, M., 1997, Internal Fragmentation: The Effects Roads, Highways, and Powerline Clearings on Movements and Mortality of Rainforest Vertebrates, Chapter 16 *in* Laurance, W.F. and Bierregaard, R.O., (eds), 1997, *Tropical Forest Remnants, Ecology, Management, and Conservation of Fragmented Communities*. The University of Chicago Press, Chicago, pages 241-255.

- Goosem, M., 2000, Effects of tropical rainforest roads on small mammals: edge changes in community composition. *Wildlife Research*, **27**: 151 163.
- Goosem, M., 2001, Effects of tropical rainforest roads on small mammals: inhibition of crossing movements. *Wildlife Research*, **28**: 351 364.
- Goosem, M., 2002, Effects of tropical roads on small mammals: fragmentation, edge effects and traffic disturbance. *Wildlife Research*, **29**: 277 289.
- Goosem, M., 2004, Linear infrastructure in the tropical rainforests of far north Queensland: mitigating impacts on fauna of roads and powerline clearings. In Lunney, D., (ed.), 2004, *Conservation of Australia's Forest Fauna* (second edition). Royal Zoological Society of New South Wales, Mosman, Australia. Pages 418 – 434.
- Goosem, M. and Marsh, H., 1997, Fragmentation of a Small-mammal Community by a Powerline Corridor through Tropical Rainforest. *Wildlife Research*, 24: 613 – 629.
- Gregory, S.V., Swanson, F.J., McKee, W.A. and Cummins, K.W., 1991, An Ecosystem Perspective of Riparian Zones. *BioScience*, **41**: 540 551.
- Guilherme, F.A.G., Oliveira-Filho, A.T., Appolinario, V. and Bearzoti, E., 2004, Effects of flooding regime and woody bamboos on tree community dynamics in a section of tropical semideciduous forest in South-Eastern Brazil. *Plant Ecology*, 174: 19 36.
- Guariguata, M.R., 1998, Response of forest tree saplings to experimental mechanical damage in lowland Panama. *Forest Ecology and Management*, **102**: 103 111.
- Guimaraes, P.R. Jr. and Cogni, R., 2002, Seed cleaning of *Cupania vernalis*(Sapindaceae) by ants: edge effects in a highland forest in south-east Brazil. *Journal of Tropical Ecology*, 18: 303 307.
- Guirado, M., Pino, J. and Roda, F., 2006, Understorey plant species richness and composition in metropolitan forest archipelagos: effects of forest size, adjacent land use and distance to the edge. *Global Ecology and Biogeography*, 15: 50 62.
- Hansen, M.J. and Clevenger, A.P., 2005, The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. *Biological Conservation*, **125**: 249 – 259.
- Harding, E.K. and Gomez, S., 2006, Positive edge effects for arboreal marsupials: an assessment of potential mechanisms. *Wildlife Research*, **33**: 121 129.

- Harper, K.A., Lesieur, D., Bergeron, Y. and Drapeau, P., 2004, Forest structure and composition at young fires and cut edges in black spruce boreal forest. *Canadian Journal of Forest Research*, 34: 289 – 302.
- Harper, K.A. and Macdonald, S.E., 2002, Structure and composition of edges next to regenerating clear-cuts in mixed-wood boreal forest. *Journal of Vegetation Science*, 13: 535 – 546.
- Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S. and Esseen, P., 2005, Edge Influence on Forest structure and Composition in Fragmented Landscapes. *Conservation Biology*, **19**: 768 – 782.
- Harrington, G.N., Freeman, A.N.D. and Crome, F.H.J., 2001, The effects of fragmentation of an Australian tropical rain forest on populations and assemblages of small mammals. *Journal of Tropical Ecology*, **17**: 225 – 240.
- Harrington, G.N., Irvine, A.K., Crome, F.H.J. and Moore, L.A., 1997, Regeneration of Large-Seeded Trees in Australian Rainforest Fragments: A Study of Higher-Order Interactions, Chapter 19 *in* Laurance, W.F. and Bierregaard, R.O., (eds), 1997, *Tropical Forest Remnants, Ecology, Management, and Conservation of Fragmented Communities*. The University of Chicago Press, Chicago, pages 292-303.
- Hartley, M.J. and Hunter, M.L. Jr., 1998, A Meta-Analysis of Forest Cover, Edge Effects, and Artificial Nest Predation Rates. *Conservation Biology*, **12**: 465 – 469.
- Haskell, D.G., 2000, Effects of forest roads on macroinvertebrate soil fauna of the southern Appalachian Mountains. *Conservation Biology*, **14**: 57 63.
- Hegarty, E.E., 1991, Leaf litter production by lianas and trees in a sub-tropical Australian rain forest. *Journal of Tropical Ecology*, 7: 201 214.
- Hibbs, D.E. and Bower, A.L., 2001, Riparian forests in the Oregon Coast Range. *Forest Ecology and Management*, **154**: 201 – 213.
- Holsinger, K.E., 2000, Demography and extinction in small populations. Chapter 4 *in* Young, A.G. and Clarke, G.M., (eds), 2000, *Genetics, Demography and Viability of Fragmented Populations*. Cambridge University Press, Cambridge, pages 55 – 72.
- Honnay, O., Verhaeghe, W. and Hermy, M., 2001, Plant community assembly along dendritic networks of small forest streams. *Ecology*, 82: 1691 – 1702.

- Honnay, O., Verheyen, K. and Hermy, M., 2002, Permeability of ancient forest edges for weedy plant species invasion. *Forest Ecology and Management*, **161**: 109 – 122.
- Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B.,
 Wright, S.J. and Loo de Lao, S.,1999, Light-Gap Disturbances, Recruitment
 Limitation, and Tree Diversity in a Neotropical Forest. *Science*, 283: 554 557.
- Hupp, C.R. and Osterkamp, W.R., 1996, Riparian vegetation and fluvial geomorphic processes. *Geomorphology*, 14: 277 – 295.
- Hyland, B.P.M., 1989, A Revision of Lauraceae in Australia (excluding *Cassytha*), *Australian Systematic Botany*, **2**: 135 367.
- Hyland, B.P.M., Whiffin, T., Christophel, D.C., Gray, B. and Elick, R.W., 2003, Australian Tropical Rain Forest Plants: Trees, Shrubs and Vines. CSIRO Publishing, Collingwood, Australia.
- Jackes, B.R. and Cairns, A., 2001, *Plants of the Tropics; Rainforest to Heath; An Identification Guide*. James Cook University, Townsville, Australia.
- Jacquemyn, H., Butaye, J. and Hermy, M., 2001, Forest plant species richness in small, fragmented mixed deciduous forest patches: the role of area, time and dispersal limitation. *Journal of Biogeography*, 28: 801 – 812.
- Jansson, R., Zinko, U., Merritt, D.M. and Nilsson, C., 2005, Hydrochory increases riparian plant species richness: a comparison between a free-flowing and a regulated river. *Journal of Ecology*, **93**: 1094 – 1103.
- Janzen, D.H., 1970, Herbivores and the number of tree species in tropical forests. *American Naturalist*, **104**: 501 – 528.
- Jones, D.L. and Clemesha, S.C., 1980, *Australian Ferns and Fern Allies*. Second Edition. The Currawong Press, Sydney, Australia.
- Jones, H. G., 1992, *Plants and microclimate: a quantitative approach to environmental plant physiology*. Second Edition. Cambridge University Press, Cambridge.
- Jules, E. S. and Rathcke, B.J., 1999, Mechanisms of Reduced Trillium Recruitment along Edges of Old-Growth forest Fragments. *Conservation Biology*, 13: 784 – 793.
- Jules, E.S. and Shahani, P., 2003, A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought. *Journal of Vegetation Science*, 14: 459 – 464.

- Kapos, V., 1989, Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology*, **5**: 173 185.
- Kapos, V., Ganade, G., Matsui, E. and Victoria, R.L., 1993, ∂¹³C as an indicator of edge effects in tropical rainforest reserves. *Journal of Ecology*, 81: 425 – 432.
- Kapos, V., Wandelli, E., Camargo, J.L. and Ganade, G.,1997, Edge-Related Changes in Environment and Plant Resources Due to Forest Fragmentation in Central Amazonia, Chapter 3 *in* Laurance, W.F. and Bierregaard, R.O., (eds), 1997, *Tropical Forest Remnants, Ecology, Management, and Conservation of Fragmented Communities*. The University of Chicago Press, Chicago, pages 33-44.
- Kellman, M., Tackaberry, R. and Rigg, L., 1998, Structure and function in two tropical gallery forest communities: implications for forest conservation in fragmented systems. *Journal of Applied Ecology*, **35**: 195 – 206.
- Kelly, D., Ladley, J.J., Robertson, A.W. and Norton, D.A., 2000, Limited forest fragmentation improves reproduction in the declining New Zealand mistletoe Peraxilla tetrapetala (Loranthaceae). Chapter 14 *in* Young, A.G. and Clarke, G.M., (eds), 2000, *Genetics, Demography and Viability of Fragmented Populations*. Cambridge University Press, Cambridge, pages 241 252.
- King, D.I. and DeGraaf, R.M., 2002, The Effect of Forest Roads on the Reproductive Success of Forest-Dwelling Passerine Birds. *Forest Science*, **48**: 391 396.
- Kira, T. and Yoda, K., 1989, Vertical Stratification in Microclimate, Chapter 3 *In* Lieth,
 H. and Werger, M.J.A., (eds), *Tropical Rain Forest Ecosystems*, Volume 2.
 Elsevior Science Publishing Company Inc., Amsterdam, The Netherlands, pages 55 71.
- Kitajima, K., 1994, Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, **98**: 419 – 428.
- Kobe, R.K., 1999, Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology*, **80**: 187 201.
- Kolb, A. and Diekmann, M., 2005, Effects of Life-History Traits on Response of Plant Species to Forest Fragmentation. *Conservation Biology*, **19**: 929 – 938.
- Kollman, J. and Buschor, M., 2003, Edge effects on seed predation by rodents in deciduous forests of northern Switzerland. *Plant Ecology*, **164**: 249 – 261.

- Korning, J. and Balslev, H., 1994, Growth and mortality of trees in Amazonian tropical rain forest in Ecuador. *Journal of Vegetation Science*, **4**: 77 86.
- Kupfer, J.A., Malanson, G.P. and Franklin, S.B., 2006, Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography*, **15**: 8 – 20.
- Larsen, T.H., Williams, N.M. and Kremen, C., 2005, Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, 8: 538 – 547.
- Laurance, W.F., 1991, Edge Effects in Tropical Forest Fragments: Applications of a Model for the Design of Nature Reserves. *Biological Conservation*, 57: 205 – 219.
- Laurance, W.F., 1994, Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. *Biological Conservation*, **69**: 23 32.
- Laurance, W.F., 1997a, Hyper-Disturbed Parks: Edge Effects and the Ecology of Isolated Rainforest Reserves in Tropical Australia, Chapter 6 *in* Laurance, W.F. and Bierregaard, R.O., (eds), 1997, *Tropical Forest Remnants, Ecology, Management, and Conservation of Fragmented Communities*. The University of Chicago Press, Chicago, pages 71 – 82.
- Laurance, W.F., 1997b, Responses of Mammals to Rainforest Fragmentation in Tropical Queensland: a Review and Synthesis. *Wildlife Research*, **24**: 603 – 612.
- Laurance, W.F., 1998, Fragments of the forest. (A report from scientists studying forest fragmentation in the Amazonia, part of the Biological Dynamics of Forest Fragments Project). *Natural History*, **107**: 35 – 38.
- Laurance, W.F., 2001, Fragmentation and Plant Communities, Chapter 13 in
 Bierregaard, R.O., Gascon, C., Lovejoy, T.E. and Mesquita, R.C.G., (eds), 2001,
 Lessons from Amazonia, The Ecology and conservation of a fragmented forest.
 Yale University Press, New Haven, pages 158 167.
- Laurance, W.F. and Bierregaard, R.O., (eds), 1997, Tropical Forest Remnants, Ecology, Management, and Conservation of Fragmented Communities. The University of Chicago Press, Chicago.
- Laurance, W.F., Laurance, S.G., Ferreira, L.V., Rankin-de Merona, J.M., Gascon, C. and Lovejoy, T.E., 1997, Biomass Collapse in Amazonian forest fragments. *Science*, 278: 1117 – 1118.

- Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M. and Laurance, S.G., 1998a, Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* **79**: 2032 – 2040.
- Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M., Laurance, S.G., Hutchings,
 R.W. and Lovejoy, T.E., 1998b, Effects of Forest Fragmentation on Recruitment
 Patterns in Amazonian tree Communities. *Conservation Biology*, 12: 460 464.
- Laurance, W.F., Delamonica, P., Laurance, S.G., Vasconcelos, H.L. and Lovejoy, T.E., 2000, Rainforest fragmentation kills big trees. *Nature*, **404**: 836.
- Laurance, W.F., Perez-Salicrup, D., Delamonica, P., Fearnside, P.M., D'Angelo, S., Jerozolinski, A., Pohl, L. and Lovejoy, T., 2001a, Rain forest fragmentation and the structure of Amazon liana communities. *Ecology*, 82: 105 – 116.
- Laurance, W.F., Williamson, G.B., Delamonica, P., Oliveira, A., Lovejoy, T.E., Gascon, C. and Pohl, L., 2001b, Effects of a strong drought on Amazonian forest fragments and edges. *Journal of Tropical Ecology*, **17**: 771 – 785.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K.,
 Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G. and Sampaio, E.,
 2002, Ecosystem Decay of Amazonian forest Fragments: a 22-Year
 Investigation. *Conservation Biology*, 16: 605 618.
- Laurance, W.F., Rankin-de Merona, J.M., Andrade, A., Laurance, S.G., D'Angelo, S., Lovejoy, T.E. and Vasconcelos, H.L., 2003, Rain-forest fragmentation and the phenology of Amazonian tree communities. *Journal of Tropical Ecology*, 19: 343 – 347.
- Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A.C., Fearnside, P.M., Ribeiro, J.E.L. and Capretz, R.L., 2006, Rain forest fragmentation and the proliferation of successional trees. *Ecology*, 87: 469 – 482.
- Lazarides, M., Cowley, K. and Hohnen, P., 1997, *CSIRO Handbook of Australian Weeds*. CSIRO Publishing, Collingwood, Australia.
- Leigh, E.G., Wright, S.J., Herre, E.A. and Putz, F.E., 1993, The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications. *Evolutionary Ecology*, 7: 76 – 102.
- Lewis, S.L., Malhi, Y. and Phillips, O.L., 2004, Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society of London B*, **359**: 437 462.

- Lieberman, D., Lieberman, M., Hartshorn, G. and Peralta, R., 1985, Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. *Journal of Tropical Ecology*, 1: 97 – 109.
- Lindenmayer, D. and Peakall, R., 2000, The Tumut experiment integrating demographic and genetic studies to unravel fragmentation effects: a case study of the native bush rat. Chapter 10 *in* Young, A.G. and Clarke, G.M., (eds), 2000, *Genetics, Demography and Viability of Fragmented Populations*. Cambridge University Press, Cambridge, pages 173 – 201.
- Lott, R.H., Harrington, G.N., Irvine, A.K. and McIntyre, S., 1995, Density-dependent Seed Predation and Plant Dispersion of the Tropical Palm *Normanbya normanbyi*. *Biotropica*, 27: 87 – 95.
- Lovei, G.L., Magura, T., Tothmeresz, B. and Kodobocz, V., 2006, The influence of matrix and edges on species richness patterns of ground beetles (Coleoptera: Carabidae) in habitat islands. *Global Ecology and Biogeography*, 15: 283 289.
- Lusk, C.H. and Del Pozo, A., 2002, Survival and growth of seedlings of 12 Chilean rainforest trees in two light environments: Gas exchange and biomass distribution correlates. *Austral Ecology*, **27**: 173 – 182.
- Mack, A.L., 1998, The Potential Impact of Small-Scale Physical Disturbance on Seedlings In a Papuan Rainforest. *Biotropica*, **30**: 547 552.
- Malcolm, J.R., 1994, Edge Effects in Central Amazonian Forest Fragments. *Ecology*, **75**: 2438 2445.
- Malcolm, J.R., 1998, A model of conductive heat flow in forest edges and fragmented landscapes. *Climatic Change*, **39**: 487 502.
- Malcolm, J.R. and Ray, J.C., 2000, Influence of Timber Extraction Routes on Central African Small-Mammal Communities, Forest Structure, and Tree Diversity. *Conservation Biology*, 14: 1623 – 1638.
- Marrinan, M.J., Edwards, W. and Landsberg, J., 2005, Resprouting of saplings following a tropical rainforest fire in north-east Queensland, Australia. *Austral Ecology*, **30**: 817 – 826.
- Marsh. D.M., and Beckman., N.G., 2004, Effects of forest roads on the abundance and activity of terrestrial salamanders. *Ecological Applications*, **14**: 1882 1891.
- Martinez-Ramos, M., Alvarez-Buylla, E., Sarukhan, J. and Pinero, D., 1988, Treefall age determination and gap dynamics in a tropical forest. *Journal of Ecology*, **76**: 700 716.

- Matlack, G.R., 1993, Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation*, **66**: 185 194.
- Matlack, G.R., 1994, Vegetation dynamics of the forest edge trends in space and successional time, *Journal of Ecology*, **82**; 113 123.
- McDonald, R.I. and Urban, D.L., 2004, Forest edges and tree growth rates in the North Carolina Piedmont. *Ecology*, **85**: 2258 2266.
- Meiners, S.J., Handel, S.N. and Pickett, S.T.A., 2000, Tree seedling establishment under insect herbivory: edge effects and inter-annual variation. *Plant Ecology*, 151: 161-170.
- Mesquita, R.C.G., Delamonica, P. and Laurance, W.F., 1999, Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biological Conservation*, **91**: 129 – 134.
- Michalski, F. and Peres, C.A., 2005, Anthropogenic determinants of primate and carnivore extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation*, **124**: 383 – 396.
- Moles, A.T. and Westoby, M., 2004, Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology*, **92**: 372 383.
- Moles, A.T. and Westoby, M., 2006, Seed size and plant strategy across the whole life cycle. *Oikos*, **11**3: 91 105.
- Mourelle, C., Kellman, M. and Kwon, L., 2001, Light occlusion at forest edges: an analysis of tree architectural characteristics. *Forest Ecology and Management*, 154: 179 192.
- Murcia, C., 1995, Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution*, **10**: 58-62.
- Murray, B.R., Kelaher, B.P., Hose, G.C. and Figueira, W.F., 2005, A meta-analysis of the interspecific relationship between seed size and plant abundance within local communities. *Oikos*, **110**: 191 – 194.
- Murren, C.J., 2002, Effects of habitat fragmentation on pollination: pollinators, pollinia viability and reproductive success. *Journal of Ecology*, **90**: 100 107.
- Murren, C.J., 2003, Spatial and demographic population genetic structure in *Catasetum viridiflavum* across a human-disturbed habitat. *Journal of Evolutionary Biology*, 16: 333 342.

- Nagaike, T., 2003, Edge Effects on Stand Structure and Regeneration in a Subalpine Coniferous Forest on Mt. Fuji, Japan, 30 Years after Road Construction. *Arctic, Antarctic, and Alpine Research*, **35**: 454 – 459.
- Nakamura, F., Yajima, T. and Kikuchi, S., 1997, Structure and composition of riparian forests with special reference to geomorphic site conditions along the Tokachi River, northern Japan. *Plant Ecology*, **133**: 209 – 219.
- Nascimento, H.E., Andrade, A.C.S., Camargo, J.L.C., Laurance, W.F., Laurance, S.G. and Ribeiro, J.E.L., 2006, Effects of the Surrounding Matrix on Tree Recruitment in Amazonian Forest Fragments. *Conservation Biology*, **20**: 853 – 860.
- Nascimento, H.E.M. and Laurance, W.F., 2004, Biomass dynamics in Amazonian forest fragments. *Ecological Applications*, **14**: S127 S138.
- Nascimento, H.E.M., Laurance, W.F., Condit, R., Laurance, S.G., D'Angelo, S. and Andrade, A.C., 2005, Demographic and life-history correlates for Amazonian trees. *Journal of Vegetation Science*, **16**: 625 – 634.
- Nelson, C.R. and Halpern, C.B., 2005, Edge-related responses of understory plants to aggregated retention harvest in the Pacific Northwest. *Ecological Applications*, 15: 196 209.
- Ness, J.H., 2004, Forest edges and fire ants alter the seed shadow of an ant-dispersed plant. *Oecologia*, **138**: 448 454.
- Newmark, W.D., 2001, Tanzanian Forest Edge Microclimatic Gradients: Dynamic Patterns. *Biotropica*, **33**: 2-11.
- Newmark, W., 2005, Diel variation in the difference in air temperature between the forest edge and interior in the Usambara Mountains, Tanzania. *African Journal of Ecology*, **43**: 177 180.
- Nichol, J.E., 1994, An examination of tropical rain forest microclimate using GIS modelling. *Global Ecology and Biogeography Letters*, **4**: 69 78.
- Nicotra, A.B., Chazdon, R.L. and Iriarte, S.V.B., 1999, Spatial Heterogeneity of Light and Woody Seedling Regeneration in Tropical Wet Forests, *Ecology*, **80**: 1908 – 1926.
- Nilsson, C., Ekblad, A., Dynesius, M., Backe, S., Gardfjell, M., Carlberg, B., Hellqvist, S. and Jansson, R., 1994, A comparison of species richness and traits of riparian plants between a main river channel and its tributaries. *Journal of Ecology*, 82: 281 295.

- Nilsson, C. and Svedmark, M., 2002, Basic Principles and Ecological consequences of changing Water Regimes: Riparian Plant Communities. *Environmental Management*, **30**: 468 – 480.
- Oke, T.R., 1987, Boundary Layer Climates, Second Edition. Methuen, New York, USA.
- Olander, L.P., Scatena, F.N. and Silver., W.L., 1998, Impacts of disturbance initiated by road construction in a subtropical cloud forest in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology and Management*, **109**: 33 49.
- Ortega, Y.K. and Capen, D.E., 2002, Roads as edges: Effects on birds in forested landscapes. *Forest Science*, **48**: 381 390.
- Osunkoya, O.O., 1994, Postdispersal survivorship of north Queensland rainforest seeds and fruits: Effects of forest, habitat and species. *Australian Journal of Ecology*, **19**: 52 – 64.
- Osunkoya, O.O., 1996, Light requirements for regeneration in tropical forest plants: Taxon-level and ecological attribute effects. *Australian Journal of Ecology*, **21**: 429 – 441.
- Osunkoya, O.O., Ash, J.E., Hopkins, M.S. and Graham, A.W., 1992, Factors affecting the survival of tree seedlings in North Queensland rainforests. *Oecologia*, **91**: 569 – 578.
- Osunkora, O.O., Ash, J.E., Graham, A.W. and Hopkins, M.S., 1993, Growth of tree seedlings in tropical rain forests of North Queensland, Australia. *Journal of Tropical Ecology*, **9**: 1 18.
- Osunkoya, O.O., Ash, J.E., Hopkins, M.S. and Graham, A.W., 1994, Influence of seed size and seedling ecological attributes on shade-tolerance of rain-forest tree species in northern Queensland. *Journal of Ecology*, **82**: 149 163.
- Paciencia, M.L.B. and Prado, J., 2005, Effects of forest fragmentation on pteridophyte diversity in a tropical forest in Brazil. *Plant Ecology*, **180**: 87 104.
- Pallant, J.F., 2005, SPSS Survival Manual: a step by step guide to data analysis using SPSS (2nd Edition). Allen and Unwin, Crows Nest, Australia.
- Parendes, L.A. and Jones, J.A., 2000, Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. *Conservation Biology*, 14: 64 – 75.
- Parsons, W.T. and Cuthbertson, E.G., 2001, *Noxious Weeds of Australia*. Second Edition. CSIRO Publishing, Collingwood, Australia.

- Pauw, A., Van Beel, S.A., Peters, H.A., Allison, S.D., Camargo, J.L.C., Cifuentes-Jara, M., Conserva, A., Restom, T.G., Heartsill-Scalley, T., Mangan, S.A., Nunez-Iturri, G., Rivera-Ocasio, E., Rountree, M., Vetter, S. and de Castilho, C.V., 2004, Physical Damage in Relation to Carbon Allocation Strategies of Tropical Forest Tree Saplings. *Biotropica*, 36: 410 413.
- Peltonen, M., 1999, Windthrows and Dead-standing Trees as Bark Beetle Breeding Material at Forest-clearcut Edge. *Scandinavian Journal of Forest Research*, 14: 505 – 511.
- Peters, H.A., Pauw, A., Silman, M.R. and Terborgh, J.W., 2004, Falling palm fronds structure Amazonian rainforest sapling communities. *Proceedings of the Royal Society B (Supplemental)*, 271: S367 – S369.
- Pettit, N.E. and Froend, R.H., 2001, Availability of seed for recruitment of riparian vegetation: a comparison of a tropical and a temperate river ecosystem in Australia. *Australian Journal of Botany*, **49**: 515 – 528.
- Philips, O.L., Hall, P., Gentry, A.H., Sawyer, S.A. and Vasquez, R., 1994, Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of Sciences of the United States of America*, **91**: 2805 – 2809.
- Phillips, O.L., Martinez, R.V., Arroyo, L., Baker, T.R., Killeen, T., Lewis, S.L., Malhi, Y., Mendoza, A.M., Neill, D., Vargas, P.N., Alexiadea, M., Ceron, C., Di Fiore, A., Erwin, T., Jardim, A., Palacios, W., Saldias, M. and Vinceti, B., 2002, Increasing dominance of large lianas in Amazonian forests. *Nature*, 418: 770 774.
- Phillips, O.L., Martinez, R.V., Mendoza, A.M., Baker, T.R. and Vargas, P.N., 2005, Large lianas as hyperdynamic elements of the tropical forest canopy. *Ecology*, 86: 1250 – 1258.
- Poorter, L., 1999, Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology*, **13**: 396 410.
- Potter, B.E., Teclaw, R.M. and Zasada, J.C., 2001, The impact of forest structure on near-ground temperatures during two years of contrasting temperature extremes. *Agricultural and Forest Meteorology*, **106**: 331 – 336.
- Primack, R.B., 1993, *Essentials of Conservation Biology*. Sinauer Associates, Inc., Massachusetts.

- Putz, F.E., 1984, The natural history of lianas on Barro Colorado Island, Panama. *Ecology*, **65**: 1713 1724.
- Putz, F.E., 1990, Growth Habits and Trellis Requirement of Climbing Palms (*Calamus* spp.) in North-eastern Queensland. *Australian Journal of Botany*, **38**: 603 608.
- Rankin-de Merona, J.M. and Hutchings, R.W.H., 2001, Deforestation Effects at the Edge of an Amazonian Forest Fragment. Chapter 9 *in* Bierregaard, R.O., Gascon, C., Lovejoy, T.E. and Mesquita, R.C.G., (eds), 2001, *Lessons from Amazonia, The Ecology and conservation of a fragmented forest*. Yale University Press, New Haven, pages 107 120.
- Rao, M., Terborgh, J. and Nunez, P., 2001, Increased Herbivory in Forest Isolates: Implications for Plant Community Structure and Composition. *Conservation Biology*, 15: 624 – 633.
- Restrepo, C. and Gomez, N., 1998, Responses of understorey birds to anthropogenic edges in a Neotropical montane forest. *Ecological Applications*, **8**: 170 183.
- Restrepo, C., Gomez, N. and Heredia, S., 1999, Anthropogenic edges, treefall gaps, and fruit-frugivore interactions in a Neotropical montane forest. *Ecology*, 80: 668 – 685.
- Reynolds, B.E., 1994, A study of weed (Lantana camara) infestation of tracks through rainforest on the Atherton Tableland, North Queensland. Unpublished Honours Thesis, James Cook University.
- Rheault, H., Drapeau, P., Bergeron, Y. and Esseen, P.A., 2003, Edge effects on epiphytic lichen in managed black spruce forest of eastern North America. *Canadian Journal of Forest Research*, **33**: 23 – 32.
- Richards, C.M., 2000, Genetic and demographic influences on population persistence:
 gene flow and genetic rescue in *Silene alba*. Chapter 16 *in* Young, A.G. and
 Clarke, G.M., (eds), 2000, *Genetics, Demography and Viability of Fragmented Populations*. Cambridge University Press, Cambridge, pages 271 291.
- Ries, L., Fletcher, R.J. Jr., Battin, J. and Sisk, T.D., 2004, Ecological Responses to Habitat Edges: Mechanisms, Models, and Variability Explained. *Annual Review* of Ecology, Evolution and Systematics, 35: 491 – 522.
- Robertson, K.M. and Augspurger, C.K., 1999, Geomorphic processes and spatial patterns of primary forest succession on the Bogue Chitto River, USA. *Journal* of Ecology, 87: 1052 – 1063.

- Roldan, A.I. and Simonetti, J.A., 2001, Plant-Mammal Interactions in Tropical Bolivian Forests with Different Hunting Pressures. *Conservation Biology*, **15**: 617 – 623.
- Rubinstein, A. and Vasconcelos, H.L., 2005, Leaf-litter decomposition in Amazonian forest fragments. *Journal of Tropical Ecology*, **21**: 699 702.
- Russell, W.H. and McBride, J.R., 2001, The relative importance of fire and watercourse proximity in determining stand composition in mixed conifer riparian forests. *Forest Ecology and Management*, **150**: 259 265.
- Sabo, J.L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Heffernan, J., Jani, A., Katz, G., Soykan, C., Watts, J. and Welter, J., 2005, Riparian zones increase regional species richness by harboring different, not more, species. *Ecology*, 86: 56 62.
- Salo, J., Kalliola, R., Hakkinene, I., Makinen, Y., Niemela, P., Puhakka, M. and Coley,
 P.D., 1986, River dynamics and the diversity of Amazon lowland forest. *Nature*,
 322: 254 258.
- Scariot, A., 2000, Seedling Mortality by Litterfall in Amazonian Forest Fragments. *Biotropica*, **32**: 662 – 669.
- Scariot, A., 2001, Effects of Landscape Fragmentation on Palm Communities. Chapter 10 *in* Bierregaard, R.O., Gascon, C., Lovejoy, T.E. and Mesquita, R.C.G., (eds), 2001, *Lessons from Amazonia, The Ecology and conservation of a fragmented forest.* Yale University Press, New Haven, pages 121 135.
- Scatena, F.N. and Lugo, A.E., 1995, Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steepland watersheds of Puerto Rico. *Geomorphology*, 13: 199 – 213.
- Schlaepfer, M.A. and Gavin, T.A. 2001, Edge Effects on Lizards and Frogs in Tropical forest Fragments. *Conservation Biology*, **15**: 1079 – 1090.
- Schnitzer, S.A., 2005, A Mechanistic Explanation for Global Patterns of Liana Abundance and Distribution. *The American Naturalist*, **166**: 262 – 276.
- Schnitzer, S.A. and Bongers, F., 2002, The ecology of lianas and their role in forests. *Trends in Ecology and Evolution*, **17**: 223 230.
- Schnitzer, S.A. and Carson, W.P., 2001, Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology*, **82**: 913 919.
- Schnitzer, S.A., Dalling, J.W. and Carson, W.P., 2000, The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology*, 88: 655 – 666.

- Schnitzer, S.A., Kuzee, M.E. and Bongers, F., 2005, Disentangling above-and belowground competition between lianas and trees in a tropical forest. *Journal of Ecology*, 93: 1115 – 1125.
- Siegenthaler, S.L., 1999, Impacts of roads and powerline corridors on microclimate and understorey vegetation in the Wet Tropics of Queensland World Heritage Area. Honours thesis, School of Tropical Environment Studies & Geography, James Cook University.
- Siegenthaler, S., and Turton, S.M., 2000, Edge effects of roads and powerlines on microclimate. *In* M. Goosem, and S. M. Turton, (Eds). *Impacts of Roads and Powerlines on the Wet Tropics of Queensland World Heritage Area*. Wet Tropics Management Authority and Rainforest CRC Report, James Cook University, pages 19 43. Available online at http://www.rainforest-crc.jcu.edu.au/reports.htm.
- Sizer, N.C., Tanner, E.V.J. and Kossmann Ferraz, I.D., 2000, Edge effects on litterfall mass and nutrient concentrations in forest fragments in central Amazonia, *Journal of Tropical Ecology*, 16, 853-863.
- Sizer, N. and Tanner, E.V.J., 1999, Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. *Biological Conservation*, 91: 135 – 142.
- Skole, D. and Tucker, C., 1993, Tropical Deforestation and Habitat Fragmentation in the Amazon: Satellite Data from 1978 to 1988. *Science*, **260**: 1905 – 1910.
- Smith, W.J., Kynaston, W.T., Cause, M.L. and Grimmett, J.G., 1991, Building Timbers: Properties and Recommendations for their Use in Queensland. Technical Pamphlet No. 1. Queensland Forest Service, Department of Primary Industries, Indooroopilly.
- Strahan, R. (ed.), 1995, *The Mammals of Australia*. Second Edition. Reed Books Australia, Chatswood, New South Wales.
- Sturman, A.P. and Tapper, N.J., 1996, *The Weather and Climate of Australia and New Zealand*. Oxford University Press, Melbourne, Australia.
- Tabarelli, M., Mantovani, W. and Peres, C.A., 1999, Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation*, 91: 119 – 127.

- Tallmon, D.A., Jules, E.S., Radke, N.J. and Mills, L.S., 2003, Of mice and men and trillium: cascading effects of forest fragmentation. *Ecological Applications*, 13: 1193 – 1203.
- TASCO, 2001, *Infrared Thermometer, THI-700L, THI-700S, Instruction Manual.* TASCO Japan Co. Ltd., Osaka, Japan.
- Terborgh, J., Lopez, L., Nunez, P.V., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D. and Balbas, L., 2001, Ecological Meltdown in Predator-Free Forest Fragment. *Science*, **294**: 1923 – 1926.
- Terborgh, J., Feeley, K., Silman, M., Nunez, P. and Balukjian, B., 2006, Vegetation dynamics of predator-free land-bridge islands. *Journal of Ecology*, 94: 253 – 263.
- Theimer, T.C., 2001, Seed scatterhoarding by white-tailed rats: consequences for seedling recruitment by an Australian rain forest tree. *Journal of Tropical Ecology*, **17**: 177 – 189.
- Theimer, T.C. and Gehring, C.A., 1999, Effects of a litter-disturbing bird species on tree seedling germination and survival in an Australian tropical rain forest. *Journal* of Tropical Ecology, 15: 737 – 749.
- Thomas, S.C., 1996, Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. *American Journal of Botany*, 83: 556 – 566.
- Tilman, D., May, R.M., Lehman, C.L. and Nowak, M.A., 1994, Habitat destruction and the extinction debt. *Nature*, **371**: 65 66.
- Tomimatsu, H. and Ohara, M., 2002, Effects of forest fragmentation on seed production of the understorey herb *Trillium camschatcense*. *Conservation Biology*, 16: 1277 – 1285.
- Tomimatsu, H. and Ohara, M., 2003, Floral visitors of *Trillium camschatense* (Trilliaceae) in fragmented forests. *Plant Species Biology*, **18**: 123 127.
- Tracey, J.G., 1982, *The Vegetation of the Humid Tropical Region of North Queensland*. CSIRO, Melbourne.
- Trombulak, S.C. and Frissell, C.A., 2000, Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities. *Conservation Biology*, **14**: 18 – 30.

- Trott, L., Goosem, S. and the Wet Tropics Management Authority, 1996, Wet Tropics in Profile, A Reference Guide to the Wet Tropics of Queensland World Heritage Area. Wet Tropics Management Authority, Cairns, Australia.
- T.S.I. Incorporated, 2002, Model 8345/8346/8347/8347A VelociCalc Air Velocity Meters, Operation and Service Manual, 1980277, Revision E. T.S.I. Incorporated, Shoreview, U.S.A.
- Tucker, N.I.J., 2001, Vegetation recruitment in a restored habitat linkage in tropical North Queensland. Masters Thesis, James Cook University.
- Tucker, N.I.J. and Murphy, T.M., 1997, The effects of ecological rehabilitation on vegetation recruitment: some observations from the Wet Tropics of North Queensland. *Forest Ecology and Management*, **99**: 133 – 152.
- Turner, I.M., 2001, *The Ecology of Trees in the Tropical Rain Forest*. Cambridge University Press, Cambridge, U.K.
- Turner, M.G., Gergel, S.E., Dixon, M.D. and Miller, J.R., 2004, Distribution and abundance of trees in floodplain forests of the Wiisconsin River: Environmental influences at different scales. *Journal of Vegetation Science*, 15: 729 – 738.
- Turton, S. and Freiburger, H.J, 1997, Edge and Aspect Effects on the Microclimate of a Small Tropical Forest Remnant on the Atherton Tableland, Northeastern Australia, Chapter 4 *in* Laurance, W.F. and Bierregaard, R.O., (eds), 1997, *Tropical Forest Remnants, Ecology, Management, and Conservation of Fragmented Communities*. The University of Chicago Press, Chicago, pages 45-54.
- Turton, S. M., Hutchinson, M. F., Accad, A., Hancock, P. E. and Webb, T., 1999, Producing fine-scale rainfall climatology surfaces for Queensland's wet tropics region. *In* Kesby, J.A., Stanley, J.M., McLean, R.F. and Olive, L.J., (eds), 1999, *Geodiversity: Readings in Australian Geography at the close of the 20th Century*. Special Publication Series No. 6, School of Geography and Oceanography, University College, ADFA, Canberra, ACT, Australia, pages 415 – 428.
- Uhl, C., Clark, K., Dezzeo, N. and Maquirino, P., 1988, Vegetation dynamics in Amazonian treefall gaps. *Ecology*, **69**: 751 763.
- Van Pelt, R., O'Keefe, T.C., Latterell, J.J. and Naiman, R.J., 2006, Riparian forest stand development along the Queets River in Olympic National Park, Washington. *Ecological Monographs*, **76**: 277 – 298.

- van Raders, R., 1999, *Rainforest Vines of the Atherton Tablelands; a Field Guide*. Malanda, Australia.
- Vasconcelos, H.L. and Laurance, W.F., 2005, Influence of habitat, litter type, and soil invertebrates on leaf-litter decomposition in a fragmented Amazonian landscape. *Oecologia*, 144: 456 – 462.
- Vasconcelos, H.L. and Luizao, F.J., 2004, Litter production and litter nutrient concentrations in a fragmented Amazonian landscape. *Ecological Applications*, 14: 884 892.
- Vernes, K., Dennis, A. and Winter, J., 2001, Mammalian Diet and Broad Hunting Strategy of the Dingo (*Canis familiaris dingo*) in the Wet Tropical Rain Forests of Northeastern Australia. *Biotropica*, **33**: 339 – 345.
- Vernes, K., Marsh, H. and Winter, J., 1995, Home-range Characteristics and Movement Patterns of the Red-legged Pademelon (*Thylogale stigmatica*) in a Fragmented Tropical Rainforest. *Wildlife Research*, 22: 699 – 708.
- Vitousek, P.M., 1984, Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology*, **65**: 285 298.
- Vos, C.C. and Chardon, J.P., 1998, Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. *Journal of Applied Ecology*, **35**: 44 – 56.
- Wahungu, G.M., Catterall, C.P. and Olsen, M.F., 1999, Selective herbivory by rednecked pademelon *Thylogale thetis* at rainforest margins: factors affecting predation rates. *Australian Journal of Ecology*, 24: 577 – 586.
- Wahungu, G.M., Catterall, C.P. and Olsen, M.F., 2002, Seedling predation and growth at a rainforest – pasture ecotone, and the value of shoots as seedling analogues. *Forest Ecology and Management*, 162: 251 – 260.
- Warburton, N.H., 1997, Structure and Conservation of Forest Avifauna in Isolated Rainforest Remnants in Tropical Australia, Chapter 13 *in* Laurance, W.F. and Bierregaard, R.O., (eds), 1997, *Tropical Forest Remnants, Ecology, Management, and Conservation of Fragmented Communities*. The University of Chicago Press, Chicago, pages 190 – 206.
- Watkins, R.Z., Chen, J., Pickens, J. and Brosofske, K.D., 2003, Effects of Forest Roads on Understorey Plants in a Managed Hardwood Landscape. *Conservation Biology*, **17**: 411 – 419.

- Watson, C.J.J., 1951, North Queensland Building Timbers and Specifications for Their Use. Queensland Forest Service Pamphlet No. 1. Government Printer, Brisbane.
- Webb, C.O. and Peart, D.R., 2000, Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology*, 88: 464 – 478.
- Westcott, D.A., Bentrupperbaumer, J., Bradford, M.G. and McKeown, A., 2005, Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, **146**: 57 – 67.
- Weston, N., and Goosem, S., 2004, Sustaining the Wet Tropics: A Regional Plan for Natural Resource Management. Volume 2A Condition Report: Biodiversity Conservation. Rainforest CRC and FNQ NRM Ltd, Cairns, Australia.
- Whelan, R.J., Ayre, D.J., England, P.R., Llorens, T. and Beyon, F., 2000, Ecology and genetics of *Grevillea* (Proteaceae): implications for conservation of fragmented populations. Chapter 15 *in* Young, A.G. and Clarke, G.M., (eds), 2000, *Genetics, Demography and Viability of Fragmented Populations*. Cambridge University Press, Cambridge, pages 253 269.
- White, E., Tucker, N., Meyers, N. and Wilson, J., 2004, Seed dispersal to revegetated isolated rainforest patches in North Queensland. *Forest Ecology and Management*, **192**: 409 – 426.
- White, G.M. and Boshier, D.H., 2000, Fragmentation in Central American dry forests: genetic impacts on *Swietenia humilis* (Meliaceae). Chapter 17 *in* Young, A.G. and Clarke, G.M., (eds), 2000, *Genetics, Demography and Viability of Fragmented Populations*. Cambridge University Press, Cambridge, pages 293 311.
- Whitmore, T.C., 1996, A review of some aspects of tropical rain forest seedling ecology with suggestions for further enquiry. Chapter 1 *in* Swaine, M.D., (ed.), 1996, *The ecology of tropical forest tree seedlings*. UNESCO Paris and the Parthenon Publishing Group, Paris and New York, pages 3 39.
- Whitmore, T.C., 1997, Tropical Forest Disturbance, Disappearance and Species Loss, Chapter1 in Laurance, W.F. and Bierregaard, R.O., (eds), 1997, Tropical Forest Remnants, Ecology, Management, and Conservation of Fragmented Communities. The University of Chicago Press, Chicago, pages 3-12.
- Williams, K.A.W., 1984, Native Plants of Queensland, Volume 2. National Library of Australia, Canberra, Australia.

- Williams, K.A.W., 1987, Native Plants of Queensland, Volume 3. National Library of Australia, Canberra, Australia.
- Williams-Linera, G., 1990a, Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology*, **78**: 356 373.
- Williams-Linera, G., 1990b, Origin and Early Development of Forest Edge Vegetation in Panama. *Biotropica*, **22**: 235 – 241.
- Wittmann, F., Junk, W.J. and Piedade, M.T.F., 2004, The varzea forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession. *Forest Ecology and Management*, **196**: 199 – 212.
- Worbes, M., Klinge, H., Revilla, J.D. and Martius, C., 1992, On the dynamics, floristic subdivision and geographical distribution of varzea forests in Central Amazonia. *Journal of Vegetation Science*, **3**: 553 – 564.
- Wright, S.J., Calderon, O., Hernandez, A. and Paton, S., 2004, Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology*, 85: 484 – 489.
- Wright, S.J. and Duber, H.C., 2001, Poachers and Forest Fragmentation Alter Seed
 Dispersal, Seed Survival, and Seedling Recruitment in the Palm *Attalea butyraceae*, with Implications for Tropical Tree Diversity. *Biotropica*, 33: 583 595.
- Wright, S.J., Muller-Landau, H.C., Condit, R. and Hubbell, S.P., 2003, Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology*, 84: 3174 3185.
- Wunderle, J.M., Willig, M.R. and Henriques, L.M.P., 2005, Avian distribution in treefall gaps and understorey of *terra firme* forest in the lowland Amazon. *Ibis*, 147: 109 129.
- Young, A. and Mitchell, N., 1994, Microclimate and vegetation edge effects in a fragmented podocarp – broadleaf forest in New Zealand. *Biological Conservation*, 67: 63 – 72.
- Young, A., Boyle, T. and Brown, T., 1996, The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology and Evolution*, 11: 413 418.
- Zar, J.H., 1999, *Biostatistical Analysis*. Fourth Edition. Prentice Hall International, Inc. and Pearson Education, Upper Saddle River, New Jersey.

Zartman, C.E. and Shaw, A.J., 2006, Metapopulation Extinction thresholds in Rain Forest Remnants. *The American Naturalist*, **167**: 177 – 189.

Appendix 1

Wood densities of tree species encountered in the vegetation survey (Chapter 5). Data 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). Wood specific gravity = wood density (kg m⁻³)/1000.

Species	Family	Wood Density (kg m ⁻³)
Trees		
Aceratium megalospermum	Eleaocarpaceae	625
Acmena graveolens	Myrtaceae	595
Acronychia vestita	Rutaceae	705
Aglaia meridionalis	Meliaceae	700 (47)*
Aglaia tomentosa	Meliaceae	700 (47)*
Alangium villosum	Alangiaceae	705
Alphitonia petriei	Rhamnaceae	515
Alstonia scholaris	Apocynaceae	400
Antirrhea tenuiflora	Rubiaceae	805 (58)*
Apodytes brachystylis	Icacinaceae	655
Archidendron whitei	Mimosaceae	705 (74)*‡
Argyrodendron peralatum	Sterculiaceae	800
Argyrodendron trifoliolatum	Sterculiaceae	925
Austromyrtus bidwillii	Myrtaceae	775 (21)*¶
Austromyrtus dallachiana	Myrtaceae	775 (21)* ¶
Austromyrtus shepherdii	Myrtaceae	775 (21)* ¶
Beilschmedia bancroftii	Lauraceae	640
Beilschmedia recurva	Lauraceae	620
Beilschmedia tooram	Lauraceae	850
Beilschmedia volckii	Lauraceae	545
Bischofia javanica	Euphorbiaceae	655
Breynia stipitata	Euphorbiaceae	690 (37)*
Brombya platynema	Rutaceae	710
Cananga odorata	Annonaceae	465

Species	Family	Wood Density (kg m ⁻³)
Cardwellia sublimis	Proteaceae	560
Carnarvonia araliifolia	Proteaceae	690
Castanospermum australe	Fabaceae	755
Castanospora alphandii	Sapindaceae	705
Celtis paniculata	Ulmaceae	705
Chionanthus axillaris	Oleaceae	935 (40)*
Chisocheton longistipitatus	Meliaceae	545
Cinnamomum laubatii	Lauraceae	480
Citronella smythii	Icacinaceae	675
Clerodendron grayi	Verbenaceae	585 (37)*
Corynocarpus cribbianus	Corynocarpaceae	690
Cryptocarya angulata	Lauraceae	755
Cryptocarya corrugata	Lauraceae	800
Cryptocarya grandis	Lauraceae	830
Cryptocarya mackinnoniana	Lauraceae	880
Cryptocarya melanocarpa	Lauraceae	775
Cryptocarya murrayi	Lauraceae	785
Cryptocarya oblata	Lauraceae	560
Cryptocarya pleurosperma	Lauraceae	690
Daphnandra repandula	Monimiaceae	675
Davidsonia pruriens	Davidsoniaceae	875
Diospiros cupulosa	Ebenaceae	1010 (122)*
Diospiros sp. "twice as flat"	Ebenaceae	1010 (122)*
Diploglottis bracteata	Sapindaceae	995
Diploglottis smithii	Sapindaceae	830 (22)*
Doryphora aromatica	Monimiaceae	560
Dysoxylum klanderi	Meliaceae	945
Dysoxylum oppositifolium	Meliaceae	880
Dysoxylum papuanum	Meliaceae	735
Dysoxylum pettigrewianum	Meliaceae	865
Elaeocarpus grandis	Elaeocarpaceae	495
Elaeocarpus largiflorens	Eleaocarpaceae	450

Species	Family	Wood Density (kg m ⁻³)
Endiandra bessaphila	Lauraceae	665
Endiandra compressa	Lauraceae	995
Endiandra globosa	Lauraceae	915
Endiandra insignis	Lauraceae	750
Endiandra leptodendron	Lauraceae	870
Endiandra monothyra	Lauraceae	800
Endiandra palmerstonii	Lauraceae	690
Endiandra sankeyana	Lauraceae	755
Endiandra sideroxylon	Lauraceae	800
Ficus congesta	Moraceae	350
Ficus copiosa	Moraceae	350
Ficus crassipes	Moraceae	350
Ficus leptoclada	Moraceae	560
Ficus pleurocarpa	Moraceae	470
Ficus septica	Moraceae	350
Ficus variegata	Moraceae	400
Ficus virens var. virens	Moraceae	400
Flindersia acuminata	Rutaceae	`530
Flindersia brayleyana	Rutaceae	575
Franciscodendron laurifolium	Sterculiaceae	450
Gardenia ovularis	Rubiaceae	850
Gessios biagiana	Cunoniaceae	640
Gillbeea adenopetala	Cunoniaceae	530
Glochidion harveyanum	Euphorbiaceae	785
Glochidion sumatrum	Euphorbiaceae	705
Guioa lasioneura	Sapindaceae	830 (22)*
Haplostichanthus sp. Johnstone River LWJ 471	Annonaceae	565 (38)*
Helicia nortoniana	Proteaceae	725 (33)*†
Hollandaea sayeriana	Proteaceae	725 (33)* †
Hylandia dockrillii	Euphorbiaceae	560

Species	Family	Wood Density (kg m ⁻³)
Irvingbaileya australis	Icacinaceae	495
Levieria acuminata	Monimiaceae	435
Litsea leefeana	Lauraceae	480
Macaranga inamoena	Euphorbiaceae	560
Mallotus paniculatus	Euphorbiaceae	690 (37)*
Melicope bonwickii	Rutaceae	465
Melicope elleryana	Rutaceae	610
Melicope vitiflora	Rutaceae	625
Melicope xanthoxyloides	Rutaceae	495
Mischocarpus lachnocarpus	Sapindaceae	830 (22)*
Myristica insipida	Myristicaceae	560
Neolitsea dealbata	Lauraceae	680
Niemeyera prunifera	Sapotaceae	610
Omalanthus novo-guineensis	Euphorbiaceae	320
Opistheolepis heterophylla	Proteaceae	610
Ostrearia australiana	Hamamelidaceae	755
Palaquium galatoxylon	Sapotaceae	560
Phaleria clerodendron	Thymelaeaceae	655 (16)§
Pilidiostigma tropicum	Myrtaceae	775 (21)*
Pitiviaster haplophylla	Rutaceae	835
Podocarpus dispermus	Podocarpaceae	580 (45)*
Polyalthia michaelii	Annonaceae	625
Polyosma hirsute	Grossulariaceae	720 (na)*
Polyscias australiana	Araliaceae	575
Polyscias elegans	Araliaceae	480
Polyscias murrayi	Araliaceae	400
Pouteria castanosperma	Sapotaceae	975
Prunus turneriana	Rosaceae	530
Pseuduvaria villosa	Annonaceae	565 (38)*
Rhodamnia sessiliflora	Myrtaceae	975
Rhodomyrtus pervigata	Myrtaceae	775 (21)*
Rhysotoechia robertsonii	Sapindaceae	830 (22)*

Species	Family	Wood Density (kg m ⁻³)
Rockinghamia angustifolia	Euphorbiaceae	800
Sarcotoechia protracta	Sapindaceae	830 (22)*
Schefflera actinophylla	Araliaceae	480
Siphonodon membranaceus	Celastraceae	835
Sloanea australis	Eleaocarpaceae	625
Sloanea macbrydei	Eleaocarpaceae	575
Symplocus cochinchinensis	Symplocaceae	545
Symplocus paucistaminea	Symplocaceae	585 (40)*
Synima cordierorum	Sapindaceae	945
Synima macrophylla	Sapindaceae	830 (22)*
Synuom glandulosum ssp. paniculosum	Meliaceae	675
Synuom muelleri	Meliaceae	625
Syzygium alliiligneum	Myrtaceae	610
Syzygium cormiflorum	Myrtaceae	770
Syzygium gustavioides	Myrtaceae	690
Syzygium sayeri	Myrtaceae	840
Tetrasynandra laxiflora	Monimiaceae	640
Toechima erythrocarpum	Sapindaceae	785
Toechima monticola	Sapindaceae	830 (22)*
Xanthophyllum octandrum	Xanthophyllaceae	800
<u>Tree Ferns</u>		
Cyathea cooperi	Cyatheaceae	Excluded
Lianas		
Austrobaileya scandens	Austrobaileyaceae	Excluded
Austrosteenisia stipularis	Fabaceae	Excluded
Cardiopteris moluccana	Cardiopteraceae	Excluded
Carronia protensa	Menispermaceae	Excluded
Cissus sterculiifolia	Vitaceae	Excluded
Cissus vinosa	Vitaceae	Excluded
Connarus conchocarpus	Connaraceae	Excluded

Species	Family	Wood Density (kg m ⁻³)
Eleagnus triflora	Eleagnaceae	Excluded
Faradaya splendida	Verbenaceae	Excluded
Ichnocarpus frutescens	Apocynaceae	Excluded
Maclura cochinchinensis	Moraceae	Excluded
Melodinus australis	Apocynaceae	Excluded
Mucuna gigantea	Fabaceae	Excluded
Neosepicaea jucunda	Bignoniaceae	Excluded
Omphalea queenslandiae	Euphorbiaceae	Excluded
Palmeria scandens	Monimiaceae	Excluded
Parsonsia latifolia	Apocynaceae	Excluded
Piper novaehollandiae	Piperaceae	Excluded
Rhamnella vitiensis	Rhamnaceae	Excluded
Sageretia hamosa	Rhamnaceae	Excluded
Salacia dispela	Hippocrataceae	Excluded
Tetracera nordtiana	Dilleniaceae	Excluded

* Family average used (obtained from Cause *et al.* 1989 and Smith *et al.* 1991). Standard deviation is shown in parentheses.

‡ Mimosaceae average excludes the genus Acacia.

¶ Myrtaceae average excludes the genera *Corymbia, Eucalyptus, Leptospermum, Lophostemon* and *Melaleuca*.

[†] Proteaceae average excludes the genera *Banksia* and *Grevillea*.

§ No data available on the family Thymelaeaceae; dataset mean used instead.

Appendix 2.

Species encountered in the vegetation survey (Chapter 5). Successional status (E = early, I = intermediate, L = late), growth habit (C = canopy tree, U = understorey tree, S = shrub, H = herb, G = grass, F = fern, V = large woody vine, V-s = slender vine, V-h = climbing herb) and propogule size (S = diameter < 1.0 cm, I = diameter 1.0 – 2.0 cm, L = diameter > 2.0 cm) and dispersal mode (B = biotic or A = abiotic) are given for each species.

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Aceratium megalospermum	Eleaocarpaceae	Ι	С	S	В
Acmena graveolens	Myrtaceae	L	С	L	В
Acronychia parviflora	Rutaceae	Ι	S	S	В
Acronychia vestita	Rutaceae	Ι	U	Ι	В
Adiantum diaphanum	Adiantaceae	L	F	S	А
Ageratum conyzoides	Asteraceae	W	W	S	А
Aglaia australiensis	Meliaceae	L	U	L	В
Aglaia meridionalis	Meliaceae	L	U	L	В
Aglaia sapindina	Meliaceae	L	U	Ι	В
Aglaia tomentosa	Meliaceae	L	U	Ι	В
Alangium villosum	Alangiaceae	L	С	S	В
Alocasia brisbanensis	Araceae	Е	Н	S	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Alphitonia petriei	Rhamnaceae	Е	С	S	В
Alphitnia whitei	Rhamnaceae	Е	С	S	В
Alpinia arctiflora	Zingiberaceae	Е	Н	L	А
Alpinia modesta	Zingiberaceae	Ι	Н	S	В
Alstonia scholaris	Apocynaceae	Е	С	L	А
Aneilema acuminatum	Commelinaceae	Е	Н	S	А
Antidesma erostre	Euphorbiaceae	Ι	U	S	В
Antirrhea tenuiflora	Rubiaceae	Ι	U	S	В
Apodytes brachystylis	Icacinaceae	L	U	S	В
Archidendron whitei	Mimosaceae	Ι	U	L	В
Archontophoenix alexandrae	Arecaceae	Ι	С	Ι	В
Ardisia brevipedata	Myrsinaceae	L	S	S	В
Ardisia pachyrrhachis	Myrsinaceae	Ι	U	S	В
Argyrodendron peralatum	Sterculiaceae	L	С	L	А
Argyrodendron trofoliolatum	Sterculiaceae	L	С	L	А
Arthropteris palasotii	Nephrolepidaceae	L	V-f	S	А
Arytera pauciflora	Sapindaceae	L	U	S	В
Asplenium australasicum	Aspleniaceae	L	F	S	А
Atractocarpus hirtus	Rubiaceae	L	S	S	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Austrobaileya scandens	Austrobaileyaceae	L	V	L	В
Austromyrtus bidwillii	Myrtaceae	L	U	Ι	В
Austromyrtus dallachiana	Myrtaceae	L	U	Ι	В
Austromyrtus shepherdii	Myrtaceae	L	U	Ι	В
Austrosteenisia stipularis	Fabaceae	Ι	V	S	
Balanophora fungosa	Balanophoraceae	L	Н	S	
Beilschmedia bancroftii	Lauraceae	L	С	L	В
Beilschmedia collina	Lauraceae	L	С	L	В
Beilschmedia recurva	Lauraceae	L	С	Ι	В
Beilschmedia tooram	Lauraceae	L	С	L	В
Beilschmedia volckii	Lauraceae	L	С	L	В
Bischofia javanica	Euphorbiaceae	L	С	S	В
Bleasdalea bleasdalei	Proteaceae	L	U	Ι	
Blechnum cartiliganum	Blechnaceae	Е	F	S	А
Bowenia spectabilis	Zamiaceae	Ι	Н	L	В
Breynia cernua	Euphorbiaceae	Е	S	S	В
Breynia stipitata	Euphorbiaceae	Е	С	S	В
Brombya platynema	Rutaceae	L	U	S	В
Bubbia semecarpoides	Winteraceae	L	U	Ι	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Caesalpinia traceyi	Caesalpiniaceae	Е	V	S	
Calamus australis	Arecaeae	Ι	V-s	S	В
Calamus caryotoides	Arecaeae	Ι	V-s	S	В
Calamus motii	Arecaeae	Ι	V-s	S	В
Callicarpa pedunculata	Verbenaceae	Е	S	S	В
Cananga odorata	Annonaceae	L	С	Ι	В
Cardiopteris moluccana	Cardiopteridaceae	L	V		
Cardwellia sublimis	Proteaceae	Е	С	S	А
Carnavonia araliifolia	Proteaceae	L	С	Ι	А
Carronia protensa	Menispermaceae	Ι	V	Ι	В
Casearia dallachii	Flacourtiaceae	L	U	S	В
Castanospermum australe	Fabaceae	Ι	С	L	В
Castanospora alphandii	Sapindaceae	Ι	С	L	В
Cayratia saponaria	Vitaceae	Е	V	S	В
Celastrus subspicata	Celastraceae	Ι	V	S	В
Celtis paniculata	Ulmaceae	Ι	С	S	В
Cephaloralea cephalobottridge	Araliaceae	Е	V	S	В
Chionanthus axillaris	Oleaceae	L	U	Ι	В
Chisocheton longistipitatus	Meliaceae	L	С	L	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal
Cinnamomum laubatii	Lauraceae	L	С	Ι	В
Cissus hypoglauca	Vitaceae	Ι	V	S	В
Cissus repens	Vitaceae	Ι	V	S	В
Cissus sterculiifolia	Vitaceae	Ι	V	S	В
Cissus vinosa	Vitaceae	Ι	V	Ι	В
Citronella moorei	Icacinaceae	L	С	Ι	В
Citronella smythii	Icacinaceae	L	С	S	В
Clematis glycinoides	Ranunculaceae	Ι	V	S	А
Clerodendron grayi	Verbenaceae	E	S	S	В
Cnesmocarpon dasyantha	Sapindaceae	L	U	Ι	В
Codiaeum variegatum var. moluccanum	Euphorbiaceae	Ε	S	S	В
Connarus conchocarpus	Connaraceae	L	V	Ι	В
Cordyline cannifolia	Agavaceae	Ε	Н	S	В
Corymborkis veratrifolia	Orchidaceae	L	S	S	А
Corynocarpus cribbianus	Corynocarpaceae	L	С	L	В
Coveniella poecilophlebia	Aspidiaceae	Ε	F	S	А
Cryptocarya angulata	Lauraceae	L	С	Ι	В
Cryptocarya corrugata	Lauraceae	L	С	Ι	В
Cryptocarya grandis	Lauraceae	L	С	Ι	В
Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
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Cryptocarya hypospodia	Lauraceae	L	С	Ι	В
Cryptocarya mackinnoniana	Lauraceae	L	С	Ι	В
Cryptocarya melanocarpa	Lauraceae	L	С	Ι	В
Cryptocarya murrayi	Lauraceae	L	С	Ι	В
Cryptocarya oblata	Lauraceae	L	С	L	В
Cryptocarya pleurosperma	Lauraceae	L	С	L	В
Cryptocarya triplinervis	Lauraceae	L	U	S	В
Cryptocarya vulgaris	Lauraceae	E	U	S	В
Cupaniopsis flagelliformis	Sapindaceae	Ι	U	Ι	В
Cyathea cooperi	Cyatheaceae	E	F	S	А
Daphnandra repandula	Monimiaceae	Ι	С	L	А
Darlingia ferruginea	Proteaceae	Ι	С	L	А
Davidsonia pruriens	Davidsoniaceae	L	U	L	В
Delarbrea michieana	Araliaceae	L	U	Ι	В
Derris trifoliolata	Fabaceae	Ι	V	L	А
Desmos goezeanus	Annonaceae	L	V	S	В
Dichapetalum papuanum	Dichapetalaceae	L	V	S	В
Dicranopteris linearis	Gleicheniaceae	Е	V-f	S	А
Diospiros cupulosa	Ebenaceae	Ι	С	Ι	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Diospiros sp. "twice as flat"	Ebenaceae	L	U	S	В
Diospiros sp. Millaa Millaa LJW 515	Ebenaceae	L	U	S	В
Diplazium dilatum	Athyriaceae	L	F	S	А
Diploglottis bracteata	Sapindaceae	L	U	L	В
Diploglottis smithii	Sapindaceae	L	U	L	В
Diploglottis smithii	Sapindaceae	Ι	С	L	В
Doryphora aromatica	Monimiaceae	L	С	Ι	А
Dysoxylum alliaceum	Meliaceae	L	С	L	В
Dysoxylum klanderi	Meliaceae	Ι	U	L	В
Dysoxylum mollisimum	Meliaceae	L	С	L	В
Dysoxylum oppositifolium	Meliaceae	L	U	S	В
Dysoxylum papuanum	Meliaceae	L	С	S	В
Dysoxylum parasiticum	Meliaceae	L	С	Ι	В
Dysoxylum pettigrewianum	Meliaceae	Ι	С	L	В
Eleagnus triflora	Eleagnaceae	Е	V	S	В
Elaeocarpus grandis	Elaeocarpaceae	Е	С	Ι	В
Elaeocarpus largiflorens	Elaeocarpaceae	Е	С	Ι	В
Embelia grayi	Myrsinaceae	Ι	V	S	В
Endiandra bessaphila	Lauraceae	L	С	Ι	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Endiandra compressa	Lauraceae	L	U	L	В
Endiandra cowleyana	Lauraceae	L	С	L	В
Endiandra globosa	Lauraceae	L	С	L	В
Endiandra hypotephra	Lauraceae	L	U	Ι	В
Endiandra insignis	Lauraceae	L	С	L	В
Endiandra leptodendron	Lauraceae	L	U	Ι	В
Endiandra monothyra	Lauraceae	L	С	Ι	В
Endiandra montana	Lauraceae	L	С	L	В
Endiandra palmerstonii	Lauraceae	L	С	L	В
Endiandra sankeyana	Lauraceae	L	С	L	В
Endiandra sideroxylon	Lauraceae	L	С	L	В
Endiandra wolfei	Lauraceae	L	С	Ι	В
Epipremnum pinnatum	Araceae	Ι	V		В
Erycibe coccinea	Convolvulaceae	L	V	Ι	В
Erythroxylum ecarinatum	Erythroxylaceae	L	С	S	В
Eupomatia barbatra	Eupomatiaceae	Ι	U		В
Eupomatia laurina	Eupomatiaceae	Ι	U	L	В
Eupomatia sp. Noah Head	Eupomatiaceae	Ι	U		В
Faradaya splendida	Verbenaceae	Ι	V	L	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Ficus congesta	Moraceae	Е	U	S	В
Ficus copiosa	Moraceae	Ι	U	S	В
Ficus crassipes	Moraceae	L	SF	Ι	В
Ficus destruens	Moraceae	L	SF	Ι	В
Ficus leptoclada	Moraceae	Е	U	S	В
Ficus pantoniana	Moraceae	L	V	Ι	В
Ficus pleurocarpa	Moraceae	L	SF	Ι	В
Ficus septica	Moraceae	Ι	U	S	В
Ficus variegata	Moraceae	L	С	L	В
Ficus virens var. virens	Moraceae	L	SF	Ι	В
Flagellaria indica	Flagellariaceae	Е	V-s	S	В
Flindersia acuminata	Rutaceae	Ι	С	L	А
Flindersia bourjotiana	Rutaceae	Ι	С	Ι	А
Flindersia brayleyana	Rutaceae	Ι	С	S	А
Fontainea picrosperma	Euphorbiaceae	Ι	U	L	В
Franciscodendron laurifolium	Sterculiaceae	L	С	Ι	В
Freycinetia excelsa	Pandanaceae	L	V-h	S	В
Freycinetia scandens	Pandanaceae	L	V-h	S	В
Gardenia merikin	Rubiaceae	L	S	L	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Gardenia ovularis	Rubiaceae	L	U	L	В
Geissois biagiana	Cunoniaceae	L	С	S	А
Gilbeea adenopetala	Cunoniaceae	Ι	С	Ι	А
Glochidion harveyanum	Euphorbiaceae	Е	С	S	В
Glochidion hylandii	Euphorbiaceae	Е	С	S	В
Glochidion philippicum	Euphorbiaceae	Е	С	S	В
Glochidion sumatranum	Euphorbiaceae	Е	С	S	В
Gmelina fasciculiflora	Verbenaceae	L	С	Ι	В
Guioa acutifolia	Sapindaceae	Е	U	S	В
Guioa lasioneura	Sapindaceae	Е	U	S	В
Gymnostachys anceps	Araceae	L	S	S	
Haplostichanthus sp. Johnstone River	Annonaceae	L	U	Ι	В
LWJ 471					
Haplostichanthus sp. Topaz LWJ 520	Annonnaceae	L	U	S	В
Harpullia frutescens	Sapindaceae	L	U	Ι	В
Harpullia rhyticarpa	Sapindaceae	L	U	Ι	В
Hedycarya loxocarya	Monimiaceae	Ι	С	S	
Helicia nortoniana	Proteaceae	L	U	S	В
Hibbertia scandens	Dilleniaceae	Е	V	S	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Hollandaea sayeriana	Proteaceae	L	U	L	В
Hylandia dockrillii	Euphorbiaceae	Ι	С	L	В
Hypserpa decumbens	Menispermaceae	Е	V	S	В
Hypserpa laurina	Menispermaceae	L	V	S	В
Hyptis capitata	Lamiaceae	W	S	S	А
Ichnocarpus frutescens	Apocynaceae	Ι	V		А
Irvingbaileya australis	Icacinaceae	L	С	L	В
Ixora baileyana	Rubiaceae	L	S	S	В
Jasminum didymum	Oleaceae	Е	V	S	В
Lantana camara	Verbenaceae	W	S	S	В
Lasianthus strigosus	Rubiaceae	L	S	Ι	В
Lastreopsis rufescens	Aspidiaceae	L	F	S	А
Leea indica	Leeaceae	Е	S	S	В
Levieria acuminata	Monimiaceae	L	U	S	В
Linospadix microcarya	Arecaceae	L	Н	S	В
Linospadix minor	Arecaceae	L	Н	Ι	В
Litsea connorsii	Lauraceae	Е	С	S	В
Litsea leefeana	Lauraceae	Ι	С	Ι	В
Macaranga inamoena	Euphorbiaceae	Е	U	S	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Macaranga subdentata	Euphorbiaceae	Е	U	S	В
Macaranga tanarius	Euphorbiaceae	Е	С	S	В
Maclura cochinchinensis	Moraceae	Е	V	S	В
Maesa dependens var. dependens	Myrsinaceae	Е	V	S	В
Mallotus paniculatus	Euphorbiaceae	Е	С	S	В
Mallotus polyadenos	Euphorbiaceae	Е	С	S	В
Marattia oreades	Marattiaceae	Е	F	S	А
Marsdenia unidentified species	Asclepiadaceae	L	V		А
Meiogyne sp. Henrietta Creek LWJ 512	Annonaceae	L	S	Ι	В
Melicope bonwickii	Rutaceae	Ε	С	S	В
Melicope broadbentiana	Rutaceae	Е	U	S	В
Melicope elleryana	Rutaceae	Е	С	S	В
Melicope vitiflora	Rutaceae	Ε	С	S	В
Melicope xanthoxyloides	Rutaceae	Ε	С	S	В
Melinus minutiflora	Poaceae	W	G	S	А
Melodinus acutifolius	Apocynaceae	Ι	V	L	В
Melodinus australis	Apocynaceae	Ι	V	S	В
Melodinus bacellianus	Apocynaceae	Ι	V	L	В
Melodorum uhrii	Annonnaceae	L	V	S	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Mischocarpus exangulatus	Sapindaceae	Ι	U	Ι	В
Mischocarpus grandissimus	Sapindaceae	Ι	U	S	В
Mischocarpus lachnocarpus	Sapindaceae	Ι	U	S	В
Mischocarpus macrocarpus	Sapindaceae	Ι	U	Ι	В
Mischocarpus stipitatus	Sapindaceae	Ι	U	Ι	В
Morinda hypotethra	Rubiaceae	Ι	V	S	В
Morinda umbellata	Rubiaceae	Ι	V	S	В
Motherwellia haplosciadea	Araliaceae	Е	V		В
Mucuna gigantea	Fabaceae	Е	V	Ι	А
Myristica insipida	Myristicaeae	L	U	Ι	В
Neiosperma poweri	Apocynaceae	L	U	Ι	В
Neolitsea dealbata	Lauraceae	Е	С	S	В
Neosepicaea jucunda	Bignoniaceae	Ι	V	L	В
Nephrolepsis cordifolia	Nephrolepidaceae	Е	F	S	А
Nephrolepsis obliterata	Nephrolepidaceae	Е	V-f	S	А
Niemeyera prunifera	Sapotaceae	L	U	L	В
Omalanthus novo-guineensis	Euphorbiaceae	Е	С	S	В
Omphalea queenslandiae	Euphorbiaceae	Ι	V	L	В
Opisteolepis heterophylla	Proteaceae	L	С	L	А

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Oplismenis compositus	Poaceae	Е	G	S	А
Oplismenis undulatafolius	Poaceae	Е	G	S	А
Ostrearia australiana	Hamamelidaceae	L	С	Ι	В
Ottochloa nodosa	Poaceae	Е	G	S	А
Palaquium galatoxylon	Sapotaceae	L	С	Ι	В
Palmeria scandens	Monimiaceae	Е	V	S	В
Pandanus monticola	Pandanaceae	L	S	L	В
Pandorea nervosa	Bignoniaceae	Ι	V	S	А
Pararistolochia australopithecus	Aristolochiaceae	L	V	S	А
Parsonsia latifolia	Apocynaceae	Е	V	L	А
Passiflora edulis	Passifloraceae	W	V	S	В
Phaleria clerodendron	Thymeliaceae	L	U	L	В
Pilidiostigma tetramerum	Myrtaceae	L	S	Ι	В
Pilidiostigma tropicum	Myrtaceae	L	U	S	В
Piper caninum	Piperaceae	Ι	V	S	В
Piper macropiper	Piperaceae	Ι	V	S	В
Piper novaehollandiae	Piperaceae	Ι	V	S	В
Pitiviaster haplophylla	Rutaceae	L	U	S	В
Pittosporum rubiginosum	Pittosporaceae	Ι	U	Ι	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Pittosporum trilobum	Pittosporaceae	Ι	U	S	В
Podocarpus dispermus	Podocarpaceae	L	U	Ι	В
Pollia macrophylla	Commelinaceae	Е	Н	S	
Polyalthia michaelii	Annonaceae	L	U	L	В
Polyosma hirsuta	Grossulariaceae	L	U	Ι	В
Polyscias australiana	Araliaceae	E	U	S	В
Polyscias elegans	Araliaceae	Ε	С	S	В
Polyscias mollis	Araliaceae	E	U	S	В
Polyscias murrayi	Araliaceae	E	С	S	В
Polyscias purpurea	Araliaceae	E	S	S	В
Pothos longipes	Araceae	Ι	V-h	Ι	В
Pouteria brownlessiana	Sapotaceae	L	С	Ι	В
Pouteria castanosperma	Sapotaceae	L	С	L	В
Pouteria obovoidea	Sapotaceae	L	С	Ι	В
Pouteria xerocarpa	Sapotaceae	Ι	U	Ι	В
Prunus turneriana	Rosaceae	Ε	С	L	В
Pseuderanthemum variable	Acanthaceae	Ι	Н	В	А
Pseuduvaria villosa	Annonaceae	L	S	Ι	В
Psychotria dallachiana	Rubiaceae	L	S	S	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Psychotria nematopoda	Rubiaceae	L	S	S	В
Psychotria sp. Utchee Creek Flecker	Rubiaceae	L	S	S	В
NQNC 5313					
Psychotria submontana	Rubiaceae	L	S	S	В
Randia tuberculosa	Rubiaceae	L	U	Ι	В
Rhamnella vitiensis	Rhamnaceae	L	V	S	
Rhaphidophora australasica	Araceae	L	V-h	S	В
Rhaphidophora petriei	Araceae	L	V-h	S	В
Rhodamnia sissiliflora	Myrtaceae	Ε	U	S	В
Rhodomyrtus macrocarpa	Myrtaceae	Ε	U	Ι	В
Rhodomyrtus pervigata	Myrtaceae	Ε	U	Ι	В
Rhysotoechia robertsonii	Sapindaceae	L	U	Ι	В
Ripogonum album	Smilacaceae	Ι	V	S	В
Rockinghamia angustifolia	Euphorbiaceae	Ι	U	Ι	В
Rubus alceifolius	Rosaceae	W	S	S	В
Rubus rosifolius/queenslandicum	Rosaceae	Ε	S	S	В
Sageretia hamosa	Rhamnaceae	Ι	V	S	А
Salacia dispela	Hippocrataceae	L	V	L	
Sanchezia parvibracteata	Acanthaceae	W	S	S	

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Sarcopetalum harveyanum	Menispermaceae	Ι	V	Ι	
Sarcopterix martyana	Sapindaceae	Е	U	S	В
Sarcotoechia protracta	Sapindaceae	L	U	L	В
Saurauia andreana	Actinidiaceae	Ι	U	Ι	В
Scaevola anantophylla	Goodeniaceae	Е	V	S	В
Schefflera actinophylla	Araliaceae	Е	U	S	В
Selaginella australiensis	Selaginaceae	L	F	S	А
Selaginella longipinna	Selaginaceae	L	F	S	А
Setococcus sp.	Poaceae	W	G	S	А
Siphonodon memranaceous	Celastraceae	L	С	L	В
Sloanea australis	Eleaocarpaceae	L	С	S	В
Sloanea langii	Eleaocarpaceae	L	С	L	В
Sloanea macbrydei	Eleaocarpaceae	L	С	S	В
Smilax calophylla	Smilacaceae	Е	V-s	S	В
Steganthera australianum	Monimiaceae	L	S	S	В
Stephania japonica	Menispermaceae	Ι	V	S	В
Stylosanthes humilis	Fabaceae	W	Н	S	
Symplocus cochinchinensis	Symplocaceae	E	U	S	В
Symplocus hayesii	Symplocaceae	L	S	Ι	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Symplocus paucistaminea	Symplocaceae	L	U	S	В
Synima cordierorum	Sapindaceae	L	U	Ι	В
Synima macrophylla	Sapindaceae	L	U	S	В
Synuom glandulosum ssp. paniculosum	Meliaceae	Е	U	S	В
Synuom muelleri	Meliaceae	Ι	U	Ι	В
Syzygium alliiligneum	Myrtaceae	L	С	L	В
Syzygium cormiflorum	Myrtaceae	L	С	L	В
Syzygium gustavioides	Myrtaceae	L	С	L	В
Syzygium johnsonii	Myrtaceae	L	С	Ι	В
Syzygium papyraceum	Myrtaceae	L	С	L	В
Syzygium sayeri	Myrtaceae	L	С	Ι	В
Tectaria confluence	Aspidiaceae	L	F	S	А
Ternstroemia cherryi	Theaceae	L	U	L	В
Tetracera nordtoniana	Dilleniaceae	Е	V	S	В
Tetrastigma nitens	Vitaceae	Ι	V	S	В
Tetrasynandra laxiflora	Monimiaceae	L	U	Ι	В
Timonius singularis	Rubiaceae	Ε	U	Ι	В
Toechima erythrocarpum	Sapindaceae	L	U	Ι	В
Toechima monticola	Sapindaceae	L	U	Ι	В

Species	Family	Successional Status	Habit	Propagule Size	Dispersal Mode
Trophis scandens	Moraceae	Ι	V	S	В
Tylophora colorata	Asclepiadaceae	Ι	V		А
Urochloa maxima	Poaceae	W	G	S	А
Ventilago ecorollata	Rhamnaceae	E	V	S	А
Wilkiea sp. Berong	Monimiaceae	Ι	U	S	В
Wilkiea sp. Boonjkee BG 5413	Monimiaceae	Ι	S	S	В
Xanthophyllum octandrum	Xanthophyllaceae	L	С	S	В

Appendix 3

Post hoc Mann-Whitney U tests to compare edge type effects for the proportion of individuals from different successional categories of understorey and canopy tree species. Significant contrasts (at the Bonferroni-corrected level of p < 0.0042) are highlighted in bold and marginally-significant comparisons are highlighted in italics.

Parameter	Size Class	Comparison	Z	<i>p</i> -value
Understorey tree species,	Trees	Powerline – highway	-2.065	0.039
% early-successional		Powerline – creek	-1.274	0.203
		Highway – creek	-3.049	< 0.001
	Saplings	Powerline – highway	-0.625	0.532
		Powerline – creek	-2.446	0.014
		Highway – creek	-2.313	0.021
	Seedlings	Powerline – highway	-0.161	0.872
		Powerline – creek	-3.070	0.002
		Highway – creek	-2.984	0.003
	All	Powerline – highway	-0.684	0.494
		Powerline – creek	-3.648	< 0.001
		Highway – creek	-4.410	< 0.001
Understorey tree species,	Trees	Powerline – highway	-2.057	0.040
% late-successional		Powerline – creek	-0.513	0.608
		Highway – creek	-2.403	0.016
	Saplings	Powerline – highway	-0.265	0.791
		Powerline – creek	-1.872	0.061
		Highway – creek	-2.365	0.018
	Seedlings	Powerline – highway	-0.362	0.718
		Powerline – creek	-2.683	0.007
		Highway – creek	-2.575	0.010
	All	Powerline – highway	-1.281	0.200
		Powerline – creek	-2.808	0.005
		Highway – creek	-4.171	< 0.001
Canopy tree species,	Trees	Powerline – highway	-1.177	0.239
% early-successional		Powerline – creek	-1.481	0.138

Parameter	Size Class	Comparison	Z	<i>p</i> -value
Canopy tree species,		Highway – creek	-0.339	0.735
% early-successional	Saplings	Powerline – highway	-0.766	0.444
(continued)		Powerline – creek	-0.328	0.743
		Highway – creek	-0.355	0.723
	Seedlings	Powerline – highway	-2.230	0.026
		Powerline – creek	-1.205	0.228
		Highway – creek	-0.927	0.354
	All	Powerline – highway	-2.018	0.044
		Powerline – creek	-1.641	0.101
		Highway – creek	-0.263	0.793

Appendix 4

Frugivorous bird species observed in small fragments on the Atherton Tablelands (Warburton 1997) or within 30 m of the Kuranda Highway, between Smithfield and Kuranda (Mr Greg Dawe, unpublished data). Species common to both lists are highlighted in bold. Birds dispersed fruit either regularly, occasionally (or intermediate between the two) or were seed predators and the maximum fruit width is the average width of the fruit of the largest-fruited plant species dispersed by each bird species (Dr Andrew Dennis *pers. comm.*). Data on seed dispersal characteristics and maximum widths of fruit dispersed were obtained from Dr Andrew Dennis (*pers. comm.*) at CSIRO, Atherton, Queensland.

Common Name	Scientific Name	Seed/Fruit	Maximum
	Dispersal		Fruit Width
			(mm)
Australian Brush-turkey	Alectura lathami	Predator	_
Barred Cuckoo-shrike	Coracina lineata	Regular	15
Black Butcherbird	Cracticus quoyi	Occasional	8.5
Bridled Honeyeater	Lichenostomus frenatus	Intermediate	7
Brown Cuckoo-dove	Macropygia amboinensis	Predator	-
Dusky Honeyeater	Myzomela obscura	Occasional	10.4
Emerald Dove	Chalcophaps indica	Predator	_
Figbird	Specotheres viridis	Regular	22
Graceful Honeyeater	Meliphaga gracilis	Occasional	6
Helmeted Friarbird	Philemon buceroides	Occasional	6.2
Lewin's Honeyeater	Meliphaga lewinii	Regular	15
Little Cuckoo-shrike	Coracina papuensis	Occasional	5.25
Macleay's Honeyeater	Xanthotis macleayana	Intermediate	8
Metallic Starling	Aplonis metallica	Regular	14
Mistletoebird	Dicaeum hirundinaceum	Regular	9.5
Pied Currawong	Strepera graculina	Regular	24
Rainbow Lorikeet	Trichoglossus haematodus	Predator	_
Silvereye	Zosterops lateralis	Regular	8

Common Name	Scientific Name	Seed/Fruit	Maximum
		Dispersal	
			(mm)
Spangled Drongo	Dicrurus hottentottus	Occasional	10.1
Spotted Catbird	Ailuroedus melanotis	Regular	17.5
Tooth-billed Catbird	Ailuroedus dentirostris	Regular	17
Topknot Pigeon	Lopholaimus antarcticus	Regular	27.9
Varied Triller	Lalage leucomela	Intermediate	10.5
Victoria's Riflebird	Ptiloris vistoriae	Regular	24.5
Wompoo Pigeon	Ptilinopus magnificus	Regular	27.1
Yellow-spotted Honeyeater	Meliphaga notata	Occasional	7.4

11. Papers Arising From the Thesis

Pohlman, C.L., Turton, S.M. and Goosem, M., *In Press*, Edge Effects of Linear Canopy Openings on Tropical Rainforest Understorey Microclimate. *Biotropica*.

This paper was accepted for publication by the journal *Biotropica* on 27th March 2006. This paper is based on Chapter 4 (Section 4.2) and Chapter 3. The galley proofs provided by *Biotropica* for correction have been presented here.

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