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

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:

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

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, with current edges 15 years old) would be more severe than those associated with creeks (eg Parendes and Jones 2000).

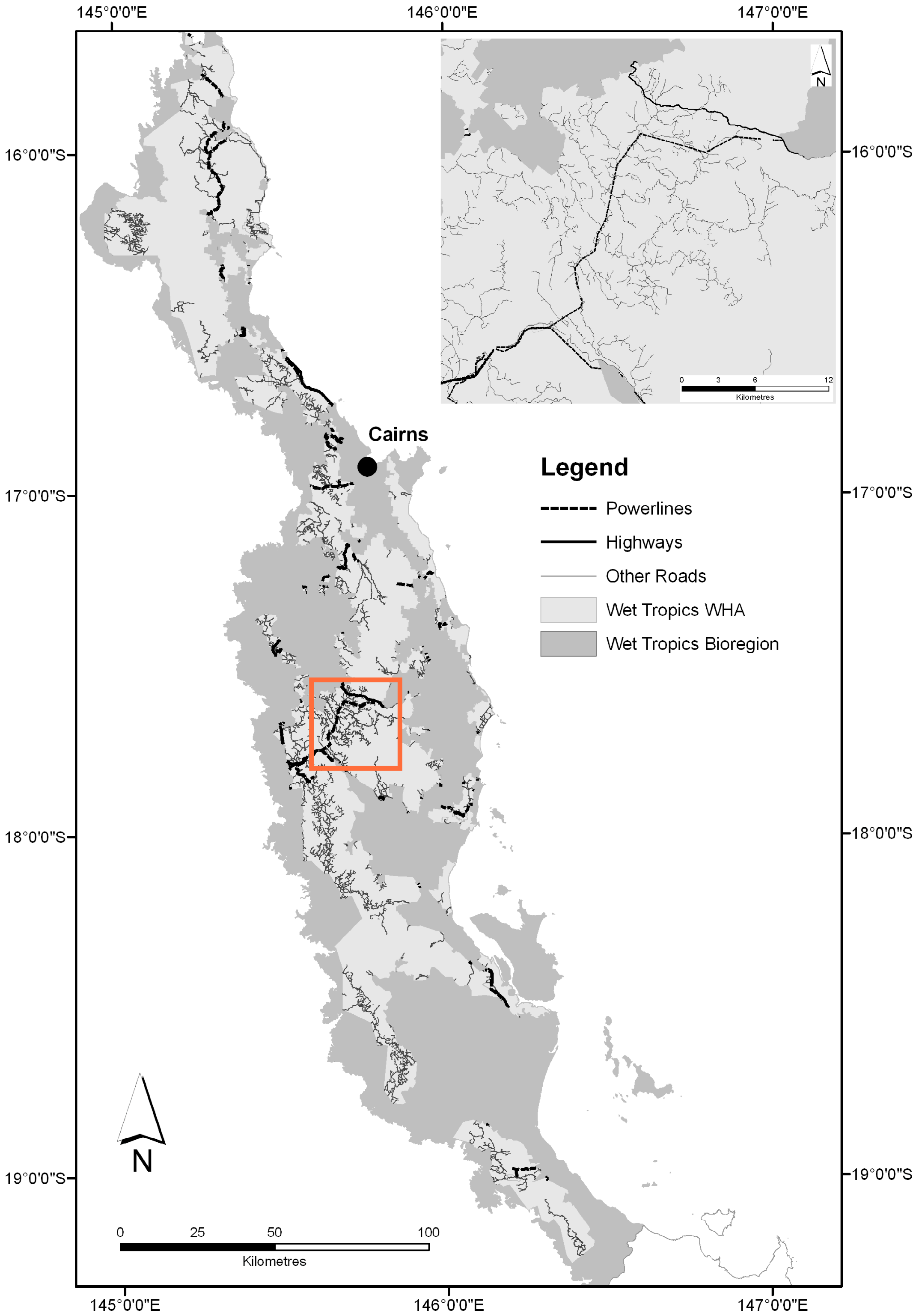


Figure 1.1. The Wet Tropics World Heritage Area of north-eastern Queensland, Australia. This area has an extensive network of clearings for linear infrastructure. The inset shows highways, powerlines and other roads within the study region (Wooroonooran National Park and South Johnstone State Forest). 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. Edge-associated 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 – 15 months 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 long-term 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 north-eastern 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 (Benitez-

Malvido 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).

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).

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	—	—

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). 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 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:

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

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

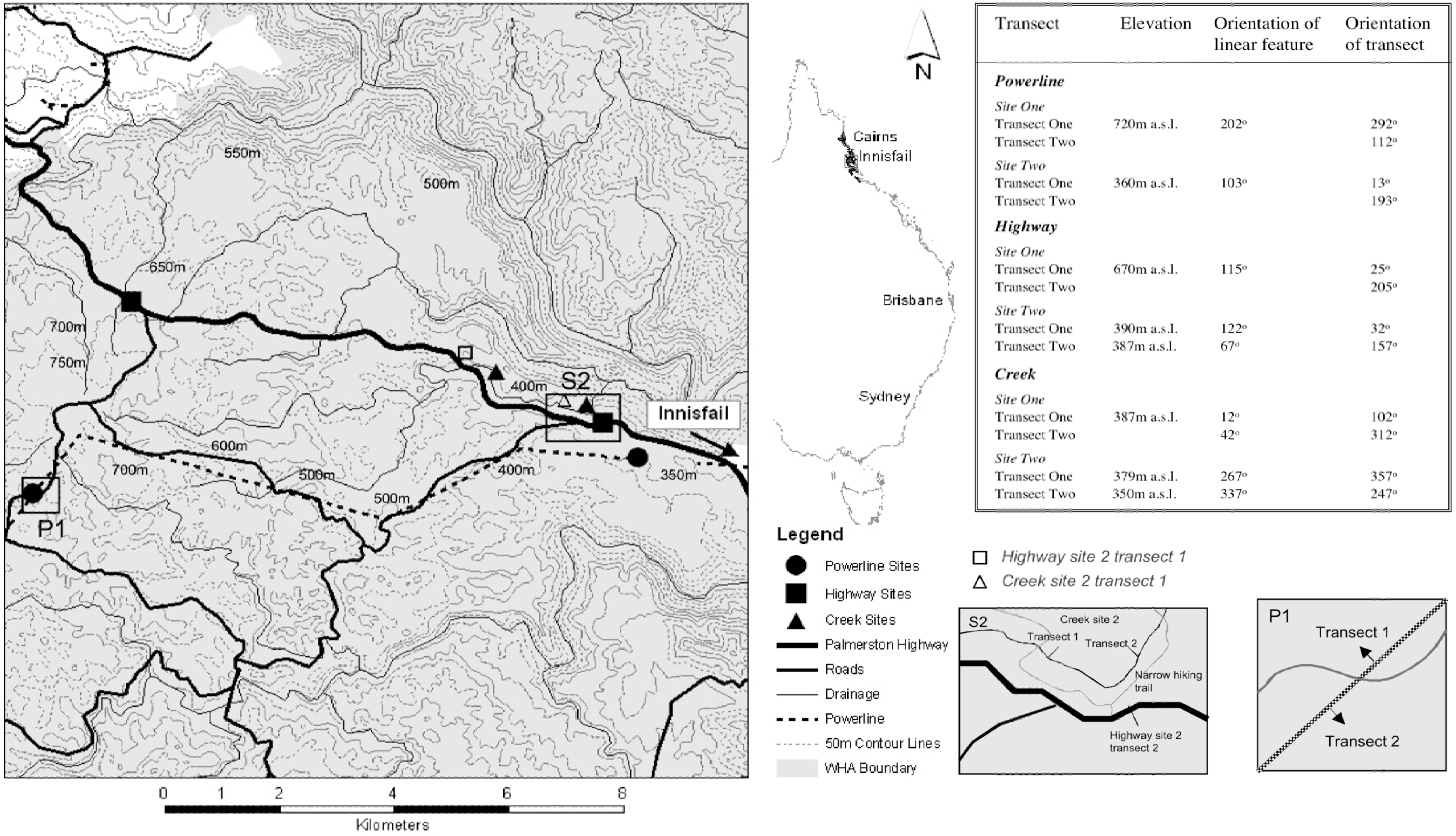
Meteorology www.bom.gov.au). The area experiences a wet season between December and May, with a peak of rainfall between January and March. Forest in this area has been disturbed by selective logging prior to the 1950s and scattered small-scale mining activities prior to the 1990s (Siegenthaler and Turton 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 taller-growing 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.



Transect	Elevation	Orientation of linear feature	Orientation of transect
Powerline			
Site One			
Transect One	720m a.s.l.	202°	292°
Transect Two			112°
Site Two			
Transect One	360m a.s.l.	103°	13°
Transect Two			193°
Highway			
Site One			
Transect One	670m a.s.l.	115°	25°
Transect Two			205°
Site Two			
Transect One	390m a.s.l.	122°	32°
Transect Two	387m a.s.l.	67°	157°
Creek			
Site One			
Transect One	387m a.s.l.	12°	102°
Transect Two		42°	312°
Site Two			
Transect One	379m a.s.l.	267°	357°
Transect Two	350m a.s.l.	337°	247°

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 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.

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-, sapling- and 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).

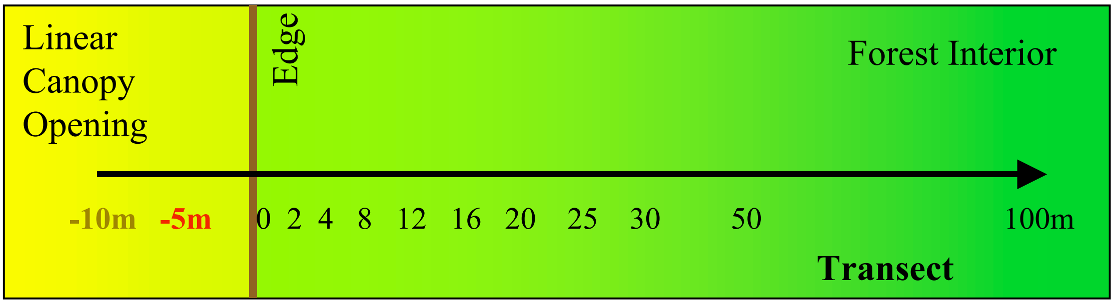


Figure 3.2. Transect layout. Measurements were made at various distances from the forest edge. Distances marked in red were only measured on the highway transects and distances marked in beige were only measured on the powerline transects.

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.

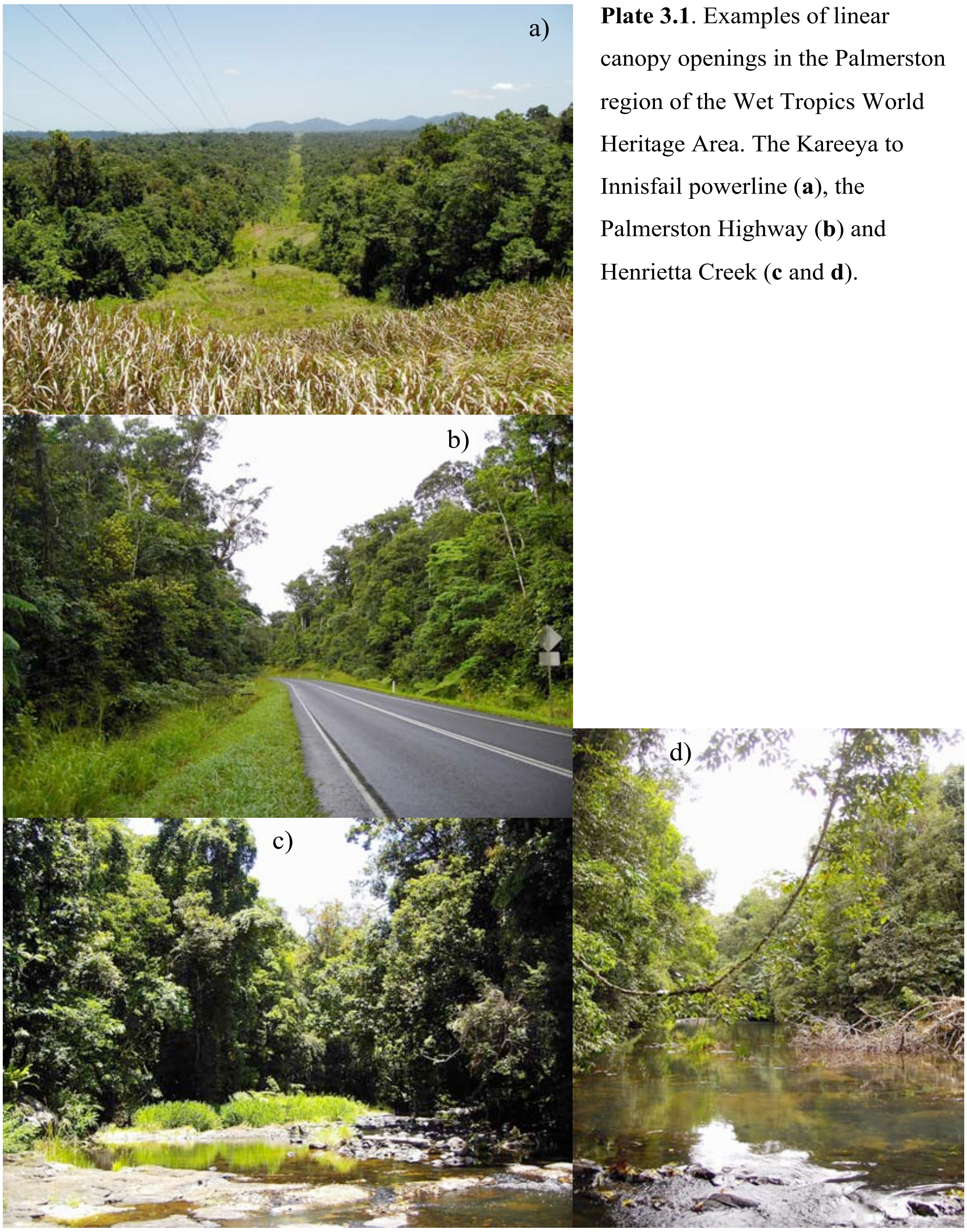


Plate 3.1. Examples of linear canopy openings in the Palmerston region of the Wet Tropics World Heritage Area. The Kareeya to Innisfail powerline (**a**), the Palmerston Highway (**b**) and Henrietta Creek (**c** and **d**).

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:

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?

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).

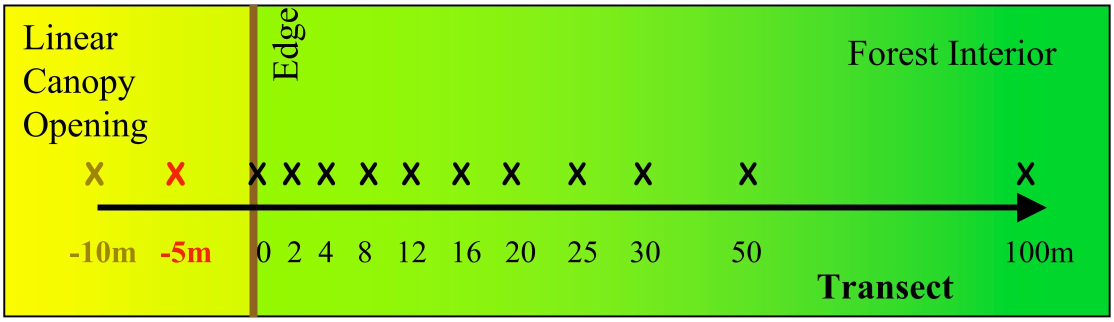


Figure 4.1. The set-up for the traverse measurements. Microclimate measurements were made at each distance marked with an "X". Distances marked in red were measured only on the highway transects and distances marked in beige were measured only on the powerline transects.

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 10th of March and the 4th of April 2004 and February 11 – 13, 2005) and remeasured in the dry season (between the 19th and 24th 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 (μmol 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 m^2 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 ^{o}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$_{30cm}$, canopy temperature, ground surface 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 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 $\text{temperature}_{160\text{cm}}$, air $\text{temperature}_{30\text{cm}}$, canopy temperature, ground surface temperature, soil temperature, $\text{VPD}_{160\text{cm}}$ and $\text{VPD}_{30\text{cm}}$ were calculated using the following formula:

$$\text{Relative Value}_{(i)} = \text{Absolute Value}_{(i)} - \text{Absolute Value}_{(100\text{m})}$$

for each distance i.

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

PAR was $\log_{10}$ 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 the dry season and highway edges in both seasons but was not elevated near creek 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).

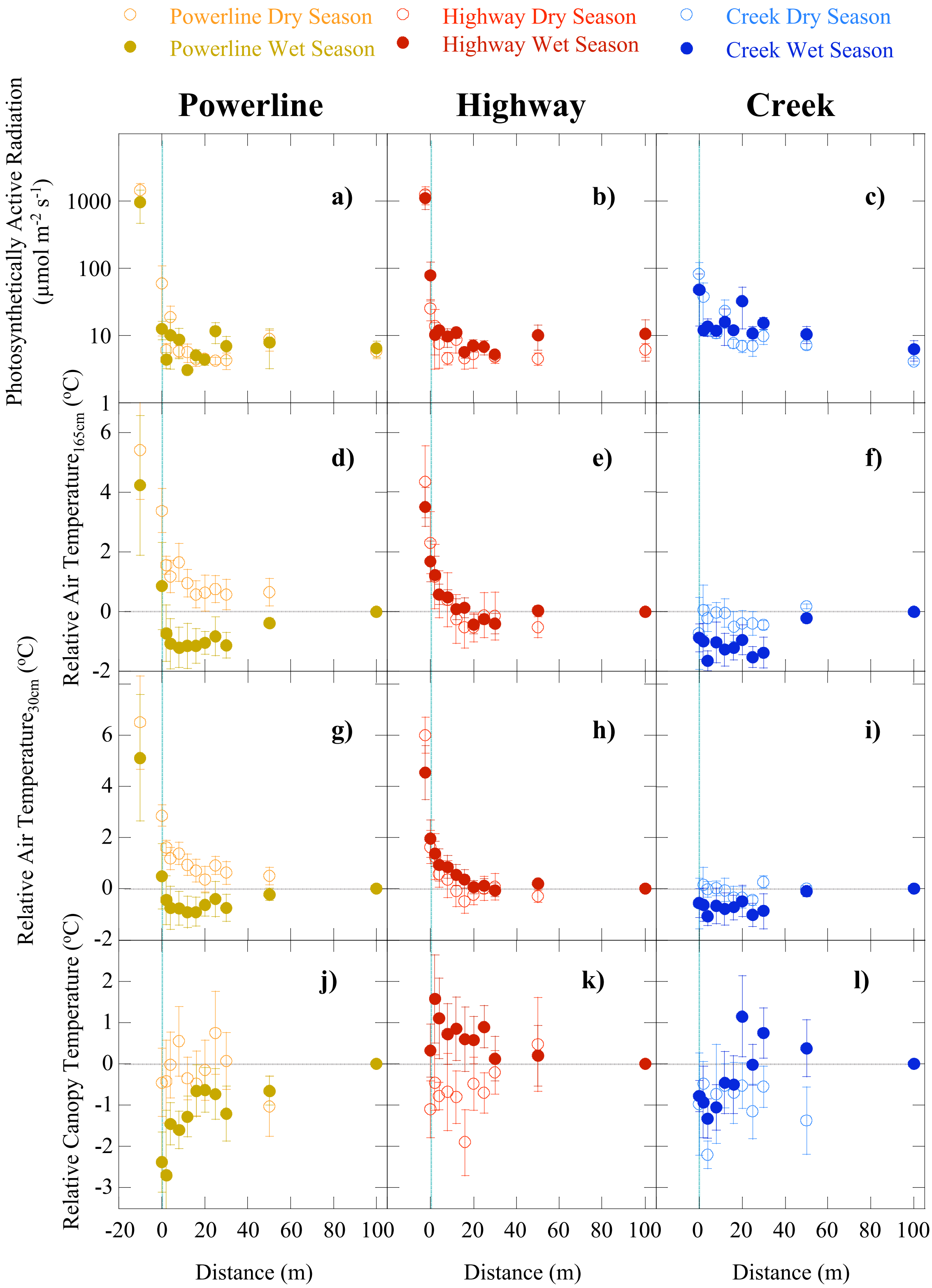
Relative canopy temperature varied with distance from the edge of the forest but the nature of the edge gradient was not consistent between edge types or seasons (Figure 4.2 j, k, l; Table 4.1). Edge gradients appeared to be relatively flat for all three edge types in the dry season; in the wet season,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

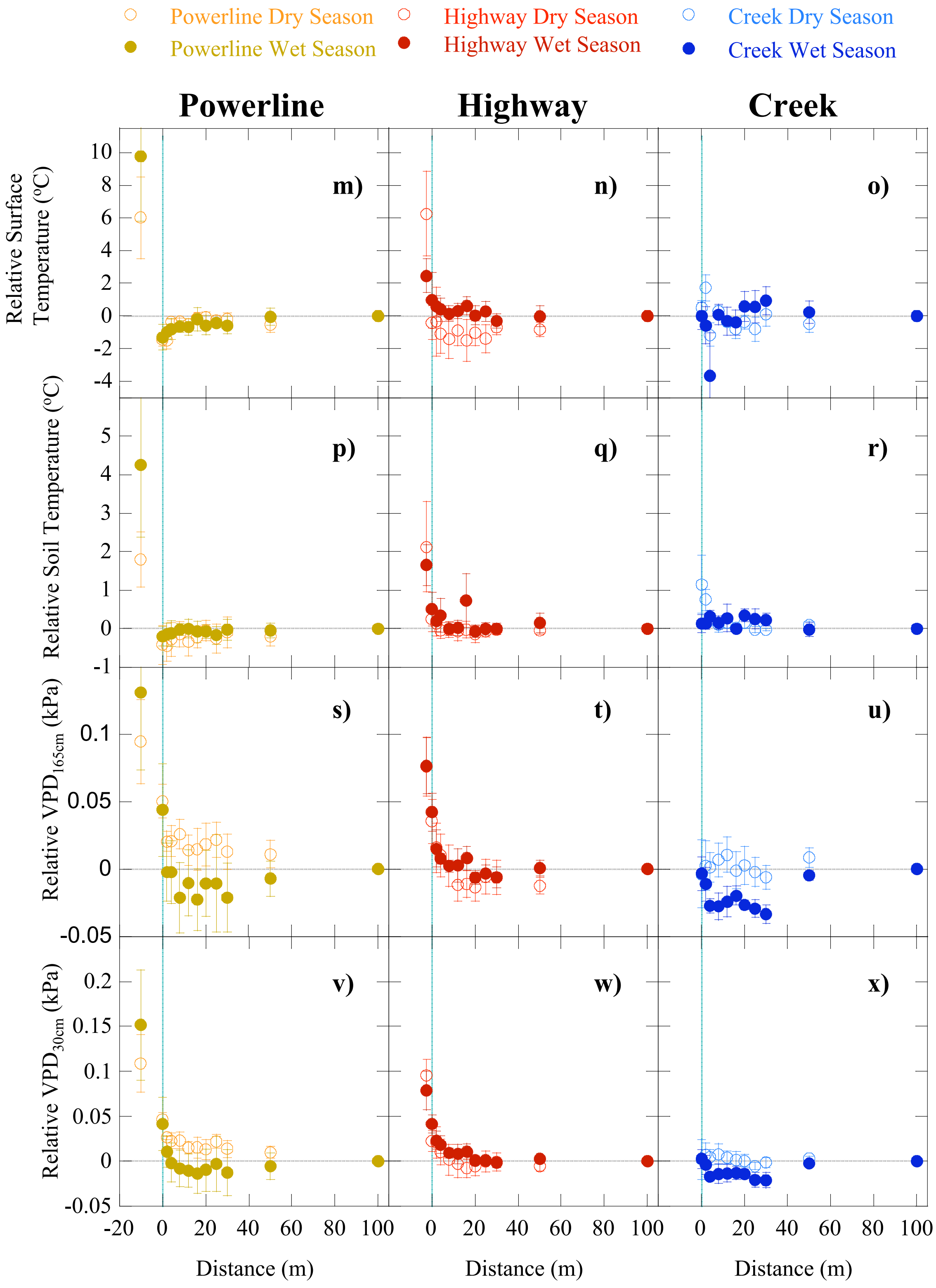
Neither air speed$_{165cm}$ nor air speed$_{30cm}$ were significantly related to distance from the edge, although both were higher in the dry season than the wet season (Figure 4.2 y, z, aa and ab, ac, ad; Table 4.1) and air speed$_{30cm}$ was lower near creeks than near powerlines and highways (ANOVA 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 of between-subject effects are highlighted in bold.

Effect	**Parameter**	***F***	**df**	***p*-value**
Distance	LogPAR (mol m^{-2} s^{-1})	16.561	1	**<0.001**
	Relative Air Temperature$_{165cm}$ (^oC)	1.515	1	0.219
	Relative Air Temperature$_{30cm}$ (^oC)	3.732	1	**0.054**
	Relative Canopy Temperature (^oC)	5.387	1	**0.021**
	Relative Surface Temperature (^oC)	1.836	1	0.177
	Relative Soil Temperature (^oC)	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_2O per g soil)	2.496	1	0.115
Edge Type	LogPAR (mol m^{-2} s^{-1})	16.787	2	**<0.001**
	Relative Air Temperature$_{165cm}$ (^oC)	13.868	2	**<0.001**
	Relative Air Temperature$_{30cm}$ (^oC)	14.126	2	**<0.001**
	Relative Canopy Temperature (^oC)	6.545	2	**0.002**
	Relative Surface Temperature (^oC)	0.963	2	0.383
	Relative Soil Temperature (^oC)	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_2O per g soil)	22.433	2	**<0.001**
Season	LogPAR (mol m^{-2} s^{-1})	1.995	1	0.159
	Relative Air Temperature$_{165cm}$ (^oC)	31.689	1	**<0.001**
	Relative Air Temperature$_{30cm}$ (^oC)	18.796	1	**<0.001**
	Relative Canopy Temperature (^oC)	1.898	1	0.170
	Relative Surface Temperature (^oC)	3.405	1	0.066
	Relative Soil Temperature (^oC)	2.501	1	0.115
	Relative VPD$_{165cm}$ (kPa)	13.795	1	**<0.001**

Effect	**Parameter**	*F*	**df**	***p*-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_2O per g soil)	54.513	1	**<0.001**
Edge Type * Season	LogPAR ($mol\ m^{-2}\ s^{-1}$)	2.330	2	0.099
	Relative Air $Temperature_{165cm}$ (^oC)	13.214	2	**<0.001**
	Relative Air $Temperature_{30cm}$ (^oC)	16.368	2	**<0.001**
	Relative Canopy Temperature (^oC)	16.924	2	**<0.001**
	Relative Surface Temperature (^oC)	4.678	2	**0.010**
	Relative Soil Temperature (^oC)	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_2O per g soil)	1.547	2	0.215


Powerline Dry Season
Powerline Wet Season
Highway Dry Season
Highway Wet Season
Creek Dry Season
Creek Wet Season
Powerline
Highway
Creek
Photosynthetically Active Radiation (μmol m^{-2} s^{-1})
Relative Air Temperature$_{165cm}$ (ºC)
Relative Air Temperature$_{30cm}$ (ºC)
Relative Canopy Temperature (ºC)
a)
b)
c)
d)
e)
f)
g)
h)
i)
j)
k)
l)
1000
100
10
1
6
4
2
0
-2
-3
-1
-20
20
40
60
80
100
Distance (m)
Distance (m)
Distance (m)



○ Powerline Dry Season
● Powerline Wet Season
○ Highway Dry Season
● Highway Wet Season
○ Creek Dry Season
● Creek Wet Season
Powerline
Highway
Creek
Relative Surface Temperature (°C)
Relative Soil Temperature (°C)
Relative VPD$_{165cm}$ (kPa)
Relative VPD$_{30cm}$ (kPa)
m)
n)
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p)
q)
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2
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-0.05
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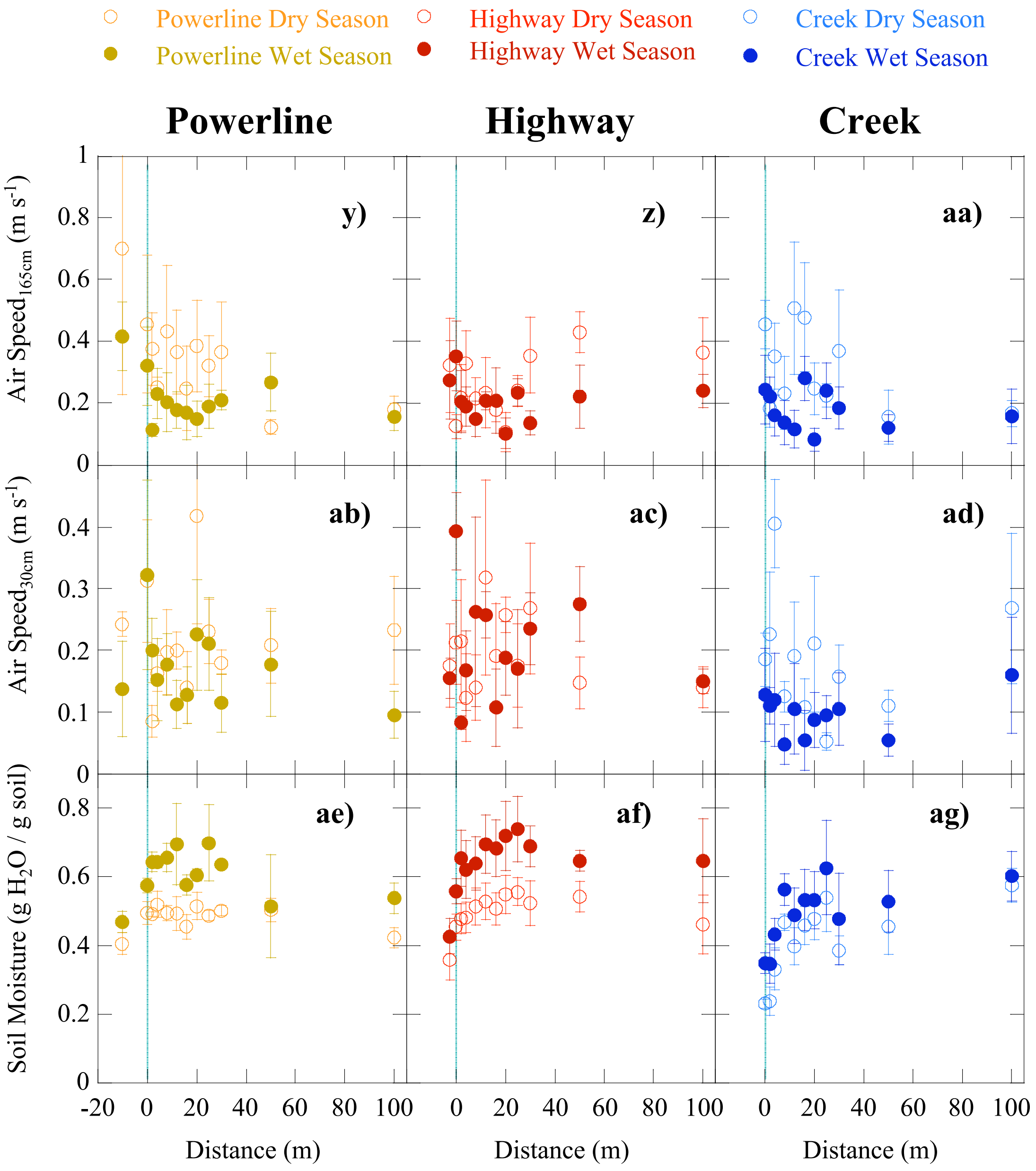


Figure 4.2. Variation in microclimatic parameters with distance from the forest edge. Values represent averages for each distance and error bars represent ±1se. Results for powerline edges are shown in panels on the left-hand side of the figure, highway results are shown in the panels in the centre of 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.

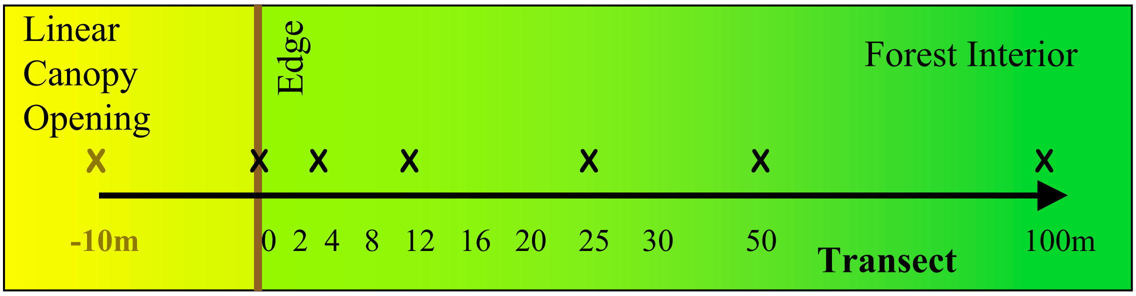


Figure 4.3. The set-up for the datalogger measurements. Measurements were made at each distance marked with an "X". Distances marked in beige were measured only on the powerline transects.

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.

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.

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

4.3.2 Results

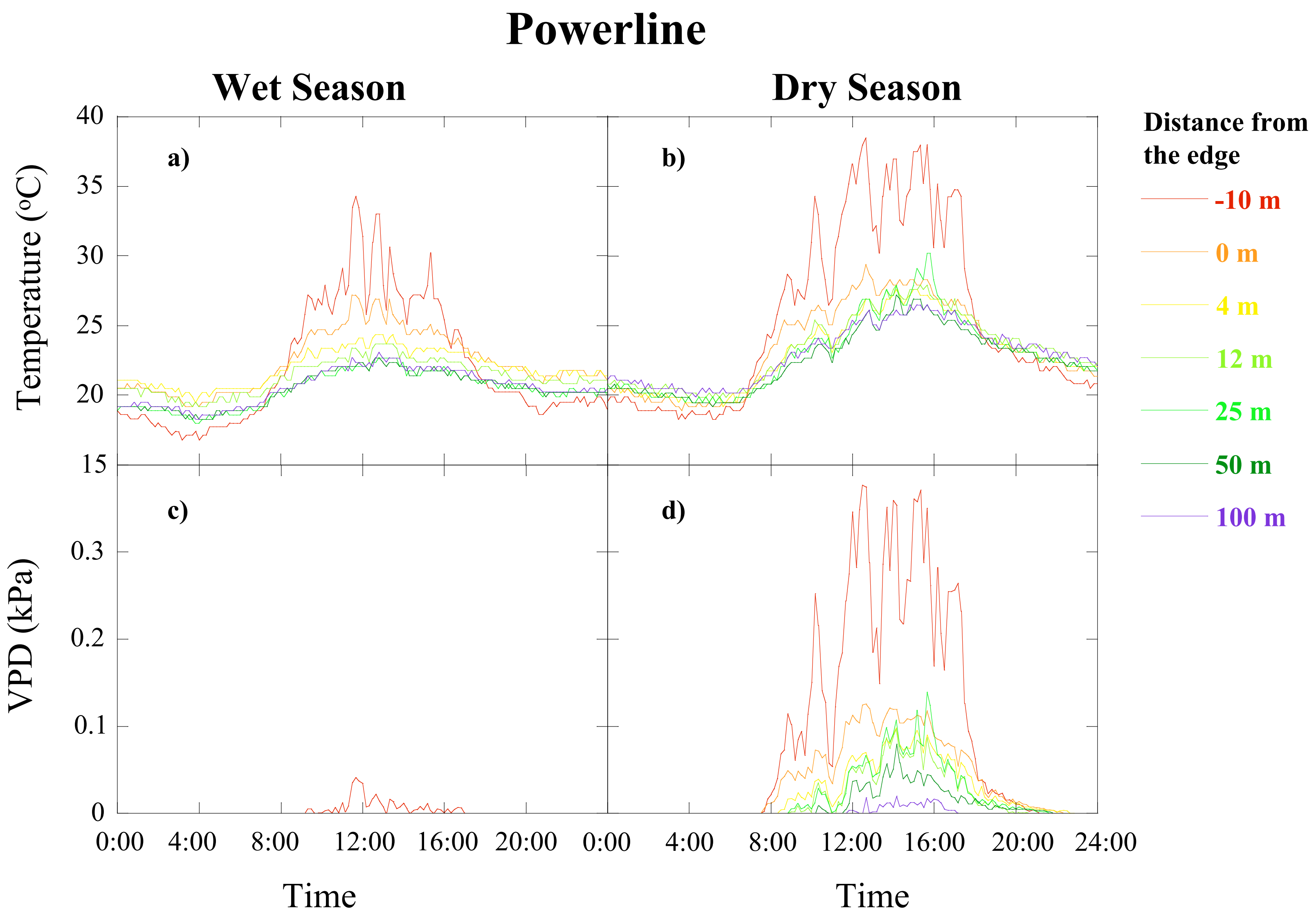
Visual assessment of the data revealed a number of qualitative differences in the diurnal patterns of air temperature, VPD and wind speed between the edges of powerlines, highways and creeks. In the dry season, positive air temperature and VPD gradients (ie higher temperature and VPD values near the 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.

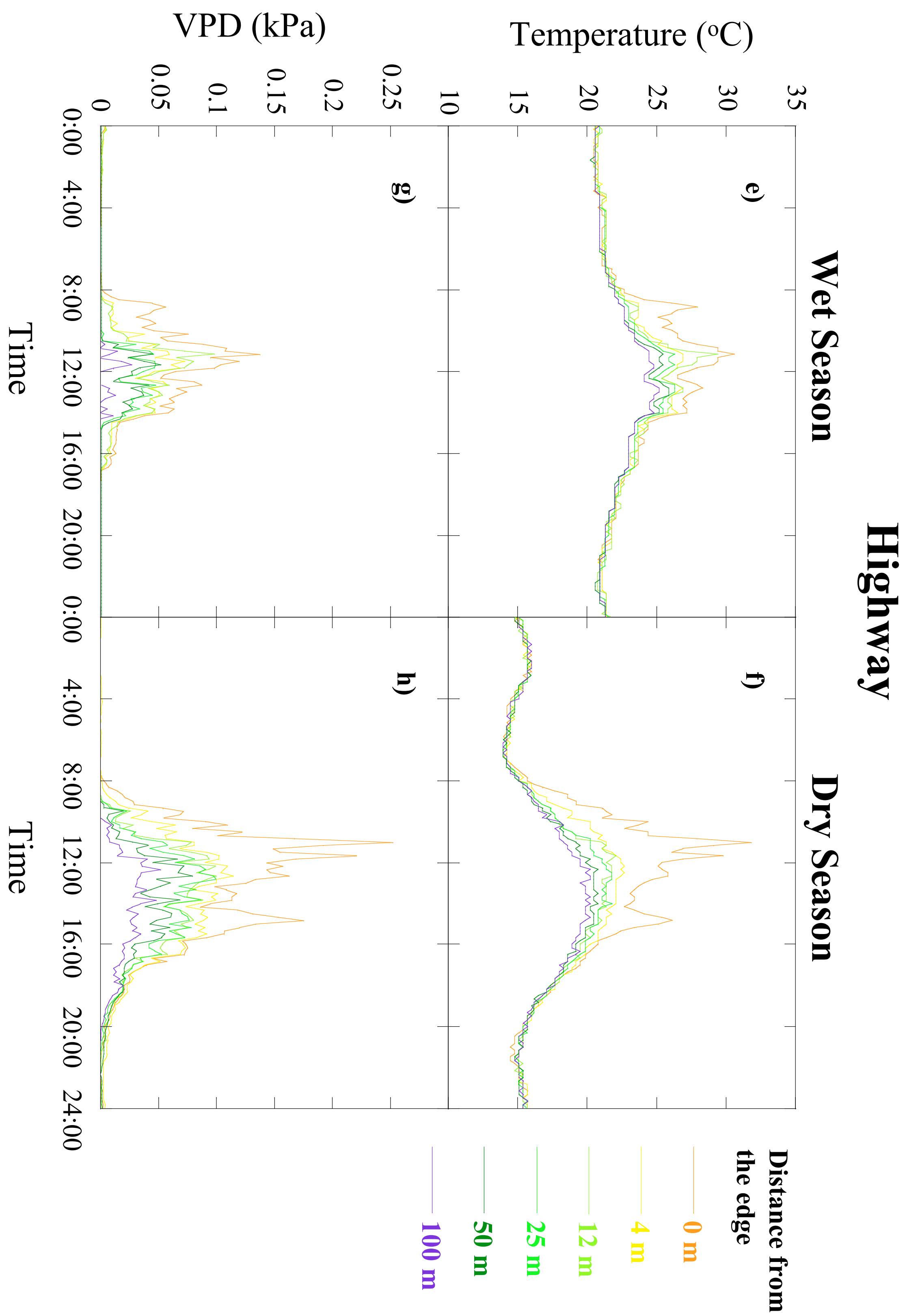
In the wet season, daytime gradients in air temperature and VPD became slightly weaker or more complex in shape and VPD gradients collapsed altogether on wet days, when all VPD values fell to 0 kPa. When positive gradients were present, these extended to between 4 and 25 m. At night, all VPD values fell 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 and to between 4 and 25 m in the wet season.


Powerline
Wet Season
Dry Season
a)
b)
c)
d)
Temperature (°C)
VPD (kPa)
40
35
30
25
20
15
0.3
0.2
0.1
0
0:00
4:00
8:00
12:00
16:00
20:00
0:00
4:00
8:00
12:00
16:00
20:00
24:00
Time
Time
Distance from the edge
-10 m
0 m
4 m
12 m
25 m
50 m
100 m


Highway
Wet Season
Dry Season
Temperature (oC)
VPD (kPa)
35
30
25
20
15
10
0.25
0.2
0.15
0.1
0.05
0
e)
f)
g)
h)
0:00
4:00
8:00
12:00
16:00
20:00
0:00
4:00
8:00
12:00
16:00
20:00
24:00
Time
Time
Distance from the edge
0 m
4 m
12 m
25 m
50 m
100 m

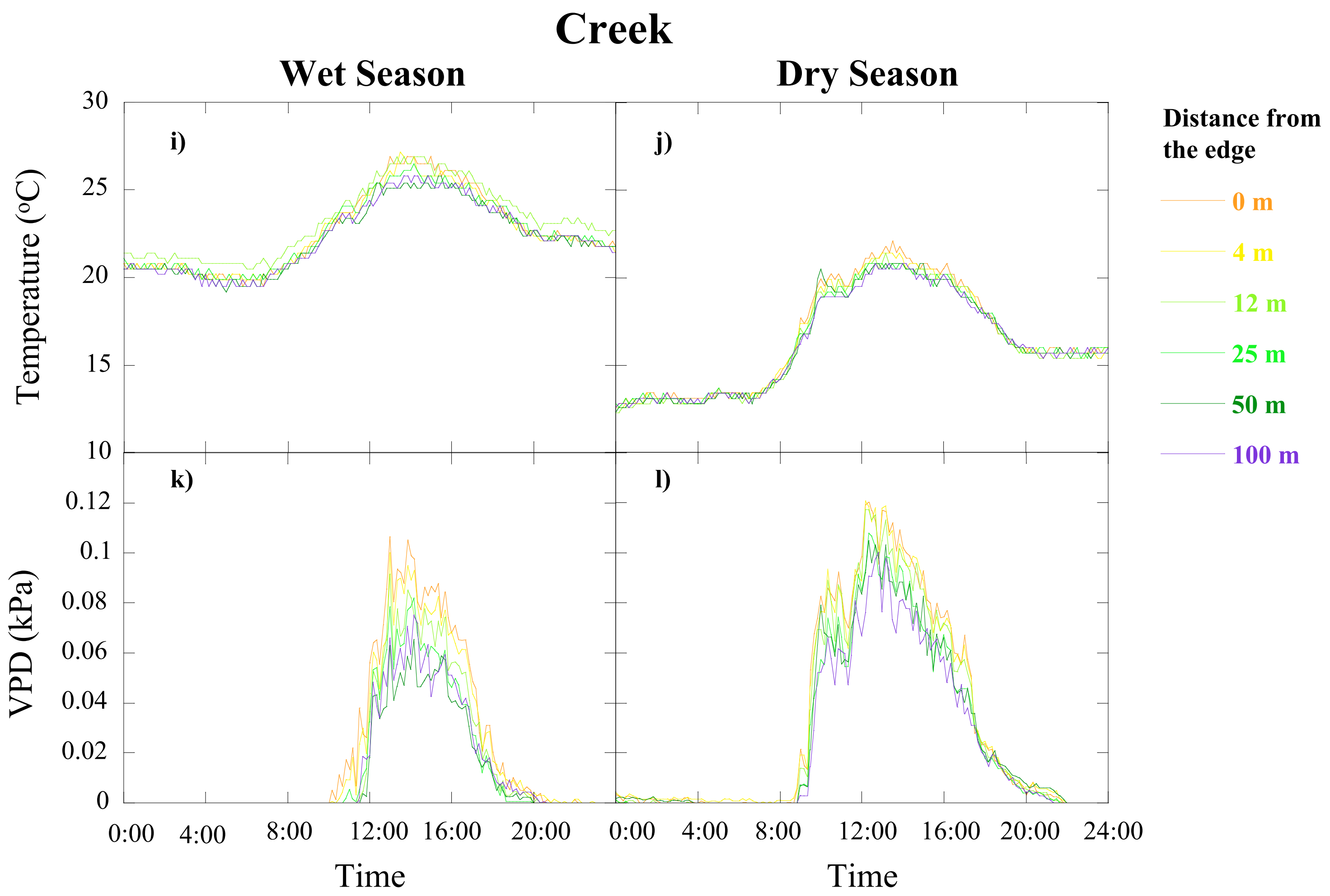


Figure 4.4. Examples of data logger measurements of air temperature and vapour pressure deficit (VPD) for a powerline transect (**a**, **b**, **c**, **d**), a highway transect (**e**, **f**, **g**, **h**) and a creek transect (**i**, **j**, **k**, **l**) in the wet and the dry season. Note the different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

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 diurnal temperature and VPD ranges. Significant effects are highlighted in bold. In cases where the edge type * season effect is significant for a parameter, the individual edge type and season effects for that parameter should be disregarded.

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

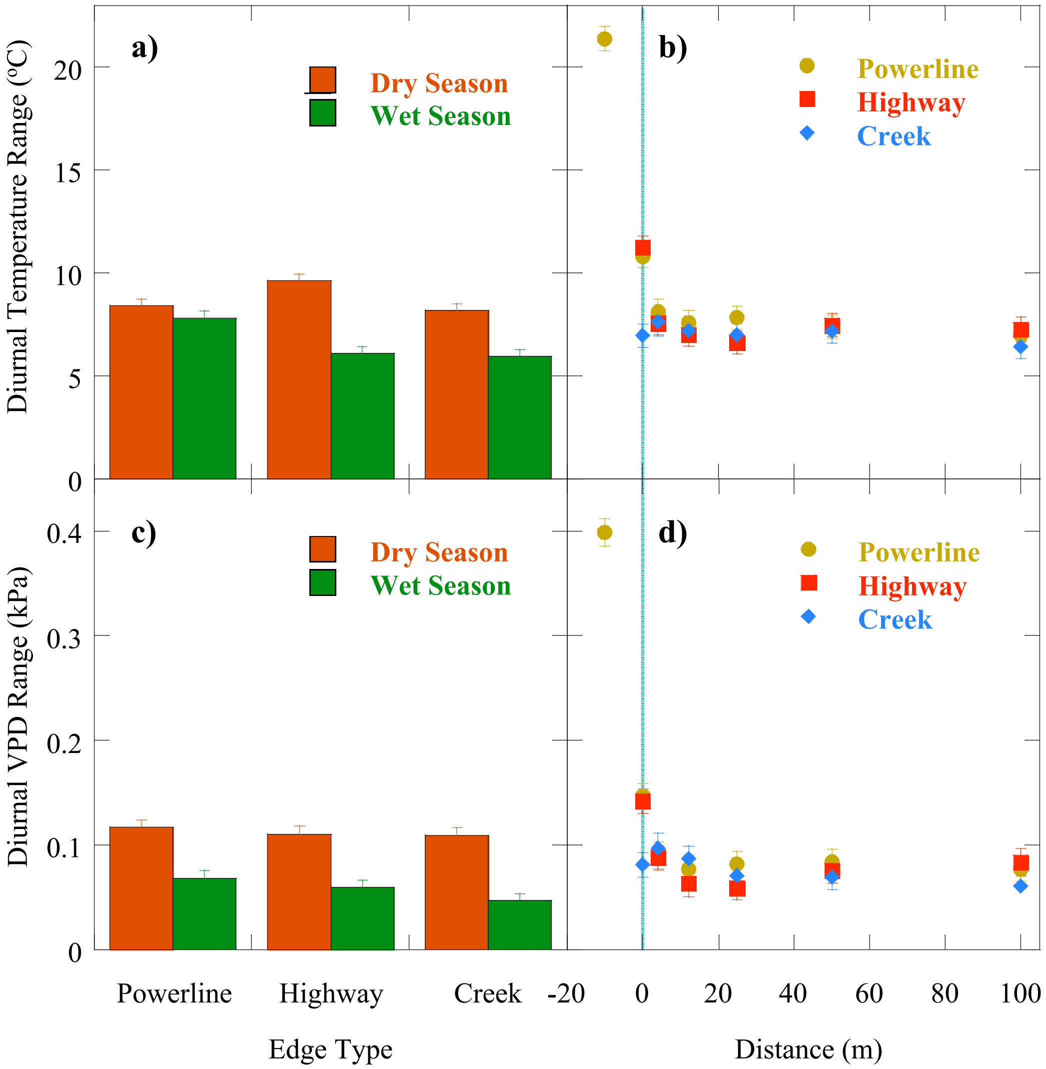


Figure 4.5. Variation in the diurnal range of air temperature (**a**, **b**) and vapour pressure deficit (**c**, **d**). Edge type by season interactions are shown in panels **a** and **c**; edge type by distance interactions are shown in panels **b** and **d**. The vertical dashed lines in panels **b** 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	*p* – 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**

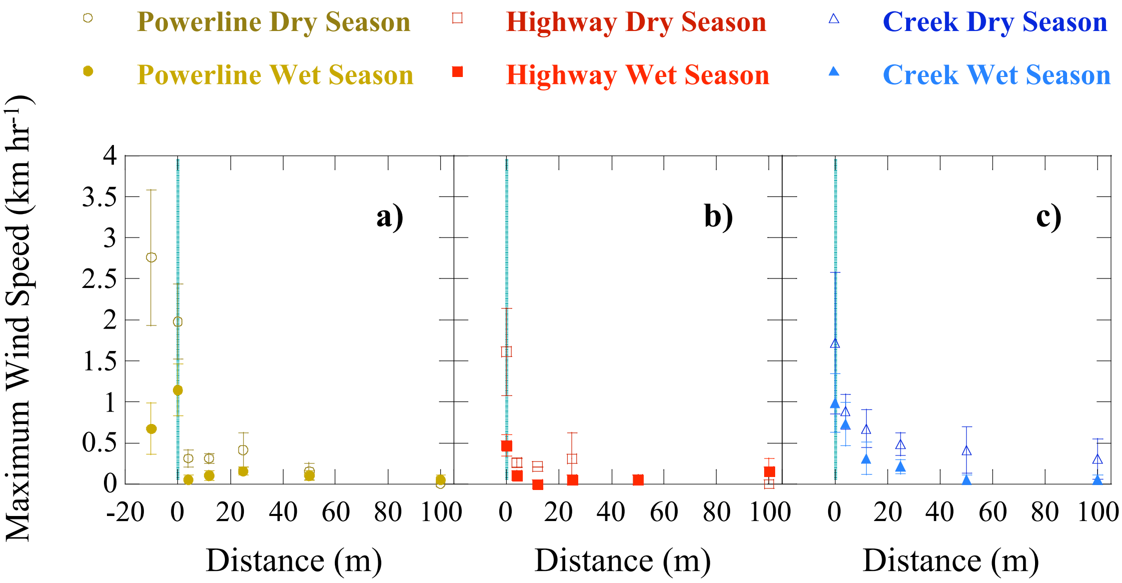


Figure 4.6. Variation in maximum wind speed measured near **a**) powerline, **b**) highway and **c**) creek edges. The vertical dashed line indicates the position of the forest edge; values for the distance of -10 m on powerline transects were not included in the statistical analyses but are shown here 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.

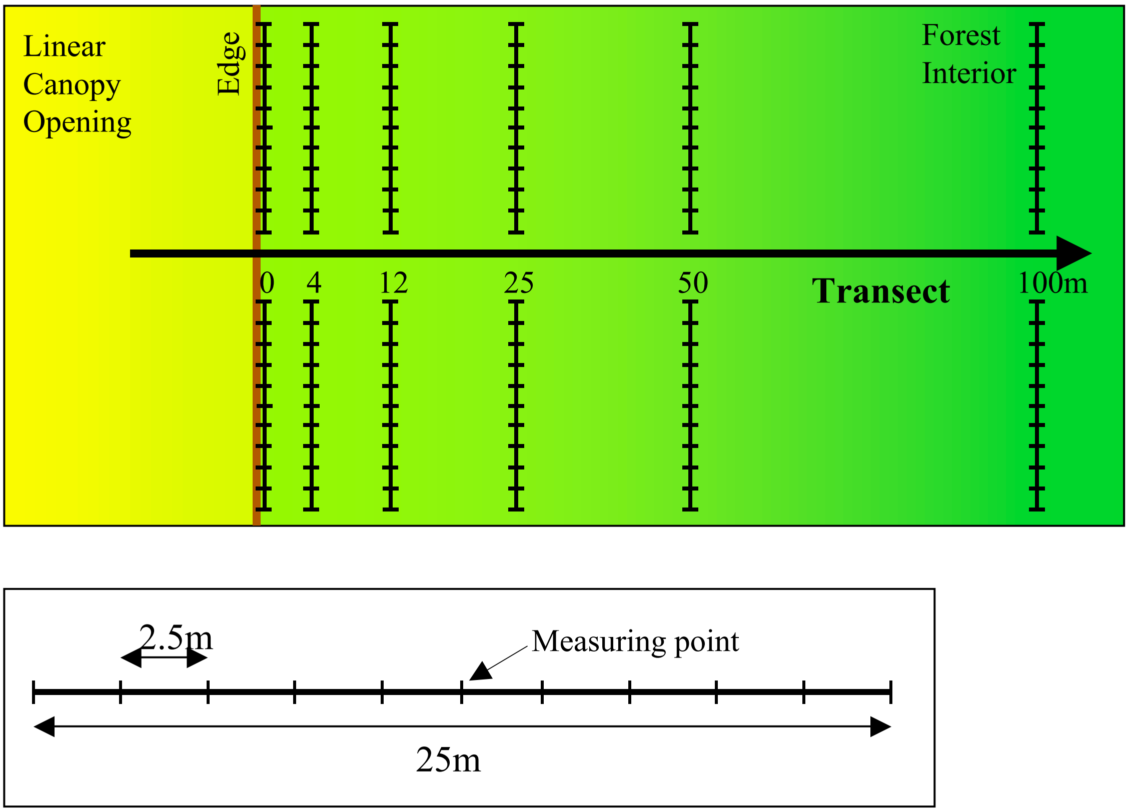


Figure 4.7. The field site survey design for the red:far red measurements. Three red:far red ratio measurements are taken within 25 cm of each measuring point and averaged.

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.

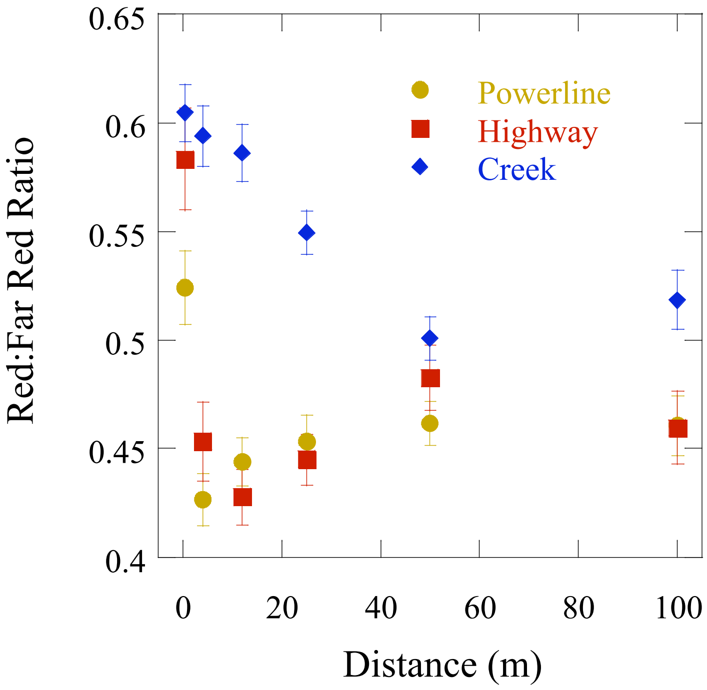


Figure 4.8. Red:Far Red ratio, means for the edge type by distance interaction. The red:far red value for the powerline at 100 m is hidden behind that of the highway at 100 m. Error bars represent ± 1 se.

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, $p = 0.631$).

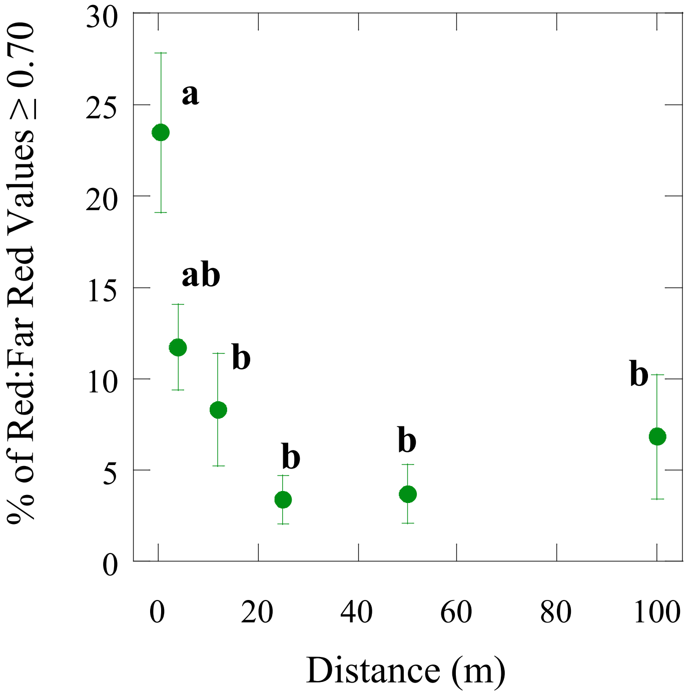


Figure 4.9. Percentage of red:far red values ≥ 0.70. Error bars represent ± 1 se. Values that share a letter are not significantly different to each other (ANOVA, Bonferroni *post hoc* test, $p < 0.05$).

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.