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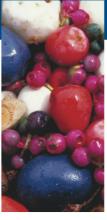
The effects of Severe Tropical Cyclone *Larry* on rainforest vegetation and understorey microclimate adjacent to powerlines, highways and streams in the Wet Tropics World Heritage Area

Catherine Pohlman and Miriam Goosem













Australian Government

Department of the Environment, Water, Heritage and the Arts

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Executive Summary

Project Objectives

Severe Tropical Cyclone *Larry* crossed the coast of Queensland on 20 March 2006, damaging a large swathe of rainforest to the west of Innisfail in the Wet Tropics World Heritage Area. Within the path of the most destructive core of Cyclone *Larry* were sites previously established for a study on the effects of human-made (powerlines and highways) and natural (streams) linear canopy openings on adjacent rainforest plant communities.

Measurements of vegetation damage and understorey microclimate (light intensity, air temperature and humidity, wind speed, soil temperature and soil moisture) were made six months following the passage of Cyclone *Larry* and were compared with measurements made at the same study sites prior to the cyclone. The purposes of these measurements were to:

- Determine whether cyclone damage to vegetation was greater near the edges of humanmade and natural linear canopy openings than in the forest interior; and
- Examine the influence of this vegetation damage (and consequently changes in rainforest canopy structure) on the microclimatic regimes experienced in the rainforest understorey.

Key Findings

- 1. Vegetation damage was slightly reduced near powerline edges, slightly elevated at intermediate distances from highway edges, and slightly elevated near stream edges, relative to the forest interior.
- 2. Changes in the understorey microclimatic regime mirrored the degree of damage to vegetation.
- 3. Where vegetation damage was greater, the understorey microclimate was brighter, warmer, drier and windier than below less-damaged areas of the forest canopy.
- 4. It is possible that the elevated damage at stream edges was due to a combination of two factors. Firstly, flood disturbance was noticeable: a number of trees near the edge were washed out by flood waters. Secondly, the species composition and forest structure near stream edges may be more vulnerable to cyclone damage, as stream edges have a greater proportion of pioneer species. Pioneer species suffered greater damage than mid- or late-successional tree species and these species also generally have a lower canopy and subcanopy foliage density than those commonly found at forest edges near powerlines or highways.
- 5. Prior to the cyclone, forest edges near powerlines and highways had developed a greater degree of edge 'sealing' than forest near stream edges (i.e. greater canopy and subcanopy foliage density) and thus reduced light availability and reduced recruitment of pioneers, weeds and other light-loving species. These 'sealed' edges may have been less prone to cyclone damage or may have offered some protection to the forest near the edge.

Management Implications and Recommendations

1. The 'sealed' forest edges near powerlines and highways appear to have offered the forest edge some degree of protection from the more severe wind damage observed near creek edges. Therefore we recommend that, for infrastructure corridors where it is not possible to minimise the footprint of the clearing (for example by raising the

- powerline above the canopy), such 'sealed' edge development should be encouraged. This could be achieved through minimising disturbance to the forest edge during infrastructure and easement maintenance.
- 2. Unfortunately, the microclimatic changes following Cyclone *Larry* have favoured the germination and growth of numerous pioneer and weed species. Initial observations suggest that the abundance of exotic plant species within the rainforest understorey has increased substantially since the cyclone. It is recommended that this situation should be monitored to identify potential problems.

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Abbreviations Used In This Report

ANCOVA...... analysis of covariance

DBH...... diameter of tree at breast height

MANOVA multivariate analysis of variance

PAR...... photosynthetically active radiation

SE..... standard error of the mean

VPD vapour pressure deficit

Glossary

South America. forest floor and the forest canopy. This foliage may comprise lateral branches from trees, crowns of saplings and shrubs as well as lianas and seedlings. Sealed edges often develop over time. as foliage growth is stimulated by higher light levels near the forest edge. Open edgeForest edge without continuous foliage between the forest floor and the forest canopy. Forest edges are 'open' when first created and may become sealed over time. Alternatively, forest edges may remain open if other factors prevent them from developing a sealed edge. Photosynthetically active radiation Sunlight between 400 and 700 nm in wavelength, required by plants for photosynthesis. Tree successional status......Approximation of the response of a tree species to both disturbance and light availability. Tree species have been classified as either early successional, mid successional or late successional in this report. Early successional species are unable to germinate in shade (i.e. beneath an intact forest canopy), have fast growth rates, require high light levels to survive and grow and are favoured by larger forest disturbances. Late successional species are able to germinate in shade, have seedlings which are able to survive in the shade, have slow growth rates and may persist as suppressed seedlings or saplings for long periods of time beneath the forest canopy. Mid successional species have properties intermediate between early and late successional species. These successional categories also correspond approximately to the positions occupied by species within a sequence of secondary forest succession that occurs when an area of primary forest is cleared. Understorey microclimateClimatic conditions experienced within approximately two metres of the forest floor; includes, but is not limited to, light level, air temperature and humidity, wind speed, soil temperature and soil moisture. Vapour pressure deficitThe difference between the moisture holding capacity of saturated air and the actual air moisture. As the air within a leaf's pores is saturated while the air outside the leaf is not, vapour pressure deficit is also a measure of the moisture stress exerted on a plant leaf.

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Mr Rigel Jensen identified plant species for the original vegetation survey and Ms Tina Lawson (Research Officer, School of Earth and Environmental Sciences, James Cook University) prepared the maps featured in this report with data from Geosciences Australia.

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Introduction

Natural and anthropogenic disturbance near linear canopy openings

Interactions between natural and anthropogenic disturbance may affect the physical structure and species composition of plant communities (Chazdon 2003). Forest fragmentation as a result of human activities has the potential to alter the ecological responses of remaining areas of forest to natural disturbances such as cyclones, fires or droughts (Laurance 1991, 1997; Laurance et al. 1997, 2001, 2002; Cochrane and Laurance 2002). In particular, trees at the forest edge may be exposed to greater levels of physical stress and wind damage than trees within continuous forest (McNaughton 1989). Elevated levels of tree damage and mortality have been reported near the edges of tropical forest fragments in central Amazonia, apparently in response to a combination of increased moisture stress and greater wind turbulence (Ferreira and Laurance 1997; Laurance et al. 1997, 1998, 2000, 2002; D'Angelo et al. 2004). Similarly, elevated levels of wind throw and tree mortality near forest edges have been reported in boreal forests (Essen 1994; Harper et al. 2005), temperate forests (Chen et al. 1992; Burton 2002; Baldwin and Bradfield 2005; Harper et al. 2005) and neotropical rainforests (Williams-Linera 1990; Leigh et al. 1993), although other studies have reported no increase in wind throw (Lin et al. 2004) or decreased wind throw (Ryall and Smith 2005) near forest or plantation edges. There have been relatively fewer studies of the effects of cyclones and intense storms on vegetation damage in fragmented forests, although elevated levels of cyclone damage to trees have been reported for rainforest edges in northeastern Australia (Laurance 1991, 1997).

Even less is known about the effects of linear infrastructure clearings on the disturbance regimes and ecology of adjacent forest. Tree mortality may be elevated near the edges of such clearings in tropical rainforest in non-cyclonic conditions (Pohlman 2006). However, it is not known whether increased wind exposure at the edges of linear clearings increases rates of vegetation damage and mortality in either normal weather conditions or during intense storms and tropical cyclones. Although there have been anecdotal reports of increased cyclone damage to rainforest near roads and railways in northeastern Australia (Webb 1958), the relationship between proximity to linear clearings and cyclone damage has never been directly examined. If severe wind storms do lead to elevated levels of tree damage and mortality near powerline edges, this may have implications for the dynamics (recruitment, growth and mortality rates [Laurance 1997; Laurance et al. 2002]) of rainforest tree communities and subsequently, their species composition and diversity (e.g. Leigh et al. 1993; Asquith and Mejia-Chang 2005).

Severe Tropical Cyclone Larry

On 20 March 2006, Severe Tropical Cyclone *Larry* passed directly over the Wooroonooran National Park in the Wet Tropics World Heritage Area of northeastern Queensland. Research sites had previously been established along the Kareeya to Innisfail powerline, along the Palmerston Highway and along Henrietta Creek; all were within the path of the most destructive core of the cyclone (Turton in prep). Initial reconnaissance indicated that these sites were severely damaged (although not completely devastated) and that most of the original site markers had survived the cyclone. This provided a rare opportunity to compare measurements taken before the cyclone with those taken after the cyclone, and to determine whether severe storm damage is greater near the edges of powerline clearings (as well as highway clearings and natural watercourses) than in the rainforest interior.

1

Research Questions

Two research questions were investigated:

- 1. Is cyclone damage to trees and saplings greater near the edges of linear canopy openings (powerline clearings, highways and watercourses) than in the rainforest interior?
- 2. What are the subsequent changes in understorey microclimate (light intensity, air temperature and humidity, soil temperature and moisture and wind speed) near the edges of linear canopy openings?

Methodology

Study Sites

Edge gradients in vegetation damage and microclimate were investigated near three types of linear canopy openings: powerlines, highways and creeks (Figure 1, Figure 2). 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. Sites were located at elevations between 350 and 720 m above sea level on fertile soils derived from basalt. Prior to Cyclone *Larry*, the forest in this area was 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 3307 mm, 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).

Two sites separated by at least three kilometres were established per edge type (powerline. highway or creek). Two transects, each running for 100 m adjacent to the forest edge were established on opposite sides of the linear canopy opening at each site. Previous studies of rainforests in northeast 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 (Siegenthaler and Turton 2000; Turton and Freiburger 1997). 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 1). To avoid confounding the effects of edge type with other environmental gradients (e.g. soil type, forest type, annual precipitation), only one linear feature per canopy opening type (powerline versus highway versus creek) was included in the study (the Kareeya to Innisfail powerline, the Palmerston Highway and Henrietta Creek). However, as the sites covered a range of elevations and were physically separated by several kilometres, these data allowed us to assess variation in the nature of the associated edge effects among the three linear canopy opening types within the study area. Full site descriptions are given in Pohlman et al. (2007). All field sites were within the area affected by the very destructive core of Tropical Cyclone *Larry* (Turton in prep).

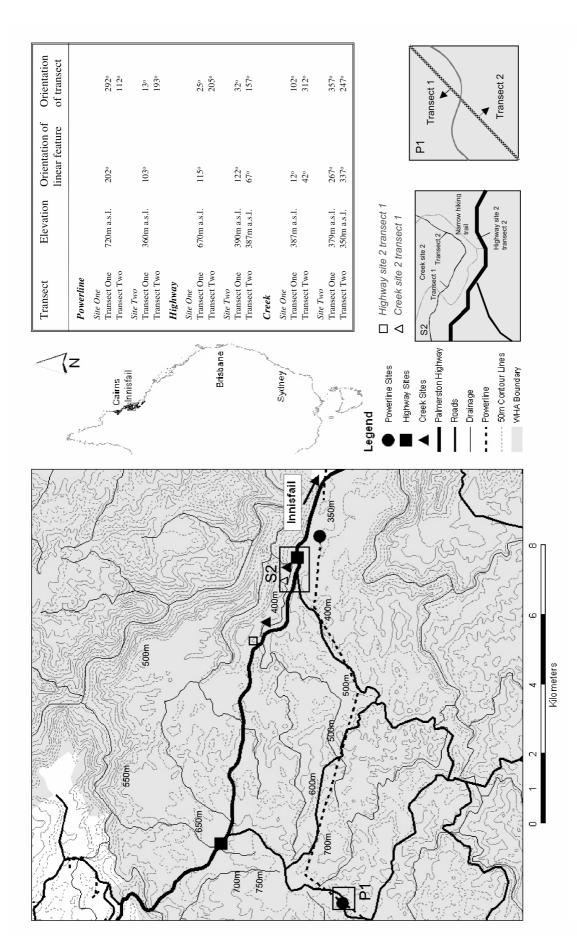


Figure 1: Study area in Wooroonooran National Park and South Johnstone State Forest. Inset P1 shows the layout of powerline site 1 and inset S2 shows the layout of creek site 2 and highway site 2, transect 2. Map produced by Tina Lawson with data from Geosciences Australia (after Pohlman *et al.* 2007).

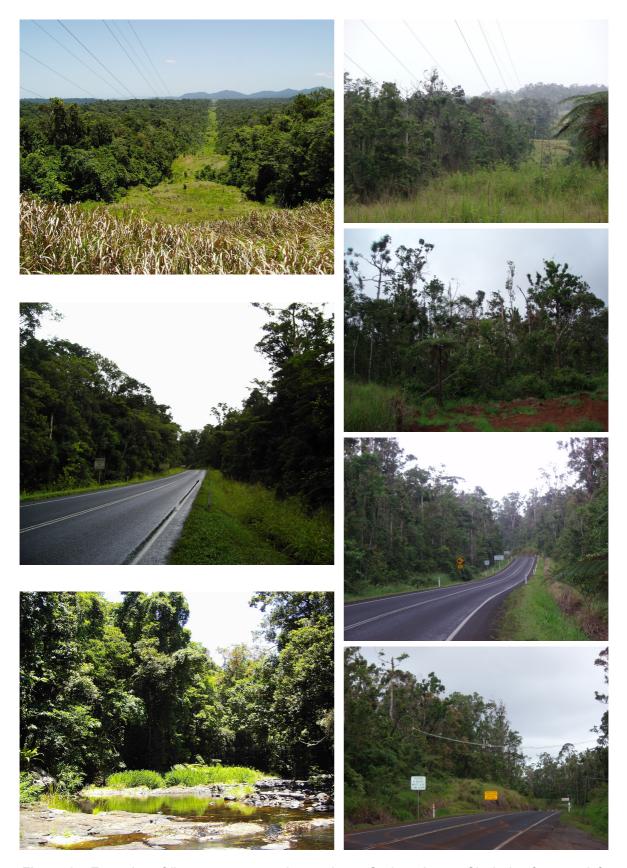


Figure 2: Examples of linear canopy openings, prior to Cyclone *Larry*. Clockwise from top left: Palmerston powerline (first three images); Palmerston Highway (following two images); Henrietta Creek; Palmerston Highway.

Vegetation Damage

Vegetation was surveyed at each transect between August 2003 and July 2005 as part of a study on the effects of linear canopy openings on vegetation structure and composition (Pohlman 2006). Trees (stems \geq 5 cm diameter at breast height [DBH]) were surveyed at 0 m, 4 m, 12 m, 25 m, 50 m and 100 m from the forest edge, within 50 m \times 1 m survey plots running parallel to the forest edge. Saplings (stems 2-4.9 cm DBH) were surveyed within 50 m \times 0.5 m subplots (placed within each tree survey plot). The diameter of all stems was measured and all trees and saplings were identified to species level by a local expert (Mr Rigel Jensen). There were no significant disturbances to the rainforest canopy within the initial survey period.

Six months after Cyclone *Larry* (7-21 September 2006), we revisited these survey plots and were able to determine the fate of 97.67% of stems \geq 5 cm DBH and 95.38% of stems 2-4.9 cm DBH, as these stems were tagged with brightly-coloured flagging tape which had survived the passage of the cyclone. As leaf resprouting and epicormic growth (*pers. obs.*) had begun by this time, we were unable to assess leaf damage. We recorded damage to branches and stems for each tree and sapling and divided trees and saplings into damage categories of increasing severity (Table 1).

To examine whether vegetation damage was elevated near the edges of linear canopy openings relative to the forest interior, we analysed the data for trees (stems ≥ 5 cm DBH) using an analysis of covariance (ANCOVA) with fixed factors edge type (powerline, highway or creek) and distance from the forest edge (0, 4, 12, 25, 50 and 100 m) and the covariates tree size (diameter at breast height [DBH]), successional status (early-successional ['pioneer' species], mid-successional and late-successional ['climax' or 'primary forest' species]), wood density and growth habit (understorey tree species and canopy tree species). The dependent variable was the damage category recorded for each individual stem. Treeferns and lianas were not included in this analysis. Data on the growth habit and successional status of each species were obtained from the literature (firstly Cooper and Cooper 1994; Hyland et al. 2003: subsequently from Williams 1984, 1987; Osunkoya 1996; Tucker and Murphy 1997; Jackes 2001; Tucker 2001; White et al. 2004) and from expert advice (Dr Steve Goosem pers. comm.). Data on the wood density of individual tree species were obtained from Osunkoya (1996), Cause et al. (1989), Hyland (1989) and from expert advice (Dr Steve Goosem, pers. comm., citing Floyd [1989] and Watson [1951]). Where the wood density of an individual species could not be obtained, a family average (obtained from data in Cause et al. 1989 and Smith et al. 1991) was used as a surrogate (Appendix 1). In the case of one species (Phaleria clerodendron, Thymelaeaceae), no wood density data was available for either the species or the family so the mean wood density of the entire dataset (Appendix 1) was used.

Data on saplings (stems 2-4.9 cm DBH) were analysed using Kruskal-Wallis tests to test for the effects of edge type (powerline, highway or creek) and distance from the edge, as well as growth habit (shrub species, understorey tree species and canopy tree species) and successional status (early-successional, mid-successional and late-successional species) on the damage category recorded for each individual stem. All statistical analyses were performed using SPSS version 11.0.4 for Macintosh.

Table 1: Damage categories for trees and saplings.

Trees (≥ 5 cm DBH)		Saplings (2-4.9 cm DBH)			
Code	Name	Description	Code	Name	Description
0	Intact	No obvious damage.	0	Intact	No obvious damage.
1	Minor branch damage	Few (< 10%) branches lost or only light branch damage sustained.	1	Minor branch damage	Few (< 10%) branches lost or only light branch damage sustained.
2	Bent	Trunk bent < 45° and unbroken.	2	Bent	Trunk bent < 45° and unbroken, tree crown clear of ground and debris.
3	Moderate branch loss	≤ 50% branches lost or heavily damaged.	3	Pinned	Trunk bent but not broken or uprooted. Substantial part of sapling beneath other debris.
4	Major branch loss	> 50% branches lost or heavily damaged.	4	Moderate branch loss	≤ 50% branches lost or heavily damaged.
5	Snapped > 10 m	Trunk snapped > 10 m height.	5	Major branch loss	> 50% branches lost or heavily damaged.
6	Snapped 2-10 m	Trunk snapped between 2 and 10 m height.	6	Snapped > 2 m	Trunk snapped > 2 m height.
7	Snapped < 2 m	Trunk snapped < 2 m height [‡] .	7	Snapped < 2 m	Trunk snapped < 2 m height.
8	Uprooted	Visible signs of uprooting [†] .	8	Uprooted	Visible signs of uprooting [†] .

[†] Trees and saplings which were washed out near creek banks were included in category 8 ('uprooted').

Understorey Microclimate

We used two complementary methods to investigate the nature of the relationship between understorey microclimate and distance from the forest edge and to explore the effect of vegetation damage from Cyclone *Larry* on these microclimatic edge gradients. Traverse measurements were used to assess the extent and severity of edge gradients in light intensity, soil temperature and soil moisture during daylight hours and data loggers were used to measure diurnal changes in microclimatic edge gradients in air temperature, vapour pressure deficit and wind speed.

Traverse Measurements

The traverse method allows the rapid measurement of spatial variation in forest understorey microclimate (Turton and Freiburger 1997). Measurements began at the outermost point of each transect and continued inwards, towards the forest interior, as swiftly as possible. Measurements were made at 0, 2, 4, 8, 12, 16, 20, 25, 30, 50 and 100 m for all transects (and at -10 m on powerline transects). Previous studies in rainforests in northeast 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; Siegenthaler and Turton 2000).

Microclimate measurements were undertaken in clear or relatively clear (cloudy or overcast but not raining) weather, between 10:00 am and 3:00 pm, to avoid the collapse of edge gradients that occurs at low solar angles (Chen *et al.* 1995; Turton and Freiburger 1997).

[‡] Trees which were flattened beneath tree-fall debris were included in category 7 ('snapped < 2 m').

Pre-cyclone measurements were made in the dry season of 2004 (September 2004; described in Pohlman *et al.* 2007). Pre-cyclone measurements included an expanded range of microclimatic parameters (Pohlman *et al.* 2007) and it took between three and five minutes to take all measurements at any one measuring point and between sixty and ninety minutes to complete a full transect. Post-cyclone measurements were made in the dry season of 2006 (5-6 October 2006), using a reduced set of parameters (the complete set of parameters could not be measured, as damage to the vegetation made it logistically impossible to carry all of the necessary equipment through the forest) and it took approximately 20-25 minutes to complete each transect.

Parameters measured were photosynthetically active radiation (PAR), soil temperature and soil moisture. Photosynthetically active radiation (PAR) (electromagnetic radiation between 400 and 700 nm in wavelength) was measured at a height of 165 cm, 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 sec⁻¹) at each point over fifteen seconds. The quantum sensor and display meter were mounted on a 165 cm-tall portable frame of PVC pipe (Figure 3). PAR was measured without simultaneous "open" controls because we were not attempting to measure canopy transmittance; we were interested instead in the mean edge gradients in light level and air speed.

Soil temperature was measured using a 5 cm soil probe (Testo 106-T1, Testo Inc. Flanders, NJ, USA). Pre-cyclone soil moisture (mL/g soil dry weight) was measured from samples taken using a bulb planter to extract soil samples to 10 cm depth. Samples were roughly homogenised and sub-sampled, then weighed prior to and after drying in an oven for a minimum of 48 hours at a temperature of 106°C (until constant weight had been achieved). Post-cyclone soil moisture was measured using a HydroSense soil moisture probe (HydroSense Soil Water Content Measurement System, Campbell Scientific Inc. Logan, UT, USA). Soil moisture measurements were transformed to allow gradients in soil moisture to be compared between years. Proportional soil moisture values were calculated using the following formula:

Proportional
$$Value_{(i)} = \frac{Absolute \ Value_{(i)}}{Absolute \ Value_{(100m)}}$$
 (Eq. 1)

for each distance i.

Thus, the value for each of these parameters at the distance of 100m (forest interior) was always 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 soil temperature (this section), air temperature and VPD (next section) were calculated using the following formula:

Relative
$$Value_{(i)} = Absolute \ Value_{(i)} - Absolute \ Value_{(100m)}$$
 (Eq. 2) for each distance *i*.

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



Figure 3: The instruments used for the traverse microclimate measurements were supported on a PVC frame. The quantum sensor was attached to the top of the frame (on a levelling mount). The person pictured is Stephen Pohlman. Photo by Catherine Pohlman.

Data for each parameter were analysed using analysis of covariance (ANCOVA) with fixed factors of edge type (powerline, highway and creek) and year (pre-cyclone [2004] and post-cyclone [2006]) and covariate of distance. Distance was included as a covariate, as it is a continuous variable that cannot be broken into discrete treatment levels. Data for PAR were log_{10} -transformed to approximate normality. Measurements taken at -10m along powerline transects were not included in the analyses, as these values introduced significant outliers into the dataset; values measured at -10 m are shown in the results section for comparison only. Transects were treated as replicates in these analyses (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) and several were also separated by some distance (Figure 1). All statistical analyses were performed using SPSS version 11.0.4 for Macintosh.

Diurnal Variation

Data loggers were used to measure diurnal variation in microclimatic edge gradients. 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. For powerline transects, an additional data logger was placed at -10 m from the forest edge. Budget constraints dictated the monitoring of one transect at a time with the data loggers available. Transects were monitored in a semi-random order for a period of at least four consecutive days in each season in which measurements were made.

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. 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 (Figure 4).

Post-cyclone measurements were made in the dry season of 2006 (between 22 August 2006 and 13 January 2007) and compared with pre-cyclone measurements taken in the dry season of 2004 (between 12 September and 22 December 2004). As there was variation in the length of time data loggers were left at each transect (due to weather and logistical constraints), a subset of four consecutive days of data (the minimum period for which each transect was monitored) was selected from the available data for each transect for each year (the four days selected were either the first four days recorded for each transect or the first four days recorded without large excessive humidity).

To examine the effects of cyclone disturbance and proximity to the forest edge on diurnal variation in air temperature and vapour pressure deficit (VPD), we examined the diurnal range for these parameters for each distance along each transect in each year, 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 year (n = 3 days * 3 edge types * 2 sites * 2 transects per site * 2 years = 72) for both air temperature and VPD. As air temperature and VPD were highly correlated with each other (Pearson correlation r = 0.931, P < 0.001), we analysed this 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 year (2004 [pre-cyclone] and 2006 [post-cyclone]). Replication was provided by sites, transects and days. Air temperature and VPD were ln(1 + x)-transformed prior to analysis to approximate normality. 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. The data collected from this point is shown in the results section for comparison only.

As the minimum value for wind speed was 0 km hr⁻¹ in all cases, we used the maximum wind speed measured at each distance for each transect over the four days' data collection period for each year as a substitute for "range" (n = 3 edge types * 2 sites * 2 transects per site * 2 years = 24). Maximum wind speed was also highly correlated with the percent of time for which wind speeds > 0 km hr⁻¹ were recorded (Spearman rank correlation -0.916, P < 0.001) and so provides a reasonable indication of the overall wind regime at each measuring point. However, this dataset contained a large number of zero values, which skewed the distribution of the data. The data could not be transformed to achieve normality, so non-parametric Kruskal-Wallis tests were used to examine the effects of edge type (powerline, highway and creek), distance (0, 4, 12, 25, 50 and 100 m) and year (pre-cyclone [2004] and post-cyclone [2006]) on maximum wind speed. Measurements at -10 m on powerline transects were not included in this analysis and are shown in the results section for comparison only.

To complement the instantaneous measurements of PAR, soil temperature and soil moisture taken using the traverse method (see previous section), gradients in air temperature and VPD were calculated for three periods within the day: morning (10:00-10:50), midday (12:00-12:50) and afternoon (14:00-14:50). Relative air temperature and relative VPD were calculated for each ten minute reading within these time periods (Eq. 2; see previous section)

and average relative values were calculated for each time period for three days per transect (N = 12 transects \times 3 days per transect \times 3 time periods per day = 108). These average hourly values were used as replicates in a MANOVA, with fixed factors of edge type (powerline, highway and creek), distance (0, 4, 12, 25 and 50 [values for 100 m were always 0 and were excluded from the analysis to allow the dataset to approximate normality]) and time of day (morning [10:00-10:50], midday [12:00-12:50] and afternoon [14:00-14:50]). Data for 2004 (pre-cyclone) and 2006 (post-cyclone) were analysed separately, as the combined dataset could not be transformed to approximate normality. All statistical analyses were performed using SPSS version 11.0.4 for Macintosh.



Figure 4: The instruments used to measure diurnal variation in microclimate were supported on a PVC frame resting on a wooden post. Instruments were attached at a height of 170 cm above the ground surface. The person pictured is Stephen Pohlman, who is standing behind and slightly upslope of the apparatus. Photo by Catherine Pohlman.

Results

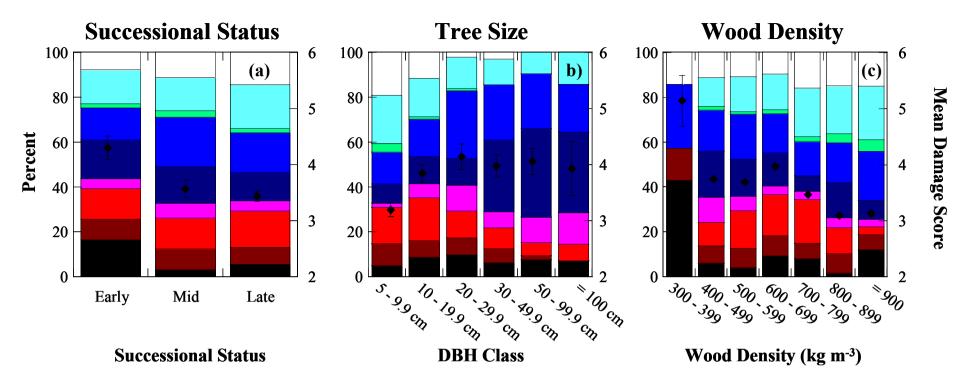
Vegetation Damage

Tree Damage

Tree damage was influenced by size (diameter at breast height [DBH]), successional status and wood density (Table 2). Early-successional tree species (i.e. pioneer tree species, which tend to be have fast growth rates, low wood density and to be favoured by high light levels and/or larger disturbances (Turner 2001) suffered greater damage than mid- or late-successional tree species (late-successional tree species [also called 'climax' species or 'primary forest species'], are species able to germinate in shade [i.e. beneath the forest canopy] and which tend to have slower growth rates, long persistence times in the seedling and sapling pools of the forest understorey and higher wood densities [Turner 2001]) (Figure 5a). There were also non-significant trends towards lesser damage with decreasing diameter (Figure 5b) and greater damage with lower wood density (Figure 5c, Table 2). In addition, there was a significant edge type \times distance interaction (Table 2); tree damage was slightly lower near powerline clearing edges (Figure 6a) and slightly higher near creek edges than in the forest interior (Figure 6c) but was not influenced by distance from highway edges (Figure 6b). However, post-hoc tests for the effects of distance within each edge type were not significant (P > 0.05).

Table 2: Cyclone damage to trees (stems ≥ 5 cm DBH). Tree damage data were analysed with ANCOVA (covariates DBH, successional status, wood density and growth habit; fixed factors edge type and distance). Significant effects are highlighted in bold and marginally significant effects are highlighted with italics.

Effect	F	d.f.	P		
Covariates					
Tree Size (DBH)	2.812	1	0.094		
Successional Status	9.586	1	0.002		
Wood Density	3.305	1	0.069		
Growth Habit	1.004	1	0.316		
Fixed Factors					
Edge Type	6.269	2	0.002		
Distance	1.863	5	0.098		
Edge Type × Distance	1.830	10	0.052		



Damage Category

Intact

Minor Branch Loss

Bent

Moderate Branch Loss

Major Branch Loss

Snapped > 10 m

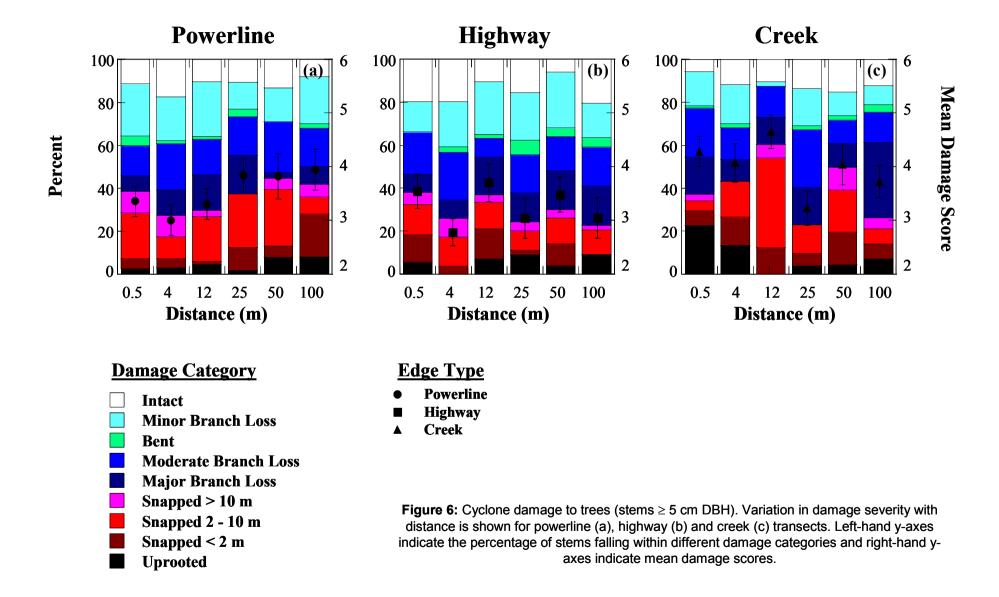
Snapped 2 - 10 m

Snapped < 2 m

Uprooted

Mean Damage Score

Figure 5: Covariates of cyclone damage to trees (stems ≥ 5 cm DBH). Damage severity was influenced by (a) successional status (p = 0.002), (b) tree size (DBH) (p = 0.094) and (c) wood density (p = 0.069). Left-hand y-axes indicate the percentage of stems falling within different damage categories and right-hand y-axes indicate mean damage scores.



Sapling Damage

Sapling damage was influenced by a number of factors (Table 3). Of the two covariates tested, sapling damage was related to growth habit but not successional status (Table 3). Sapling damage tended to be greater in species with taller adult stature: sapling damage was greatest in tree species that reach the canopy when fully grown, intermediate in tree species that only occur in the understorey as adults and least in shrub species (Figure 7). Of the main factors examined (edge type and distance from the forest edge), the edge type \times distance interaction was significant (Table 3). Sapling damage was lower near the very edge (0 m) of powerline clearings (Figure 8a) and higher near creek edges (Figure 8c) than in the forest interior and elevated between 12 and 25 m from highway edges (Figure 8b).

Table 3: Cyclone damage to saplings (stems 2-5 cm DBH). Sapling damage data were analysed with Kruskal-Wallis tests. Significant effects are highlighted in bold and marginally significant effects are highlighted with italics.

Effect	χ²	d.f.	P				
Covariates							
Growth Habit	13.606	2	0.001				
Successional Status	4.253	2	0.119				
Fixed Factors							
Edge Type	1.591	2	0.451				
Distance	8.059	5	0.153				
Edge Type × Distance	37.571	17	0.003				

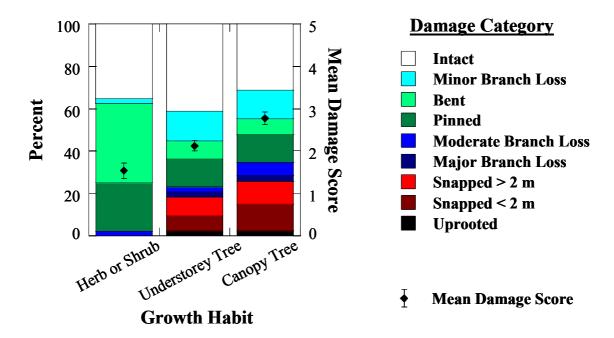
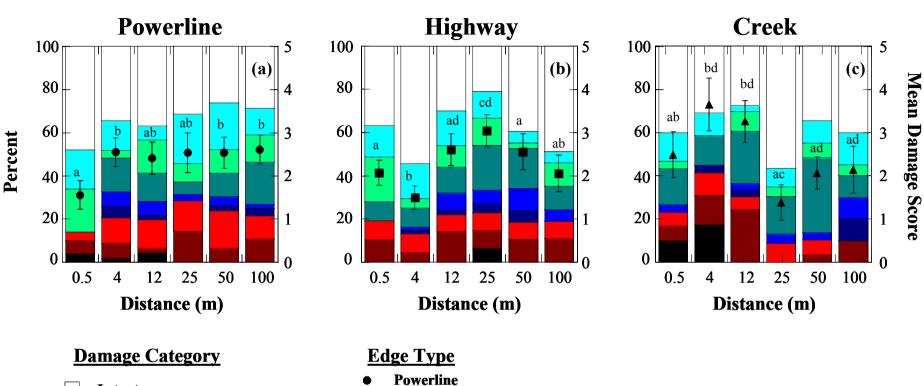


Figure 7: Covariate of cyclone damage to saplings (stems 2-4.9 cm DBH). Cyclone damage varied between species with differing growth habits (P = 0.001) Left-hand y-axes indicate the percentage of stems falling within different damage categories and right-hand y-axes indicate mean damage scores.



- Intact
- Minor Branch Loss
- Bent
- Pinned
- Moderate Branch Loss
- Major Branch Loss
- \blacksquare Snapped > 2 m
- Snapped < 2 m
- Uprooted

- Highway
- ▲ Creek

Figure 8: Cyclone damage to saplings (stems 2-4.9 cm DBH). Variation in damage severity with distance is shown for powerline (**a**), highway (**b**) and creek (**c**) transects. Left-hand *y*-axes indicate the percentage of stems falling within different damage categories and right-hand *y*-axes indicate mean damage scores. Symbols which share letters were not significantly different (P > 0.05, post-hoc Mann-Whitney U tests).

Understorey Microclimate

Traverse Measurements

Vegetation damage caused by Severe Tropical Cyclone *Larry* affected the direction and severity of microclimatic edge gradients measured near the edges of powerlines, highways and streams. Photosynthetically active radiation (PAR) was bimodally distributed; values of PAR measured six months after Cyclone *Larry* were much greater than those measured before the cyclone (t = 31.468, P < 0.001). Data for PAR for 2004 (pre-cyclone) and 2006 (post-cyclone) were thus analysed separately. Prior to the cyclone, there was a strong increase in light intensity near the edges of all three types of linear canopy openings (covariate distance, F = 11.581, d.f. = 1, P = 0.001; Figure 9 a, b, c), although creek edges had greater light availability than powerline or highway edges (main effect edge type, F = 7.889, d.f. = 2, P = 0.001). After the cyclone, the edge gradients in light intensity had disappeared (covariate distance, F = 0.814, d.f. = 1, P = 0.369; Figure 9), although light availability was still marginally higher along creek transects than along powerline or highway transects (main effect edge type, F = 2.783, d.f. = 2, P = 0.066).

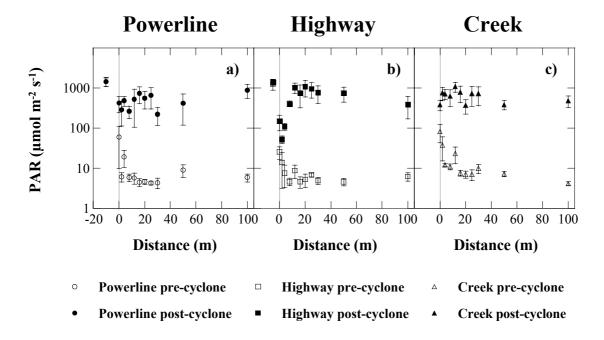


Figure 9: Photosynthetically active radiation (PAR) for (a) powerline, (b) highway and (c) creek transects, measured in the dry seasons eighteen months before (open symbols) and six months after (closed symbols) Cyclone *Larry*. Note the log-scale on the *y*-axis. Dashed vertical lines indicate the position of the forest edge. Values represent means ± 1 SE.

Gradients in soil temperature differed among edge types and between years (edge type \times year interaction, F=12.743, d.f. = 2, P<0.001; Figure 10). Although the effect of distance on relative soil temperature was not significant (covariate distance, F=2.871, d.f. = 1, P=0.091), some trends were apparent. Near powerline edges, soil temperatures tended to be slightly lower near the very edge of the forest (within ~4 m of the edge) than in the forest interior and this pattern was only slightly altered after the cyclone (Figure 10a), possibly due to a slightly higher level of vegetation damage within the forest interior (Figure 6a) exposing the forest to greater light availability and harsher microclimate. Near highway edges, soil

temperatures were slightly elevated at the very edge (within ~2 m of the edge) of the forest prior to the cyclone; six months after the cyclone, soil temperatures were lower near the forest edge and elevated at intermediate distances (~ 12-30 m) relative to the forest interior (Figure 10b). Again this may relate to the larger amounts of damage to saplings at these intermediate distances allowing greater light penetration and thus soil temperature to rise. In contrast, near creek edges, soil temperatures were slightly elevated at the very edge of the forest (within ~4 m of the edge) prior to the cyclone, whereas, six months after the cyclone, soil temperatures were greater in the interior of the forest than within 50 m of the edge (Figure 10c).

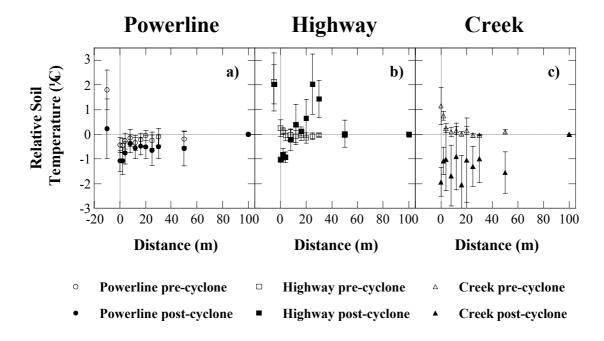


Figure 10: Relative soil temperature for (a) powerline, (b) highway and (c) creek transects, measured in the dry seasons eighteen months before (open symbols) and six months after (closed symbols) Cyclone *Larry*. Dashed vertical lines indicate the position of the forest edge and dashed horizontal lines indicate the relative value of measurements taken in the forest interior (100 m). Values represent means ±1 SE.

Soil moisture tended to be lower near the forest edge than in the forest interior (covariate distance, F = 3.785, d.f. = 1, P = 0.053; Figure 11), although gradients in soil moisture differed among edge types and between years (edge type × year interaction, F = 9.496, d.f. = 2, P < 0.001). Prior to the cyclone, soil moisture tended to decrease slightly from powerline edges to the forest interior but six months after the cyclone, this gradient had reversed and soil moisture was slightly lower near powerline edges than in the forest interior (Figure 11a). There was no clear gradient in soil moisture near highway edges prior to the cyclone but soil moisture was slightly lower near the very edge of the forest (~ 0.4 m) six months after the cyclone (Figure 11b). Soil moisture was lower near creek edges than in the forest interior both before and after the cyclone, although soil moisture obtained interior values closer to the edge after the cyclone than before the cyclone (Figure 11c).

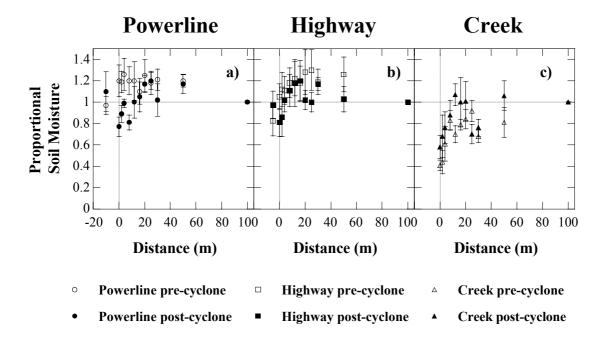


Figure 11: Proportional soil moisture for (a) powerline, (b) highway and (c) creek transects, measured in the dry seasons eighteen months before (open symbols) and six months after (closed symbols) Cyclone *Larry*. Dashed vertical lines indicate the position of the forest edge and dashed horizontal lines indicate the relative value of measurements taken in the forest interior (100 m). Values represent means ±1 SE.

Diurnal Variation

Severe Tropical Cyclone *Larry* altered both the absolute values of and the edge gradients in the diurnal ranges of air temperature and vapour pressure deficit (VPD). The direction of edge gradients differed between years (distance \times year interaction; Pillai's trace = 0.090, F = 3.521, d.f. = 10, P < 0.001); in addition, diurnal ranges of air temperature and VPD differed among edge types and between years (edge type \times year interaction; Pillai's trace = 0.051, F = 4.820, d.f. = 4, P = 0.001), although the three-way interaction was not significant (edge type \times distance \times year interaction; Pillai's trace = 0.019, F = 0.359, d.f. = 0.359, d.f. = 20, P = 0.996). Prior to the cyclone, diurnal ranges of air temperature and VPD were slightly greater near the very edges of powerlines and highways than in the forest interior (Figure 12 a, b, d, e), but did not vary with distance from creek edges (Figure 12 c, f). After the cyclone, these gradients had reversed, and diurnal ranges of air temperature and VPD were lower near the edges of powerlines, highways and streams than in the forest interior. The edge type \times year interaction detected in the MANOVA was not supported by the *post hoc* tests of between-subject effects for the individual parameters (Table 4); neither air temperature nor VPD displayed significant edge type \times year interactions in these tests.

Maximum wind speed generally decreased from the forest edge to the forest interior, for all three edge types (Figure 13 a, b, c; Table 5). Wind speeds were greater along creek transects than along powerline or highway transects, both prior to the cyclone and six months after it. Additionally, although wind speed was greater after the cyclone than before the cyclone, this increase was greatest along creek transects and least along powerline transects (Figure 13, a, b, c; Table 5) and the increase in wind speeds along highway transects was somewhat greater at intermediate distances than near the edge or in the forest interior (Figure 8b). In general, wind speed was greater for distances between 4 and 100 m

from the forest edge after the cyclone than before the cyclone (Figure 13, a, b, c; Table 5), indicating a greater penetration of wind into the forest interior after the cyclone.

Edge gradients in relative air temperature and relative VPD differed between years and among edge types (Table 6). Prior to the cyclone, air temperature and VPD were higher near the forest edge than in the forest interior, but this increase was greater near powerline and highway edges than near stream edges (edge type x distance interaction; Pillai's trace = 0.132, F = 4.223, d.f. = 16, P < 0.001; Table 6; Figure 14 a, b, c, g, h, i). In addition, the magnitude of edge gradients increased between morning and afternoon (time of day main effect; Pillai's trace = 0.038, F = 4.653, d.f. = 4, P = 0.001; Table 6; Figure 14 a, b, c, g, h, i). Six months after the cyclone, edge gradients in air temperature and VPD varied with time of day and among edge types (edge type \times distance \times time of day; Pillai's trace = 0.111, F = 1.626, d.f. = 32, P = 0.016; Table 6; Figure 14 d, e, f, j, k, l). Along powerline transects, air temperature and VPD were lower near the edge than in the forest interior and this edge gradient was strongest in the morning and, although still present at midday and in the afternoon, intermediate distances displayed higher temperature and VPD compared to the forest interior (Figure 14 d, j). Along highway transects, air temperature and VPD were lower near the forest edge than in the forest interior and this gradient was strongest in the morning and lesser in the afternoon (Figure 14 e, k). Along creek transects, air temperature and VPD were slightly higher near the forest edge (between 4 and 50 m from the edge) than in the forest interior in the morning but were lower near the edge than in the forest interior at midday and in the afternoon, with the exception of the 50 m point at 2:00 pm, which displayed higher values of air temperature and VPD than either the edge or the forest interior (Figure 14 f, I).

Table 4: Tests of between-subject effects (distance, edge type and year) for the MANOVA on diurnal temperature (°C) and VPD (kPa) ranges. Significant effects have been highlighted in bold.

Factor	Parameter	F	d.f.	P
Edge Type	In (1 + diurnal temperature range)	0.617	2	0.540
	In (1 + diurnal VPD range)	1.607	2	0.202
Distance	In (1 + diurnal temperature range)	1.767	5	0.119
	In (1 + diurnal VPD range)	1.769	5	0.118
Year	In (1 + diurnal temp)	292.747	1	< 0.001
	In (1 + diurnal VPD range)	264.864	1	< 0.001
Edge Type × Distance	In (1 + diurnal temperature range)	0.896	10	0.537
	In (1 + diurnal VPD range)	0.417	10	0.939
Edge Type × Year	In (1 + diurnal temperature range)	2.632	2	0.073
	In (1 + diurnal VPD range)	1.557	2	0.212
Distance × Year	In (1 + diurnal temperature range)	5.877	5	< 0.001
	In (1 + diurnal VPD range)	5.864	5	< 0.001
Edge Type × Distance	In (1 + diurnal temperature range)	0.544	10	0.859
× Year	In (1 + diurnal VPD range)	0.547	10	0.856

Table 5: Wind speed (km hr⁻¹) results table. Each effect analysed with Kruskal-Wallis tests (or Mann-Whitney U tests for 'Year'). Significant effects are highlighted in bold.

Effect	χ²	d.f.	P
Edge Type	18.602	2	< 0.001
Distance	35.534	5	< 0.001
Year	1684.000 [†]	1	0.003
Edge Type × Distance	59.902	17	< 0.001
Edge Type × Year	30.004	5	< 0.001
Distance × Year	52.728	11	< 0.001
Edge Type × Distance × Year	81.712	35	< 0.001

[†] Mann-Whitney U test.

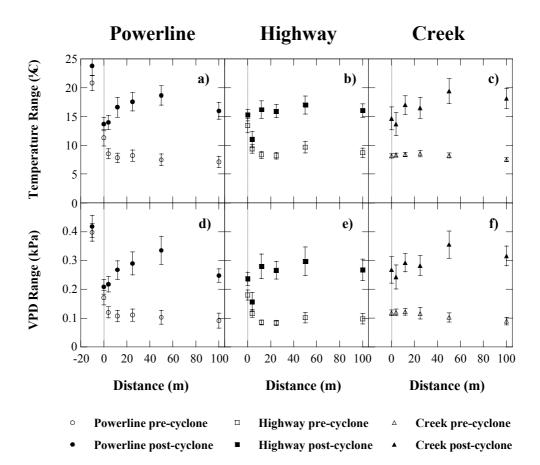


Figure 12: Diurnal temperature range (a, b, c) and diurnal vapour pressure deficit (VPD) range (d, e, f) for powerline (a, d), highway (b, e) and creek (c, f) transects in the dry seasons eighteen months before (open symbols) and six months after (closed symbols) Cyclone *Larry*. Dashed vertical lines indicate the position of the forest edge. Values represent means ± 1 SE.

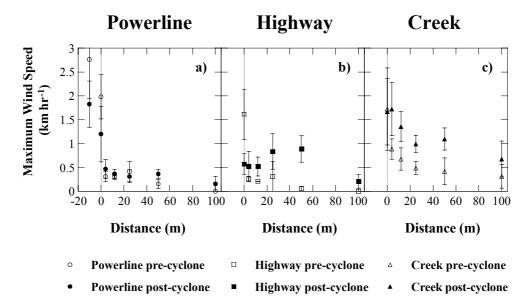


Figure 13: Maximum wind speed for powerline (a), highway (b) and creek (c) transects in the dry seasons eighteen months before (open symbols) and six months after (closed symbols) Severe Tropical Cyclone *Larry*. Dashed vertical lines indicate the position of the forest edge. Values represent means ± 1 SE.

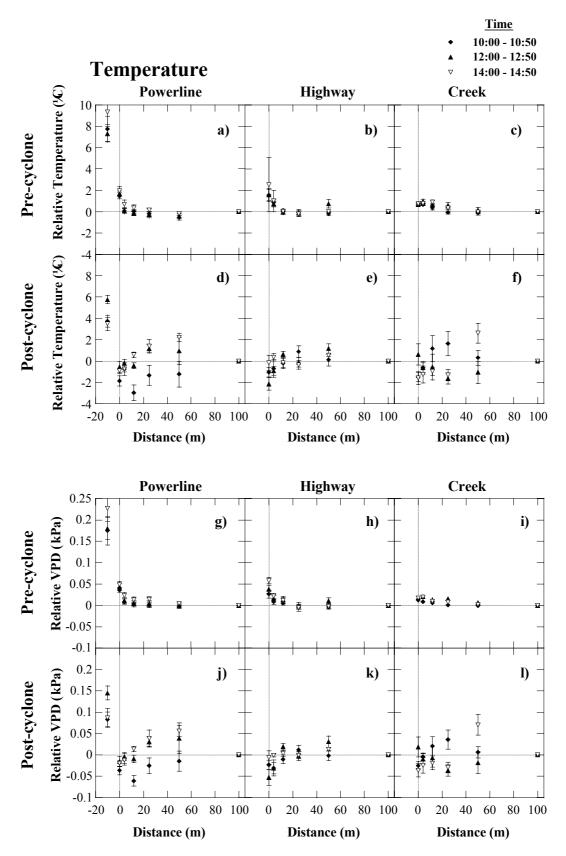


Figure 14: Edge gradients in air temperature and VPD in the morning (10:00-10:50), at midday (12:00-12:50) and in the afternoon (14:00-14:50). Dashed vertical lines indicate the position of the forest edge and dashed horizontal lines indicate the relative value of measurements made in the forest interior (100 m). Values represent means \pm 1 SE.

Table 6: Tests of between-subject effects (distance, edge type and time of day) for the MANOVA on relative air temperature (°C) and relative VPD (kPa). Data for 2004 (pre-cyclone) and 2006 (post-cyclone) were analysed separately. Significant effects (α = 0.05) are highlighted in bold.

Effect	Parameter	Pre-cyclone (2004)			Post-cyclone (2006)		
		F	d.f.	P	F	d.f.	P
Edge Type	Relative Temperature (°C)	4.136	2	0.017	0.298	2	0.742
Edge Type	Relative Vapour Pressure Deficit (kPa)	1.441	2	0.238	0.180	2	0.835
Dietonee	Relative Temperature (°C)	47.035	4	< 0.001	7.131	4	< 0.001
Distance	Relative Vapour Pressure Deficit (kPa)	39.206	4	< 0.001	8.983	4	< 0.001
Time of Day	Relative Temperature (°C)	3.845	2	0.022	2.272	2	0.104
Time of Day	Relative Vapour Pressure Deficit (kPa)	8.882	2	< 0.001	2.768	2	0.064
Edge Type ×	Relative Temperature (°C)	6.874	8	< 0.001	0.820	8	0.585
Distance	Relative Vapour Pressure Deficit (kPa)	5.006	8	< 0.001	1.209	8	0.292
Edge Type ×	Relative Temperature (°C)	1.122	4	0.345	6.614	4	< 0.001
Time of Day	Relative Vapour Pressure Deficit (kPa)	1.201	4	0.310	5.111	4	< 0.001
Distance ×	Relative Temperature (°C)	0.743	8	0.653	1.773	8	0.080
Time of Day	Relative Vapour Pressure Deficit (kPa)	0.707	8	0.685	1.651	8	0.108
Edge Type ×	Relative Temperature (°C)	0.696	16	0.799	2.565	16	0.001
Distance × Time of Day	Relative Vapour Pressure Deficit (kPa)	0.559	16	0.914	2.602	16	0.001

Discussion

Vegetation Damage

Effect of proximity to linear clearings

Damage to trees was slightly reduced near powerline edges and slightly elevated near creek edges, relative to the forest interior (Figure 6). Similarly, sapling damage was reduced near powerline edges and elevated near creek edges, relative to the forest interior but was also elevated at intermediate distances from highway edges (Figure 8). These results contradicted our initial hypothesis that vegetation damage from Cyclone *Larry* would be generally greater near the edges of linear canopy openings than in the forest interior; vegetation damage was elevated near creek edges, but not near anthropogenic edges (powerlines and highways). In light of the literature documenting greater wind damage near forest edges in tropical, temperate and boreal forests (Williams-Linera 1990; Laurance 1991, 1997; Chen *et al.* 1992; Leigh *et al.* 1993; Essen 1994; Ferreira and Laurance 1997; Laurance *et al.* 1997, 1998, 2000, 2002; Burton 2002; D'Angelo *et al.* 2004; Baldwin and Bradfield 2005; Harper *et al.* 2005), this result is surprising, although such patterns are not entirely ubiquitous (e.g. Lin *et al.* 2004; Ryall and Smith 2005). Few of these studies, however, have specifically examined the damage caused by severe wind storms.

The severe winds associated with Cyclone *Larry* (gusts to 294 km hr⁻¹ at Bellenden Ker [Bureau of Meteorology 2007]) appear to have caused vegetation destruction so severe that it overrode any smaller-scale landscape effects (Everham and Brokaw 1996), although effects caused by larger-scale topographic features were evident (Turton in prep). Although elevated cyclone damage has previously been detected near forest edges bordering agricultural land on the Atherton tablelands (approximately 20 km west of our study sites) (Laurance 1991, 1997), this damage was caused by a category 3 cyclone, with maximum wind gusts of 176 km hr⁻¹ (Unwin *et al.* 1988), which caused less severe vegetation damage in the study area than Cyclone *Larry* (Unwin *et al.* 1988; Turton in prep). If forest edges do influence the vulnerability of vegetation to cyclone damage, this effect may be confined to areas of less severe overall cyclone damage. A study of broader landscape patterns associated with Cyclone *Larry* is currently underway. This project, also funded by Powerlink, is examining cyclone damage over a wider area of the Palmerston region using remote sensing techniques applied to satellite and aerial photographic imagery to examine tree fall severity and direction and vegetation indices (Goosem *et al.* in prep.).

Effect of tree size and successional status

Tree damage was more severe for early successional tree species. This is consistent with the trend towards increasing damage with decreasing wood density, as early successional species tend to have lower wood densities (Osunkoya 1996; Turner 2001; Falster and Westoby 2005; van Gelder et al. 2006; Osunkoya et al. 2007). Tree damage also tended to be more severe in larger trees than in smaller trees. Damage to saplings was greater for individuals from taller-growing species (canopy trees) than for shorter-growing species (understorey trees and shrubs), although damage did not differ among species from different successional stages. We could not assess the effects of wood density on sapling damage, but wood density tends to be greater in species with shorter stature, at least among shade-tolerant species (Falster and Westoby 2005; van Gelder et al. 2006). As wood density is negatively correlated with damage rates (Falster 2006), these data suggest that, unsurprisingly, species with higher wood density (and thus greater resistance to damage under non-cyclonic conditions), suffered lower rates of cyclone damage than species with lower wood density. Similar patterns of greater cyclone damage to species with lower wood

density and/or greater damage to pioneer species have been detected in many previous studies around the world (e.g. Zimmerman *et al.* 1994; Everham and Brokaw 1996; Ostertag *et al.* 2005; Franklin *et al.* 2004), although Grove *et al.* (2000) observed greater cyclone damage in old-growth stands than in second-growth stands in the Daintree area of northeastern Queensland after Tropical Cyclone *Rona*.

Cyclone damage tended to be greater for trees with larger diameters (Figure 5b). This relationship appeared to take the form of a threshold response, rather than a simple linear correlation, with trees less than approximately 20 cm in diameter experiencing lower cyclone damage than trees with larger diameters. However, this relationship was not significant at the $\alpha = 0.05$ level and there was a higher proportion of snapped and uprooted trees in the smaller size classes than in the larger size classes. In contrast, the proportion of trees with significant branch damage was greater amongst larger trees than amongst smaller trees. This pattern of damage suggests that larger trees, which tend to have larger crowns and thus greater crown exposure in the canopy (Poorter *et al.* 2006), suffered greater crown damage but less major stem damage (snapping and uprooting) than smaller trees (with correspondingly smaller crowns and thus lower crown exposure). It is possible that much of the damage suffered by smaller trees was due to falling branches and other debris from the forest canopy, while much of the damage to larger trees was due to the direct effects of strong winds from the cyclone (e.g. Everham and Brokaw 1996).

Effects of 'sealed' edges

The different edge patterns that were observed in the current study (i.e. slightly reduced tree and sapling damage near powerlines, slightly elevated tree and sapling damage near creeks and slightly elevated sapling damage at intermediate distances from highway edges) may also have resulted from differences in pre-cyclone edge conditions among edge types. Prior to Cyclone *Larry*, there were higher proportions of smaller trees and saplings near the forest edge than in the forest interior, for all three edge types, as well as increased abundances of lianas and weeds (Pohlman 2006). Forest near creek edges, however, had a more open canopy structure (which allowed a greater penetration of light and wind into the forest understorey), a greater proportion of pioneer species and a greater abundance of lianas than forest near powerline or highway edges (Pohlman 2006). These differences were ascribed to differences in the degree of edge 'sealing' that occurred in the time since the current forest edges were created.

Edge sealing occurs when the increased light availability at a newly-formed forest edge encourages the growth of foliage on remaining trees, as well as the growth of saplings, seedlings and lianas, until a 'wall of vegetation' covers the forest edge from the ground to the forest canopy (Laurance et al. 2002; Harper et al. 2005). Sealed edges have been found to decrease the severity of some, though not all, microclimatic and biotic edge effects (e.g. Camargo and Kapos 1995; Kapos et al. 1997; Cadenasso and Pickett 2000, 2001; Harper et al. 2005). Prior to Cyclone Larry, forest edges near powerlines and highways were more sealed than forest edges near creeks. Edges near anthropogenic linear clearings had a higher foliage density (measured indirectly through a decrease in the red : far red ratio), reduced recruitment of pioneer species and less dramatic increases in understorey light availability and the abundance of lianas than forest near creek edges (Pohlman 2006). These differences in edge sealing may have been due to differences in the frequency of physical disturbance to the forest edge. Creek edges may be subject to periodic flood disturbance, whilst powerline and highway edges have not been significantly disturbed in approximately fifteen years (although highway edges may receive some disturbance from periodic highway maintenance activities) (Pohlman et al. 2007).

The greater proportion of pioneer species and the open edge structure near creeks, as well as the sandier soil found near creek edges (Pohlman et al. 2007) may have increased the

vulnerability of trees and saplings to damage from Cyclone Larry. Although Cyclone Larry was a 'dry' cyclone, in that it was not associated with heavy rainfall (Turton in prep), sections of the creek bank appeared to have been washed away or undermined during post-cyclone floods (personal observation), which may have accounted for a large proportion of the greater number of uprooted trees and saplings near creek edges (Figures 6c, 8c). As pioneer species also suffered greater cyclone damage, the relatively elevated abundance of these species near creek edges is also likely to have contributed to the high cyclone damage observed near creek edges. Conversely, the relatively lower abundance of pioneer species and more sealed edge structure near powerline and highway edges may have offered some protection from cyclone damage. A thin strip of edge vegetation with foliage slightly more intact than that in the forest interior was observed near highway edges (personal observation: see also Figure 9b, where lowered PAR is evident near highway edges) although not near powerline edges. It is possible that the lower proportion of large trees (which were more vulnerable to cyclone damage than smaller trees) left vegetation at the edge less exposed to damage from falling branches and canopy debris and, in addition, that the relatively low proportion of pioneer species near powerline and highway edges (as compared with creek edges) also decreased the vulnerability of these forest edges.

Understorey Microclimate

Prior to Cyclone *Larry*, edge gradients were present in understorey microclimate. For example, light availability increased towards the forest edge, although this increase was greatest near creek edges (Figure 9). Prior to the cyclone there were only very slight changes in soil temperature at the very edge of the forest (Figure 10) and soil moisture was lower near creek edges (Figure 11c), possibly due to higher sand content (and thus lower moisture holding capacity) of soil near the creek edge (Pohlman *et al.* 2007). However, edge gradients in air temperature and vapour pressure deficit were obvious, being elevated at the forest edge near powerlines and highways but not creeks, while the strength of these gradients increased between morning and afternoon (Figure 14). Additionally, the diurnal ranges of temperature and vapour pressure deficit were greater at the edge of the forest, near powerlines and highways but not creeks (Figure 12). Finally, wind speed increased near the forest edge, although this increase was greatest near creek edges (Figure 13). Following Cyclone *Larry*, the severe damage to the forest canopy led to an increase in light availability and wind speed in the forest understorey (Figures 9, 13) and the loss or alteration of numerous microclimatic edge gradients.

Following the cyclone, edge gradients in light availability were lost (Figure 10), with the exception of a decrease in light availability near highway edges (Figure 10b) that was associated with a thin strip of edge vegetation that was less damaged than the surrounding forest (personal observation). Edge gradients in the diurnal ranges of air temperature and vapour pressure deficit were reversed after the cyclone (Figure 12); temperature and VPD were lower near the forest edge than in the forest interior, for all three edge types. Maximum wind speeds were elevated near the forest edge both before and after the cyclone, but both the absolute values of wind speed and the magnitude of the edge gradients in wind speed increased near creek edges and highway edges following the cyclone. Edge gradients in air temperature and vapour pressure deficit observed during daylight hours (Figure 14) became more complex after the cyclone.

Increases in light availability and wind speed in the forest understorey reflect the severe cyclone damage to the rainforest canopy (Turton 1992; Turton and Siegenthaler 2004). The high foliage density of intact rainforest canopies moderates the microclimate experienced in the rainforest understorey, decreasing light intensity and wind speed and increasing humidity (e.g. Ray *et al.* 2005). Prior to the cyclone, light levels measured in the forest interior were approximately < 0.2-7 % of those measured in the open. Six months following the cyclone,

interior light measurements had risen to approximately 3-100 % of open values. This dramatic increase in light availability in the forest understorey was complemented by increases in wind speed and diurnal ranges of air temperature and vapour pressure deficit. In contrast to light availability, increases in wind speed were not accompanied by the loss of edge gradients (Figure 9). The persistence of edge gradients in wind speed indicates that, even after the cyclone, certain edge processes were still operating in the forest understorey. The increase in the absolute values of wind speed reflects the importance of canopy structure for the wind regime experienced in the forest understorey (e.g. Ray et al. 2005). Similarly, the increase in wind speeds at intermediate distances from highway edges is consistent with the combined effects of increased tree and sapling damage found at those distances.

Changes in edge gradients of air temperature and vapour pressure deficit (Figures 12 and 14) may reflect the degree of damage to the forest canopy. Although the diurnal edge gradients became more complex after the cyclone (Figure 14), there is a general trend towards a reversal of the edge gradients present before the cyclone. Prior to the cyclone, both the diurnal ranges of temperature and VPD (Figure 12) and the diurnal edge patterns (Figure 14) tended to show positive edge gradients (i.e. values were greater near the edge than in the forest interior) near powerline and highway edges. Following the cyclone, edge gradients became negative (i.e. values were lower near the forest edge than in the forest interior) near powerline and highway edges. It is possible that the slightly lower vegetation damage near powerline edges (Figures 6a and 8a) and the strip of vegetation with relatively intact foliage near highway edges (personal observation) provided a slightly more closed canopy (and thus a greater degree of insulation from the prevailing temperature, sunlight and wind conditions) near the forest edge than in the more extensively damaged forest interior. Changes in edge gradients near creeks appeared slightly less pronounced, but were roughly consistent with those measured near powerlines and highways. Given the greater vegetation damage observed near creek edges (Figures 6c and 8c), this pattern in unlikely to be a direct result of differences in canopy damage between the creek edge and the forest interior. However, prior to the cyclone, the lack of edge gradients in air temperature and VPD near creeks was ascribed to a buffering effect of increased evaporative cooling from the flowing water within the creek itself (Pohlman et al. 2007) and it is possible that this mechanism is still operating to reduce the extremes of temperature and VPD experienced near the severely damaged creek edge.

Cyclone Larry and Linear Canopy Openings

Contrary to our initial expectations, cyclone damage was not greater near the edges of powerlines and highways than in the forest interior, although cyclone damage was elevated near creek edges. The greater degree of vegetation 'sealing' of forest edges near powerlines and highways, as well as the relatively low abundance of tree species with traits associated with increased vulnerability to wind damage (e.g. low wood density and early successional status) and the greater proportion of trees with smaller diameters near the forest edge, may have offered some degree of protection from the more severe cyclone damage observed near creek edges. Additionally, flood damage near the creek edges probably amplified the wind effects.

The severe canopy damage caused by Cyclone *Larry* led to dramatic changes in the microclimate of the rainforest understorey. Light availability increased dramatically after the cyclone, as did wind speed and the diurnal ranges of air temperature and vapour pressure deficit. Slightly less severe vegetation damage near the edges of powerlines and highways led to slightly reduced temperature and VPD extremes, relative to the forest interior. The increase in light availability since the cyclone has been sufficient to allow the germination and growth of numerous pioneer and weed species (*personal observation*) and it is possible that

the increased wind speeds (and continued presence of edge gradients in wind speed) may facilitate the invasion of weed species into the rainforest (e.g. Bellingham *et al.* 2005), as many weed species of more open habitats are wind-dispersed. Species common in the Palmerston powerline clearing and along the road and highway edges such as Guinea grass (*Urochloa maxima*) and molasses grass (*Melinus minutiflora*) and a variety of herbaceous weeds (Goosem 2006; Pohlman 2006) are wind-dispersed and have been observed colonising the cyclone-disturbed areas (*personal observations*). Recovery of the forest canopy may lead to a decrease in the abundance of pioneer and weed species (e.g. Burslem *et al.* 2000), however, should weed species capable of interfering with canopy recovery become established, this process may be considerably slowed, if not stalled altogether (Gascon *et al.* 2000). In the linear infrastructure clearings of this area, weed species such as the grasses mentioned above, as well as the scramblers *Lantana camara* and *Rubus alceifolius* have a tendency to suppress the regeneration of rainforest tree seedlings (Reynolds 1994; Werren 2001; Goosem and Turton 2006). The post-cyclone situation therefore requires close monitoring.

Recommendations

We make the following recommendations:

- 1. Where it is not possible to minimise the footprint of linear infrastructure corridors (e.g. to clear only the area around the base of each transmission line tower), a 'sealed' edge structure should be maintained. The sealed edge structure near powerlines and highways appears to have offered some degree of protection from the more severe wind damage observed near creek edges. A sealed edge structure may be encouraged and maintained through measures which minimise the disturbance to the forest edge during infrastructure and easement maintenance (e.g. avoid mechanical disturbance to the forest edge; avoid the use of fire near rainforest edges [e.g. Cochrane and Laurance 2002]).
- 2. Microclimatic changes following Cyclone Larry may favour the germination and growth of numerous pioneer and weed species and initial observations suggest that the abundance of exotic plant species within the rainforest understorey has increased substantially since the cyclone. We recommend that this situation be monitored, in order to identify potential problems (e.g. incursions of scrambling weeds [e.g. Lantana camara, Rubus alceifolius] or grasses into the forest).

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Appendix 1

Wood densities of tree species encountered in the vegetation survey

Data obtained from Osunkoya (1996), Cause *et al.* (1989), Hyland (1989) and from expert advice (Dr Steve Goosem, *pers. comm.*, citing Floyd 1989 and Watson 1951).

Species	Family	Wood Density (kg m ⁻³)
Aceratium megalospermum	Eleaocarpaceae	625
Acmena graveolens	Myrtaceae	595
Acronychia vestita	Rutaceae	705
Aglaia meridionalis	Meliaceae	700 (47) [†]
Aglaia tomentosa	Meliaceae	700 (47) [†]
Alangium villosum	Alangiaceae	705
Alphitonia petriei	Rhamnaceae	515
Alstonia scholaris	Apocynaceae	400
Antirrhea tenuiflora	Rubiaceae	805 (58) [†]
Apodytes brachystylis	Icacinaceae	655
Archidendron whitei	Mimosaceae	705 (74) ^{† ‡}
Argyrodendron peralatum	Sterculiaceae	800
Argyrodendron trifoliolatum	Sterculiaceae	925
Austromyrtus bidwillii	Myrtaceae	775 (21) ^{† §}
Austromyrtus dallachiana	Myrtaceae	775 (21) ^{† §}
Austromyrtus shepherdii	Myrtaceae	775 (21) ^{† §}
Beilschmedia bancroftii	Lauraceae	640
Beilschmedia recurva	Lauraceae	620
Beilschmedia tooram	Lauraceae	850
Beilschmedia volckii	Lauraceae	545
Bischofia javanica	Euphorbiaceae	655
Breynia stipitata	Euphorbiaceae	690 (37) [†]
Brombya platynema	Rutaceae	710
Cananga odorata	Annonaceae	465
Cardwellia sublimis	Proteaceae	560
Carnarvonia araliifolia	Proteaceae	690
Castanospermum australe	Fabaceae	755
Castanospora alphandii	Sapindaceae	705
Celtis paniculata	Ulmaceae	705
Chionanthus axillaris	Oleaceae	935 (40) [†]
Chisocheton longistipitatus	Meliaceae	545

Species	Family	Wood Density (kg m ⁻³)
Cinnamomum laubatii	Lauraceae	480
Citronella smythii	Icacinaceae	675
Clerodendron grayi	Verbenaceae	585 (37) [†]
Corynocarpus cribbianus	Corynocarpaceae	690
Cryptocarya angulata	Lauraceae	755
Cryptocarya corrugata	Lauraceae	800
Cryptocarya grandis	Lauraceae	830
Cryptocarya mackinnoniana	Lauraceae	880
Cryptocarya melanocarpa	Lauraceae	775
Cryptocarya murrayi	Lauraceae	785
Cryptocarya oblata	Lauraceae	560
Cryptocarya pleurosperma	Lauraceae	690
Daphnandra repandula	Monimiaceae	675
Davidsonia pruriens	Davidsoniaceae	875
Diospiros cupulosa	Ebenaceae	1010 (122) [†]
Diospiros sp. "twice as flat"	Ebenaceae	1010 (122) [†]
Diploglottis bracteata	Sapindaceae	995
Diploglottis smithii	Sapindaceae	830 (22) [†]
Doryphora aromatica	Monimiaceae	560
Dysoxylum klanderi	Meliaceae	945
Dysoxylum oppositifolium	Meliaceae	880
Dysoxylum papuanum	Meliaceae	735
Dysoxylum pettigrewianum	Meliaceae	865
Elaeocarpus grandis	Elaeocarpaceae	495
Elaeocarpus largiflorens	Eleaocarpaceae	450
Endiandra bessaphila	Lauraceae	665
Endiandra compressa	Lauraceae	995
Endiandra globosa	Lauraceae	915
Endiandra insignis	Lauraceae	750
Endiandra leptodendron	Lauraceae	870
Endiandra monothyra	Lauraceae	800
Endiandra palmerstonii	Lauraceae	690
Endiandra sankeyana	Lauraceae	755
Endiandra sideroxylon	Lauraceae	800
Ficus congesta	Moraceae	350
Ficus copiosa	Moraceae	350
Ficus crassipes	Moraceae	350
Ficus leptoclada	Moraceae	560

Species	Family	Wood Density (kg m ⁻³)
Ficus pleurocarpa	Moraceae	470
Ficus septica	Moraceae	350
Ficus variegata	Moraceae	400
Ficus virens var. virens	Moraceae	400
Flindersia acuminata	Rutaceae	530
Flindersia brayleyana	Rutaceae	575
Franciscodendron laurifolium	Sterculiaceae	450
Gardenia ovularis	Rubiaceae	850
Gessios biagiana	Cunoniaceae	640
Gillbeea adenopetala	Cunoniaceae	530
Glochidion harveyanum	Euphorbiaceae	785
Glochidion sumatrum	Euphorbiaceae	705
Guioa lasioneura	Sapindaceae	830 (22) [†]
Haplostichanthus sp. Johnstone River LWJ 471	Annonaceae	565 (38) [†]
Helicia nortoniana	Proteaceae	725 (33) ^{† ¶}
Hollandaea sayeriana	Proteaceae	725 (33) ^{† ¶}
Hylandia dockrillii	Euphorbiaceae	560
Irvingbaileya australis	Icacinaceae	495
Levieria acuminata	Monimiaceae	435
Litsea leefeana	Lauraceae	480
Macaranga inamoena	Euphorbiaceae	560
Mallotus paniculatus	Euphorbiaceae	690 (37) [†]
Melicope bonwickii	Rutaceae	465
Melicope elleryana	Rutaceae	610
Melicope vitiflora	Rutaceae	625
Melicope xanthoxyloides	Rutaceae	495
Mischocarpus lachnocarpus	Sapindaceae	830 (22) [†]
Myristica insipida	Myristicaceae	560
Neolitsea dealbata	Lauraceae	680
Niemeyera prunifera	Sapotaceae	610
Omalanthus novo-guineensis	Euphorbiaceae	320
Opistheolepis heterophylla	Proteaceae	610
Ostrearia australiana	Hamamelidaceae	755
Palaquium galatoxylon	Sapotaceae	560
Phaleria clerodendron	Thymelaeaceae	655 (16) [¿]
Pilidiostigma tropicum	Myrtaceae	775 (21) [†]
Pitiviaster haplophylla	Rutaceae	835

Species	Family	Wood Density (kg m ⁻³)
Podocarpus dispermus	Podocarpaceae	580 (45) [†]
Polyalthia michaelii	Annonaceae	625
Polyosma hirsute	Grossulariaceae	720 (na) [†]
Polyscias australiana	Araliaceae	575
Polyscias elegans	Araliaceae	480
Polyscias murrayi	Araliaceae	400
Pouteria castanosperma	Sapotaceae	975
Prunus turneriana	Rosaceae	530
Pseuduvaria villosa	Annonaceae	565 (38) [†]
Rhodamnia sessiliflora	Myrtaceae	975
Rhodomyrtus pervigata	Myrtaceae	775 (21) [†]
Rhysotoechia robertsonii	Sapindaceae	830 (22) [†]
Rockinghamia angustifolia	Euphorbiaceae	800
Sarcotoechia protracta	Sapindaceae	830 (22) [†]
Schefflera actinophylla	Araliaceae	480
Siphonodon membranaceus	Celastraceae	835
Sloanea australis	Eleaocarpaceae	625
Sloanea macbrydei	Eleaocarpaceae	575
Symplocus cochinchinensis	Symplocaceae	545
Symplocus paucistaminea	Symplocaceae	585 (40) [†]
Synima cordierorum	Sapindaceae	945
Synima macrophylla	Sapindaceae	830 (22) [†]
Synuom glandulosum ssp. paniculosum	Meliaceae	675
Synuom muelleri	Meliaceae	625
Syzygium alliiligneum	Myrtaceae	610
Syzygium cormiflorum	Myrtaceae	770
Syzygium gustavioides	Myrtaceae	690
Syzygium sayeri	Myrtaceae	840
Tetrasynandra laxiflora	Monimiaceae	640
Toechima erythrocarpum	Sapindaceae	785
Toechima monticola	Sapindaceae	830 (22) [†]
Xanthophyllum octandrum	Xanthophyllaceae	800

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

[‡] Mimosaceae average excludes the genus *Acacia*.

[§] Myrtaceae average excludes the genera Corymbia, Eucalyptus, Leptospermum, Lophostemon and Melaleuca.

[¶] Proteaceae average excludes the genera Banksia and Grevillea.

[¿] No data available on the family Thymelaeaceae; dataset mean used instead.

Further information

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