

Edge Effects Disrupt Vertical Stratification of Microclimate in a Temperate Forest Canopy¹

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Abstract: Forest edge structure plays a key role in modulating microclimatic edge responses. However, empirical evidence for this is derived almost entirely from ground-based measurements, rather than measurements across the vertical canopy profile. Intuitively, canopy organisms are not only exposed to altered lateral-edge processes but also vertical influences from the hot, dry canopy edge above. The question then is “what is the influence of edge formation on vertical stratification of edge microclimate?” Here, we undertake a novel test of edge influence on vertical stratification of microclimate across the full vertical profile from ground level to upper canopy in a New Zealand temperate rain forest. We hypothesized that there would be a breakdown of vertical stratification at the edge and “compression” of the abiotic envelope experienced by organisms. We deployed 25 data loggers at five heights from canopy down to ground level (0, -2, -4, -8, -16 m) at each of five distances from edge (0, -2, -4, -8, -16 m) and quantified incident light, air temperature, and vapor pressure deficit relative to an external control. As predicted, we found strong evidence of a breakdown of vertical stratification at the edge for all microclimate variables. In generalized linear mixed models there was a significant interaction between vertical height and distance from edge, with microclimate differentials increasing in magnitude from edge to interior at ground level but decreasing in magnitude from edge to interior at canopy level. Attenuation of edge effects was lower above ground level, suggesting that past evidence of microclimatic edge effects based on ground-level measurements may underestimate the full extent of edge influence on vertical stratification of microclimate in forest remnants.

FOREST FRAGMENTATION and edge formation expose forest remnants to the climatic extremes of adjacent habitats (Laurance 2004), resulting in significant changes to edge microclimate (Chen et al. 1999). Microclimatic variables such as air temperature, vapor pressure deficit, and light intensity can all vary

greatly from the edge to the interior of forest remnants, due to increased penetration of solar radiation and wind (Chen et al. 1993a, b, Young and Mitchell 1994, Chen et al. 1995). It is well recognized that the magnitude and extent of these effects is dependent not only on edge structure but also on surrounding

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landscape context (Harper et al. 2005, Ewers and Didham 2006a). It has even been suggested that such “matrix” effects might be more important under some circumstances than edge structure in determining fragment microclimate (Denyer et al. 2006, Vanwallegghem and Meentemeyer 2009, Pinto et al. 2010, Wright et al. 2010), even if the matrix is only a narrow linear opening such as a road or power-line corridor (Pohlman et al. 2007).

Consequently, both edge closure (the density and vertical distribution of vegetation at the edge) and edge contrast (the difference in canopy height and vegetation structure between forest and matrix) play key roles in modulating microclimatic edge responses (Canham et al. 1990, Matlack 1993, Chen et al. 1995, Heithecker and Halpern 2007). For example, recently created edges typically have an open structure, with no substantial lateral crown spread of remnant trees or regrowth of understory vegetation, and edge effects can penetrate large distances into the forest (Chen et al. 1993a, b, Matlack 1993, Didham and Lawton 1999). By contrast, at long-established “closed” edges there can be well-developed regrowth that provides effective buffering of forest microclimate, regardless of matrix contrast (Brothers and Spingarn 1992, MacDougall and Kellman 1992, Didham and Lawton 1999, Mourelle et al. 2001).

The empirical evidence base for these effects is drawn almost entirely from ground-based measurements of altered microclimate gradients in the forest understory, rather than measurements across the whole vertical canopy profile. Intuitively, the forest canopy interface has a hot, dry, sunlit microclimate and would not be expected to respond in the same way as the forest understory to edge formation. Other zones within the vertical canopy profile will be influenced not only by lateral edge processes but also by vertical influences from the canopy above. The question then becomes “what is the influence of edge formation on vertical stratification of edge microclimate?” In many respects, we see this question as fundamental to the influence of edge closure and edge contrast on forest microclimate. In fact, temporal changes in vegetation structure and leaf properties at the

lateral edge of the forest (Mourelle et al. 2001) might well be a direct analogue of those that occur in the upper canopy to maximize photosynthetic capacity at the tree scale (Hollinger 1989). It is certainly well recognized that canopy architecture and the vertical distribution of foliage (Hollinger 1989, Parker 1997, Parker and Brown 2000, Parker et al. 2002, Parker et al. 2004, Dial et al. 2011) have a strong effect on light penetration (Sampson and Smith 1993, Mourelle et al. 2001) and turbulent atmospheric mixing in forests (Juang et al. 2008). The same almost certainly occurs at the lateral forest edge, but it is poorly studied.

Unfortunately, there has been almost a complete divide between edge microclimate studies that sample intensively in the horizontal dimension but incorporate limited or no vertical dimension (Chen et al. 1993a, b, 1995, 1999, Didham and Lawton 1999, Heithecker and Halpern 2007, Vanwallegghem and Meentemeyer 2009) versus canopy microclimate studies that sample intensively along a vertical profile but incorporate only a limited number of sampling locations (Parker et al. 2002, Mariscal et al. 2004, Parker et al. 2004, Juang et al. 2008, Rambo and North 2008). Exceptions to this have typically focused on modeling turbulent wind flow processes and eddying in forest gaps (Miller et al. 1991, Detto et al. 2008), particularly with application to the impact of logging and thinning on gap microclimate in forestry operations (Zhu et al. 2003, Miller et al. 2007, Rambo and North 2009, Gauthier and Jacobs 2010). Only very rarely has a three-dimensional approach to the measurement of edge microclimate been attempted within forest remnants, and even then it has only involved near-surface understory (Delgado et al. 2007, Ewers and Banks-Leite 2013) or subcanopy (Camargo and Kapos 1995, Dignan and Bren 2003) measurements.

The lack of empirical data limits generalizations about the impact of edge effects on vertical stratification of microclimate. Nevertheless, from the negative slopes of edge effects commonly observed at ground level, combined with the a priori expectation of null edge responses in upper canopy micro-

climate (assuming these areas are already “edgeline” in their microclimate anyway), we might predict that there would be a breakdown of vertical stratification at the forest edge. It is intriguing that, in a mathematical model of conductive heat flow across clear-cut forest edges in central Amazonia, Malcolm (1998) concluded that edge formation should indeed result in a more even temperature distribution across vertical height strata at the forest edge than in the forest interior. However, a limited comparison of real measurements of vapor pressure deficit (VPD) at five subcanopy heights (1.5–10 m in a forest 30 m tall) across six distances from edge (ca 12–100 m) in central Amazonia found that VPD actually increased more with height near the edge than in control areas (Camargo and Kapos 1995), leaving a question mark over the empirical generality of Malcolm’s (1998) model conclusions for edge microclimate.

Here, we undertook an explicit empirical test of edge influence on vertical stratification of microclimate across the full vertical profile from ground level to upper canopy. We carefully avoided edges where vertical canopy height declined toward the forest edge, so that our comparisons were not confounded by physical spatial compression of vertical height as opposed to compression of the abiotic envelope experienced by organisms living at the edge (cf. Parker et al. 2002). Our aim was to avoid a spurious geometric definition of “stratification” in the traditional sense of discrete, definable vegetation strata that can be categorized at fixed vertical heights above the ground but instead use the functional definition of Parker and Brown (2000) that “stratification” is a representation of the asymmetry, or heterogeneity, of functional attributes among two or more “zones” of the continuous vertical profile. With respect to microclimatic conditions within forests, vertical stratification (in this sense) might typically be represented as a narrow “bright zone” in the upper canopy with a high mean and low coefficient of variation (CV) in light, temperature, and VPD, below which there is a broad “transition zone” with rapidly changing mean values and high CV, and finally a near-ground

“dim zone” with a low mean and low CV of microclimate variables (see figure 5 in Parker and Brown [2000]). By contrast, a breakdown in vertical stratification near the edge might be observed as the relative similarity of microclimatic conditions across the entire vertical profile. We hypothesized that if such a breakdown in vertical stratification of microclimate occurred at the forest edge, then we would observe a significant interaction effect between the slopes of edge effects at different heights above ground.

MATERIALS AND METHODS

Study Site

The study was conducted at the north-facing edge of a large (1,060 ha) tract of forest near the headwaters of the Kakapo Brook, a tributary of the Waiau River in the Hurunui District of the central South Island, New Zealand. The study area is part of the Glynn Wye high-country cattle station, consisting of a mosaic of managed grazing land and remnant forest, at various altitudes from 600 to 1,700 m above sea level (asl). With the exception of the high alpine areas (elevation >1,300 m, ca. 15% of the landscape), the region was in continuous southern beech forest (*Nothofagus* spp.) before human settlement. Since settlement, large tracts of forest have been cleared and converted to farmland, leaving just 40% of the study area covered by remnants of the original forest (Ewers et al. 2007). Land conversion involved burning and mechanical clearance for pastoral agriculture ca. 80–100 yr ago, rather than logging. The forest edge sampled in this study was a mixed silver beech (*N. menziesii*), red beech (*N. fusca*), and mountain beech (*N. solandri* var. *cliffortioides*) forest located at ca. 700 m asl, and no timber harvesting had ever been conducted in this forest. Although tree height in the study area varied considerably (from ca. 10 to 25 m, depending on soil conditions and elevation), the study edge was selected for its uniformity of canopy height (16 m) right up to the well-demarcated edge with the adjacent grassland matrix habitat. Edge vegetation structure was dense, but there was almost no regeneration of woody

plants in the grassland due to continued grazing pressure from cattle, deer, goats, and sheep.

Experimental Design

Microclimate was measured at five distances from the forest edge into the forest interior (0, -2, -4, -8, and -16 m), but individual sampling points were not in a straight-line transect, they were offset laterally along the edge by up to 30 m. A logarithmic (base 2) sampling scale was applied, reflecting the a priori expectation that the rate of change in microclimate variables would be most rapid close to the forest edge (Didham and Lawton 1999). A north-facing edge was selected because microclimatic edge effects are typically found to be most severe at this aspect in the Southern Hemisphere (Young and Mitchell 1994, Norton 2002, Dignan and Bren 2003). At each distance, microclimate data loggers were established at five vertical heights from the upper canopy edge (0 m) down to the forest floor (0, -2, -4, -8, and -16 m), 25 data loggers in total, deployed in a continuous response surface design. Tree heights at the randomly selected sampling points were 16 m (± 25 cm) in all cases. This sampling protocol was used to contrast edge microclimate gradients among different vertical strata and to contrast horizontal microclimate gradients in from the forest edge with vertical microclimate gradients down from the forest canopy interface.

Data loggers at ground level (-16 m) were placed on wooden stakes approximately 5 cm above the forest floor, making sure that the sensors were not covered by ground-layer vegetation. Data loggers in the canopy (0, -2, -4, and -8 m) were established by hoisting a self-leveling wooden platform into the forest canopy on a single-line pulley system. Unlike other studies (e.g., Rambo and North 2008) we avoided attaching data loggers directly to the trunks of trees, so that we could minimize trunk and branch influences on microclimate. Lines were placed in the canopy using a line-throwing crossbow, and each microclimate data logger was independently placed on a separate line. A typical vertical vegetation

profile at each sampling point consisted of a dense but patchy understory herb layer with scattered clumps of *Blechnum* spp. sword ferns, a shrub layer and midstory of mixed *Nothofagus* spp. saplings, under a canopy of large *Nothofagus* spp. trees.

Placement of the five upper-canopy (0 m) data loggers posed a special challenge, because platforms could not be hoisted right up to the rope attachment point at the upper edge of the canopy (and pulling on the rope inevitably meant that the actual rope attachment point was usually at -1 m, rather than at 0 m). Consequently, a 75 m length of static rope 10 mm thick was placed tautly between adjacent tree crowns, and the individual pulley lines for the upper canopy data loggers were established perpendicularly over top of this fixed line. To obtain the correct vertical height at the upper canopy edge, the sensors were bolted to the end of a PVC pipe 3 m long, which was then inserted through the self-leveling wooden platform so that 2 m of the pipe projected above the platform and the remaining 1 m of the pipe projected below the platform. The lower portion of the pipe was carefully weighted to act as a counterbalance to the microclimate sensors. Each self-leveling platform was then raised to -2 m, so that the projecting pole elevated the microclimate sensors to exactly 0 m. An additional guy rope was attached to the bottom of the pole to make fine leveling adjustments in orientation. This elaborate setup for the upper canopy data loggers was carefully designed to prevent the units projecting too high, or pulling down through the canopy and causing foliage to cover the sensors (as would have occurred at even -5 cm).

In this study, we were not principally interested in the absolute values of abiotic variables (because these can vary greatly from day to day) but instead in relative differentials between edge distances versus the open-area control readings, and between vertical heights versus the open-area control. The control data logger was established in a flat, open grassland, 256 m from the nearest forest remnant, and the sensors were bolted to a wooden pole arbitrarily placed at 1 m above ground level.

Measurement of Microclimate Variables

Microclimate variables were recorded at the 26 sampling points between 28 February and 7 March 2003 using microloggers (Hobo H08-series, Onset Computer Corporation). We followed the rationale of Turton (1985) that new shoot growth nears its maximum for the growing season by late February to early March in montane *Nothofagus* forest, and this is also the warmest month, so an understanding of microclimatic variation at this time is most relevant to plant ecophysiology and forest dynamics. Microloggers were placed in rainproof containers with good airflow and were protected from direct solar radiation by an insulated sun shield. Air temperature (°C) and relative humidity (RH, %) were recorded by internal sensors (Hobo) (following calibration of the 26 microloggers in a common-garden setting), and light intensity was measured using external light sensors designed at the University of Canterbury. Recordings were made at 5-min intervals. Subsequently RH was converted to vapor pressure deficit (VPD, mb) using Tetens Equation for the relationship between temperature (T , in °C) and the partial pressure of water vapor (e_s):

$$e_s = 6.1078 \exp \left[\frac{17.269T}{T + 237.3} \right] \quad (1)$$

VPD (calculated as: $e_s - [\text{RH} \cdot e_s / 100]$) is a better measure of evaporative and transpirational stresses on plants than RH alone (De Freitas and Enright 1995). Unfortunately, the RH sensor in one data logger failed (0 m distance, -2 m height), and VPD data for this one location were excluded from analysis. The light sensors employed a photodiode with a 30° receptive angle and were capped with a semi-opaque, 1 cm³ Perspex cube to diffuse ambient light onto the sensor. Light sensors recorded a voltage signal at the micrologger that was proportional to ambient solar radiation, and each of the 26 sensors was individually calibrated to photon flux density (PFD, $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$).

For the purposes of analyses, three measures of relative microclimate differentials were calculated at each location. Air tempera-

ture differentials and VPD differentials were calculated for each location using individual data logger values minus the matrix control (open area) value recorded at the same time interval and averaged for all 5-min readings during the 4 hr after the solar transit (i.e., 1245–1645 hours) (Figure 1). This period represented the hottest part of the day when standing microclimate gradients were maximal. Averaging during this period avoided the overestimation of maximum microclimate differentials that can occur due to spurious variation in factors such as cloud cover and sun flecks. By contrast, proportion incident light was calculated as forest PFD divided by matrix control PFD and averaged for all 5-min readings within the 4-hr period ± 2 hr of the solar transit (i.e., 1045–1445 hours) to account for the narrow receptive angle of the sensor.

In addition to relative microclimate differentials between locations, three measures of variability in microclimate were calculated between vertical strata at differing distances from the forest edge. Variability in VPD and variability in PFD were both measured as the coefficient of variation (CV) in 5-min readings during their respective 4-hr sampling periods each day. Variability in air temperature was expressed as the daily temperature range (maximum daily temperature during the 4 hr after the solar transit minus minimum daily temperature during the 4 hr before dawn) (Figure 1).

Statistical Analyses

We tested the interactive effects of height above ground and distance from forest edge on microclimate variables using linear mixed effects model analyses in R version 2.13.1 (R Development Core Team 2011). For all six microclimate variables, six average daily values were obtained and these were used to compare differences in microclimate between heights and distances (i.e., days were the replicates, not 5-min readings). LOCATION was included as a random effect in each model to account for nonindependence of repeated daily measures at each sampled location. Log₂ distance from forest edge (EDGE) and log₂

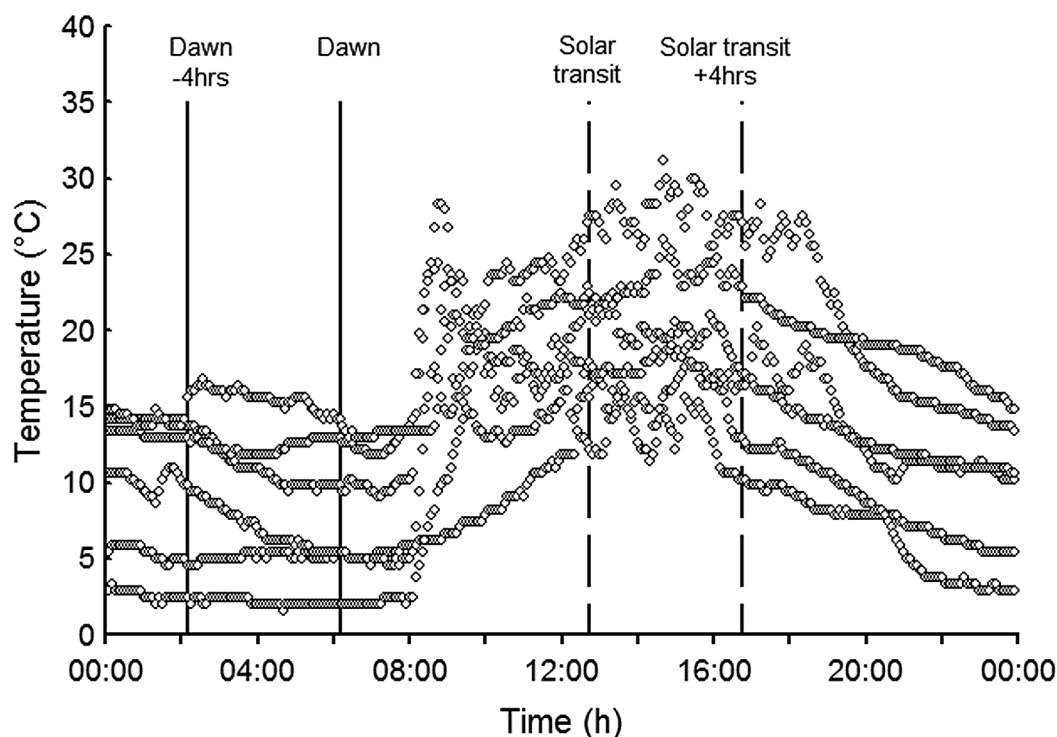


FIGURE 1. Daily variation in air temperature at the open pasture control site during the sampling period. Different symbols indicate measurements taken on different days. Vertical lines indicate the time intervals within which values for temperature and vapor pressure deficit were drawn. Incident light was recorded within the 4-hr period ± 2 hr of the solar transit (see Materials and Methods for further explanation).

distance from forest edge squared (EDGE^2) were included as fixed continuous variables, reflecting the potential nonlinear response of microclimate to distance from forest edge. We chose to include \log_2 height above ground (HEIGHT) as a fixed categorical factor with five levels, rather than as a continuous variable, because we explicitly wanted to test how the slopes of edge responses varied between midstory and canopy levels, compared with the ground-level edge response slopes measured in most previous edge microclimate studies. We included interaction effects between \log_2 height by \log_2 distance from forest edge ($\text{HEIGHT}:\text{EDGE}$) and \log_2 height by \log_2 distance from forest edge squared ($\text{HEIGHT}:\text{EDGE}^2$) as fixed effects to estimate variation in the slope of edge effects with height above ground. In a sensitivity analysis, the alternative approach of treating

height above ground as a continuous polynomial predictor had no qualitative influence on the conclusions presented here (results not shown).

For each microclimate variable we first fitted a linear mixed effects model with Gaussian error structure using the nlme package in R and tested the assumptions of normality and homoscedasticity of variances (Bolker et al. 2009). In no cases were the assumptions met, so we tested effects using generalized linear mixed effects models (GLMMs) in the lme4 package in R. In the GLMMs, a Poisson distribution (with log link function) was specified for microclimate differentials and microclimate variability (temperature differential, temperature variability, VPD differential, VPD variability, and PFD variability), except where a binomial distribution (with logit link function) was specified for proportion data

(proportion incident light). For models where there was significant overdispersion of model residuals, an observation-level vector (OBS) was added to the model as a random factor (Jiang 2007, Bolker et al. 2009).

To determine the minimum adequate factors in each model we took an information-theoretic approach to model simplification (Burnham and Anderson 2002). This approach allows comparison of multiple models with reduced subsets of fixed factors and their interactions, enabling the most parsimonious model(s) to be identified. This is achieved through fitting competing models to the same data set and then ranking them by the lowest AICc scores (AIC scores corrected for small sample size) using the AICcmodavg package in R 2.13.1. Models within two AICc units of the lowest AICc score were considered to have equivalent likelihood of being the model with the greatest explanatory power (Burnham and Anderson 2002).

RESULTS

Ambient conditions at the pasture control site over the course of the study were typical of late summer weather in mountainous terrain of the central South Island, with low overnight temperatures (daily minimum: 1.60°C–14.09°C) and moderate to warm daytime temperatures (daily maximum: 16.76°C–31.12°C) (Figure 1). All relative microclimate differentials and measures of variability in air temperature, vapor pressure deficit, and light across vertical strata showed strongly contrasting effects of height above ground and distance from forest edge (Figure 2).

Air Temperature

For air temperature, the minimum adequate GLMM included a significant height by distance from edge interaction effect (Table 1, a). At ground level, air temperature differentials calculated relative to the pasture control site showed larger reductions in the interior than the edge (i.e., increased significantly in magnitude from edge to interior), whereas the reverse occurred in the upper canopy, with air temperature differentials decreasing

significantly in magnitude from edge to interior (Figure 2a; Table 2, a). This interaction effect resulted in the strong vertical stratification of air temperature observed at –16 m inside the forest (a vertical gradient of over 3°C) becoming “compressed” and unstructured at the forest edge (a vertical gradient of less than 1.5°C), although temperatures even in the upper canopy were still 1°C below those at the open-pasture control site (Figure 2a). A similar trend was observed for variability in absolute air temperature as well (Figure 2b), with a significant height by distance from edge interaction effect in one of the two most parsimonious GLMM models (Table 1, b). Temperature variability at the forest edge and in the upper canopy was typically higher than in the interior forest understory. However, the statistical difference in slopes of edge effects among heights was comparatively weak due to high variability in diurnal temperature range among days, and a model with a common edge slope was the minimum adequate model in the GLMM analysis (Table 2, b; Figure 2b).

Vapor Pressure Deficit

For vapor pressure deficit, there was a significant height by distance from edge interaction effect in the minimum adequate GLMM for calculated VPD differentials (Figure 2c; Table 1, c). At ground level, VPD differentials were up to twice as high in the forest interior as at the forest edge, and the reverse was true for the upper forest canopy (Figure 2c; Table 2, c). Variability in VPD also showed a strong interaction effect between height and distance from edge (Table 1, d), but trends were less clear-cut beyond the general finding of higher variability in VPD at the forest edge and in the upper canopy compared with the interior forest understory (Figure 1d).

Incident Light

For light conditions, there was not only a significant height by distance from edge interaction effect, but edge responses were also highly nonlinear (Table 1, e; Figure 2e). Proportion incident light declined rapidly

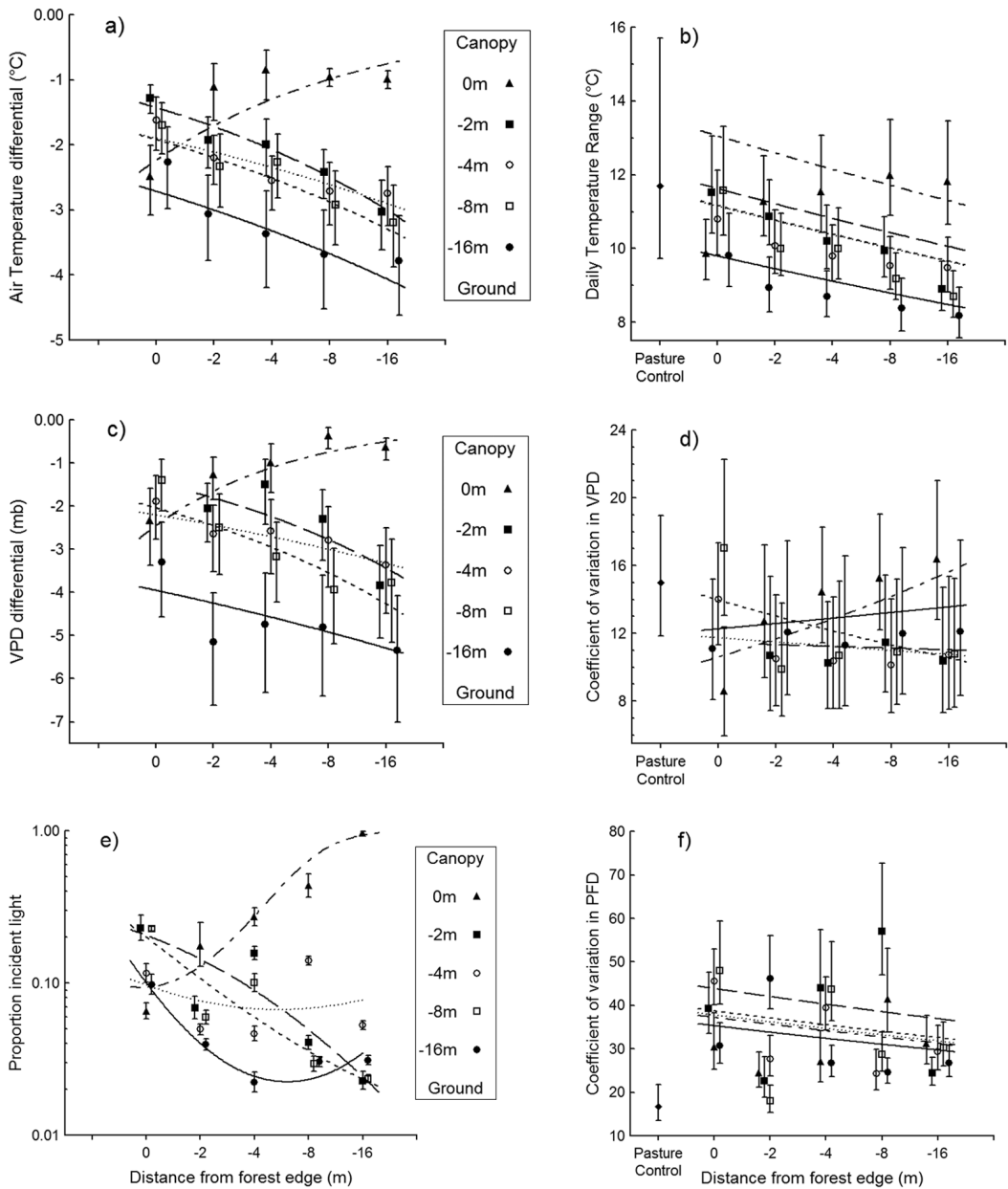


FIGURE 2. Breakdown of the vertical stratification of microclimate at the edge of a southern beech forest in New Zealand. Microclimate differentials (relative to an open-area pasture control site) are shown for (a) average daily air temperature, (c) average daily vapor pressure deficit (VPD), and (e) proportion incident light. Variability in absolute microclimate is shown for (b) average daily temperature range, (d) coefficient of variation (CV) of VPD, and (f) CV of photon flux density (PFD). Fitted lines for each height above ground are derived from the GLMM analysis: -16 m (solid circle, solid line), -8 m (open square, short-dash line), -4 m (open circle, dotted line), -2 m (solid square, long-dash line), and 0 m upper canopy (solid triangle, dash-dot line). Points are slightly offset along the x-axis to avoid overlapping error bars. Variability in microclimate is shown for the pasture control site also but was not included in GLMM model fitting.

TABLE 1
Model Simplification Procedure to Select the Best-Fit Generalized Linear Mixed Effects Model(s) for Each Microclimate Response Variable, Based on Akaike Information Criterion (AIC) Comparisons

| Model No. | Model ^a | K | AICc | ΔAICc | Akaike Weight |
|---|---|----|---------------|-------------|---------------|
| (a) Average daily temperature differentials | | | | | |
| a.1 | HEIGHT+EDGE+HEIGHT:EDGE | 11 | 59.00 | 0.00 | 0.66 |
| a.2 | HEIGHT+EDGE+EDGE ² +HEIGHT:EDGE | 12 | 61.26 | 2.25 | 0.21 |
| a.3 | HEIGHT+EDGE | 7 | 62.82 | 3.82 | 0.10 |
| a.4 | HEIGHT | 6 | 65.65 | 6.64 | 0.02 |
| (b) Average daily temperature range | | | | | |
| b.1 | HEIGHT+EDGE | 7 | 53.22 | 0.00 | 0.50 |
| b.2 | HEIGHT+EDGE+HEIGHT:EDGE | 11 | 54.64 | 1.42 | 0.24 |
| b.3 | HEIGHT | 6 | 55.25 | 2.03 | 0.18 |
| b.4 | HEIGHT+EDGE+EDGE ² +HEIGHT:EDGE | 12 | 56.98 | 3.77 | 0.08 |
| (c) Average daily VPD differentials | | | | | |
| c.1 | HEIGHT+EDGE+HEIGHT:EDGE | 11 | 76.75 | 0.00 | 0.73 |
| c.2 | HEIGHT+EDGE+EDGE ² +HEIGHT:EDGE | 12 | 78.77 | 2.02 | 0.26 |
| c.3 | HEIGHT+EDGE+EDGE ² +HEIGHT:EDGE+HEIGHT:EDGE ² | 16 | 85.77 | 9.01 | 0.01 |
| (d) Coefficient of variation in VPD | | | | | |
| d.1 | HEIGHT+EDGE+HEIGHT:EDGE | 11 | 144.45 | 0.00 | 0.48 |
| d.2 | HEIGHT+EDGE+EDGE ² +HEIGHT:EDGE | 12 | 145.21 | 0.75 | 0.33 |
| d.3 | HEIGHT | 6 | 147.69 | 3.23 | 0.10 |
| d.4 | HEIGHT+EDGE+EDGE ² +HEIGHT:EDGE+HEIGHT:EDGE ² | 16 | 148.76 | 4.31 | 0.06 |
| d.5 | HEIGHT+EDGE | 7 | 149.66 | 5.20 | 0.04 |
| (e) Proportion incident light | | | | | |
| e.1 | HEIGHT+EDGE+EDGE ² +HEIGHT:EDGE+HEIGHT:EDGE ² | 16 | 348.80 | 0.00 | 0.91 |
| e.2 | HEIGHT+EDGE+EDGE ² +HEIGHT:EDGE | 12 | 353.37 | 4.56 | 0.09 |
| e.3 | HEIGHT+EDGE+HEIGHT:EDGE | 11 | 362.54 | 13.73 | 0.00 |
| (f) Coefficient of variation in PFD | | | | | |
| f.1 | HEIGHT+EDGE | 8 | 465.49 | 0.00 | 0.53 |
| f.2 | HEIGHT | 7 | 466.14 | 0.65 | 0.38 |
| f.3 | HEIGHT+EDGE+HEIGHT:EDGE | 12 | 469.66 | 4.17 | 0.07 |
| f.4 | HEIGHT+EDGE+EDGE ² +HEIGHT:EDGE | 13 | 471.99 | 6.50 | 0.02 |
| f.5 | HEIGHT+EDGE+EDGE ² +HEIGHT:EDGE+HEIGHT:EDGE ² | 17 | 475.47 | 9.98 | 0.00 |

Note: K, number of parameters in the model; ΔAICc, change in AICc relative to the best (i.e., lowest) AICc score; Akaike Weight, relative probability of each model being the best model, out of the models compared. For the sake of brevity, models with ΔAICc > 10 are not shown here. **Boldface** values indicate models that are within 2 AICc units of the best-fit model.

^a All GLMM models include “(1|LOCATION)” as a random effect. In addition, models in (e)–(f) also include an observation-level random vector “(1|OBS)” to account for overdispersion of model residuals.

from edge to interior at all vertical heights, except in the upper canopy where proportion incident light increased rapidly from edge to interior (Figure 2e). Variability in light environment (PFD) also changed with distance from edge, but there was a uniform slope of edge response at all vertical heights in the minimum adequate GLMM (Table 1, f; Table 2, f). Variability in PFD declined from edge to interior at all heights, but even in the interior forest understory it was still higher than in the open-area control site (Figure 2f).

DISCUSSION

At the dense, closed edge of a cool-temperate rain forest, gradients in understory microclimate attenuated logarithmically with increasing distance from edge to interior, with average reductions of 4°C air temperature, 5 mb vapor pressure deficit, and 98% incident light, relative to an external open-area control. These findings are qualitatively typical of those recorded in the majority of previous studies of edge microclimate based on ground-level measurements, both in New

TABLE 2

Estimated Model Coefficients of the Best-Fit Generalized Linear Mixed Effects Model for Each Microclimate Response Variable (as Indicated by the Model No. from Table 1)

| Model No. | Parameter | Estimate | SE | z | Pr(> z) | |
|---|-----------------------------------|----------|-------|---------|----------|-----|
| (a) Average daily temperature differentials | | | | | | |
| a.1 | (Intercept) | 0.998 | 0.241 | 4.142 | <0.001 | *** |
| | HEIGHT.canopy-8 | -0.346 | 0.275 | -1.256 | 0.209 | |
| | HEIGHT.canopy-4 | -0.356 | 0.278 | -1.281 | 0.200 | |
| | HEIGHT.canopy-2 | -0.642 | 0.298 | -2.157 | 0.031 | * |
| | HEIGHT.canopy-0 | -0.196 | 0.284 | -0.689 | 0.491 | |
| | EDGE | 0.101 | 0.068 | 1.476 | 0.140 | |
| | HEIGHT.canopy-8:EDGE | 0.034 | 0.104 | 0.330 | 0.742 | |
| | HEIGHT.canopy-4:EDGE | 0.005 | 0.106 | 0.052 | 0.959 | |
| | HEIGHT.canopy-2:EDGE | 0.085 | 0.111 | 0.770 | 0.441 | |
| | HEIGHT.canopy-0:EDGE | -0.373 | 0.130 | -2.870 | 0.004 | ** |
| (b) Average daily temperature range | | | | | | |
| b.1 | (Intercept) | 2.282 | 0.110 | 20.778 | <0.001 | *** |
| | HEIGHT.canopy-8 | 0.131 | 0.082 | 1.598 | 0.110 | |
| | HEIGHT.canopy-4 | 0.129 | 0.082 | 1.574 | 0.115 | |
| | HEIGHT.canopy-2 | 0.170 | 0.081 | 2.100 | 0.036 | * |
| | HEIGHT.canopy-0 | 0.287 | 0.079 | 3.627 | <0.001 | *** |
| | EDGE | -0.036 | 0.018 | -2.056 | 0.040 | * |
| (c) Average daily VPD differentials | | | | | | |
| c.1 | (Intercept) | 1.374 | 0.301 | 4.568 | <0.001 | *** |
| | HEIGHT.canopy-8 | -0.661 | 0.235 | -2.817 | 0.005 | ** |
| | HEIGHT.canopy-4 | -0.584 | 0.234 | -2.499 | 0.012 | * |
| | HEIGHT.canopy-2 | -0.993 | 0.344 | -2.889 | 0.004 | ** |
| | HEIGHT.canopy-0 | -0.480 | 0.248 | -1.933 | 0.053 | † |
| | EDGE | 0.073 | 0.055 | 1.339 | 0.181 | |
| | HEIGHT.canopy-8:EDGE | 0.111 | 0.088 | 1.264 | 0.206 | |
| | HEIGHT.canopy-4:EDGE | 0.029 | 0.090 | 0.327 | 0.744 | |
| | HEIGHT.canopy-2:EDGE | 0.140 | 0.119 | 1.175 | 0.240 | |
| | HEIGHT.canopy-0:EDGE | -0.470 | 0.126 | -3.720 | <0.001 | *** |
| (d) Coefficient of variation in VPD | | | | | | |
| d.1 | (Intercept) | 2.507 | 0.281 | 8.926 | <0.001 | *** |
| | HEIGHT.canopy-8 | 0.129 | 0.112 | 1.157 | 0.247 | |
| | HEIGHT.canopy-4 | -0.044 | 0.116 | -0.381 | 0.703 | |
| | HEIGHT.canopy-2 | -0.071 | 0.156 | -0.456 | 0.649 | |
| | HEIGHT.canopy-0 | -0.145 | 0.116 | -1.248 | 0.212 | |
| | EDGE | 0.025 | 0.032 | 0.768 | 0.443 | |
| | HEIGHT.canopy-8:EDGE | -0.095 | 0.046 | -2.053 | 0.040 | * |
| | HEIGHT.canopy-4:EDGE | -0.047 | 0.047 | -0.993 | 0.321 | |
| | HEIGHT.canopy-2:EDGE | -0.034 | 0.059 | -0.578 | 0.563 | |
| | HEIGHT.canopy-0:EDGE | 0.072 | 0.046 | 1.585 | 0.113 | |
| (e) Proportion incident light | | | | | | |
| e.1 | (Intercept) | -2.146 | 0.157 | -13.633 | <0.001 | *** |
| | HEIGHT.canopy-8 | 0.830 | 0.162 | 5.119 | <0.001 | *** |
| | HEIGHT.canopy-4 | 0.013 | 0.181 | 0.074 | 0.941 | |
| | HEIGHT.canopy-2 | 0.927 | 0.160 | 5.779 | <0.001 | *** |
| | HEIGHT.canopy-0 | 0.102 | 0.175 | 0.584 | 0.559 | |
| | EDGE | -1.206 | 0.212 | -5.696 | <0.001 | *** |
| | EDGE ² | 0.231 | 0.054 | 4.239 | <0.001 | *** |
| | HEIGHT.canopy-8:EDGE | 0.369 | 0.264 | 1.399 | 0.162 | |
| | HEIGHT.canopy-4:EDGE | 0.869 | 0.265 | 3.279 | 0.001 | ** |
| | HEIGHT.canopy-2:EDGE | 0.705 | 0.255 | 2.761 | 0.006 | ** |
| | HEIGHT.canopy-0:EDGE | 1.244 | 0.246 | 5.047 | <0.001 | *** |
| | HEIGHT.canopy-8:EDGE ² | -0.163 | 0.070 | -2.330 | 0.020 | * |
| | HEIGHT.canopy-4:EDGE ² | -0.164 | 0.067 | -2.452 | 0.014 | * |

TABLE 2 (continued)

| Model No. | Parameter | Estimate | SE | z | Pr(> z) | |
|-----------|-----------------------------------|----------|-------|--------|----------|-----|
| | HEIGHT.canopy-2:EDGE ² | -0.247 | 0.068 | -3.654 | <0.001 | *** |
| | HEIGHT.canopy-0:EDGE ² | 0.022 | 0.063 | 0.345 | 0.730 | |
| (f) | Coefficient of variation in PFD | | | | | |
| f.1 | (Intercept) | 3.546 | 0.142 | 25.034 | <0.001 | *** |
| | HEIGHT.canopy-8 | 0.109 | 0.113 | 0.965 | 0.335 | |
| | HEIGHT.canopy-4 | 0.086 | 0.113 | 0.757 | 0.449 | |
| | HEIGHT.canopy-2 | 0.234 | 0.113 | 2.078 | 0.038 | * |
| | HEIGHT.canopy-0 | 0.070 | 0.113 | 0.620 | 0.535 | |
| | EDGE | -0.043 | 0.025 | -1.708 | 0.088 | † |

Note: SE, standard error of parameter estimates; z, z-score testing whether the parameter estimate is significantly different from zero; Pr(>|z|), probability of the observed z-score being greater than the critical value at †, $P < .10$; *, $P < .05$; **, $P < .01$; and ***, $P < .001$. The model intercept represents the ground-level value, and the coding for the remaining height categories is represented as “canopy minus 8 m,” “canopy minus 4 m,” and so on.

Zealand (Young and Mitchell 1994, Davies-Colley et al. 2000, Norton 2002, Denyer et al. 2006) and elsewhere (Chen et al. 1999, Dignan and Bren 2003, Vanwalleghe and Meentemeyer 2009). However, these “typical” edge responses bear little resemblance to the edge gradients in microclimate that we observed at subcanopy and canopy levels. In fact, relative differentials for all three microclimate variables exhibited a highly significant interaction effect between vertical height above ground and distance from forest edge. Microclimate differentials recorded at ground level increased significantly in magnitude from edge to interior, whereas values recorded at canopy level actually decreased significantly in magnitude from edge to interior. Although these results are based on a single sampled edge, our initial findings provide compelling evidence for a compression of the abiotic envelope at the forest edge and an edge-induced breakdown in the vertical stratification of forest microclimate. We discuss the implications (and limitations) of these findings for understanding landscape influences on microclimatic conditions in forest remnants.

Edge Effects on Microclimate across the Vertical Profile

Our a priori hypothesis was that there would be significant negative slopes of edge effects

observed at ground level but only weak or no edge responses observed in the upper canopy, based on the reasoning that the upper canopy might already be “edgeline” in microclimatic conditions anyway and thus may be little affected by lateral edge influence. This hypothesis proved to be only partially correct for air temperature, VPD, and incident light measurements.

AIR TEMPERATURE. For air temperature, the forest understory varied from 1°C to 4°C cooler than the open-area reference site as distance from edge increased from 0 to 16 m. Although edge effects are known to extend much farther than this (Chen et al. 1999, Ewers and Didham 2006b, 2008), and therefore we inevitably sampled only part of the edge response curve, these understory values were fairly typical of the -1°C to -3°C differentials recorded for cool-temperate rain forest interiors (Davies-Colley et al. 2000, Norton 2002, Denyer et al. 2006). By contrast, much shallower edge gradients in air temperature were observed in the subcanopy, and in the upper canopy the edge to interior gradient was reversed, with air temperature increasing significantly toward the forest interior. These differing edge response functions across vertical strata produced the predicted breakdown of vertical stratification at the forest edge, but it was surprising that the compression of vertical microclimatic conditions was as much due to edge influence on canopy

microclimate as it was to edge influence on understory microclimate.

As far as we are aware, a reversal of microclimate edge-response functions from ground level to upper canopy has not previously been recorded. These microclimate responses are almost certainly due to the strong influence of leaf area index (LAI) on edge penetration of wind and solar radiation, as shown for example in conductive heat flow models at the forest edge (Malcolm 1998), but we acknowledge that we lack the mechanistic basis to prove this hypothesis without appropriate measures of LAI or the vertical distribution of foliage density. It is interesting that Malcolm (1998) alluded to the upper canopy as an “edge” where heat flow occurs both horizontally from the adjacent clear-cut as well as vertically from the atmosphere above. Moreover, in his earlier two-dimensional model of the “additive” effects of multiple edges on understory versus overstory vegetation density, Malcolm (1994) predicted that additive edge influences would produce rounded response isopleths at the right-angle corners of abrupt forest edges. This is exactly the phenomenon we observed for temperature at the interface of lateral and upper canopy edges. However, Malcolm (1994) stopped short of making a direct link between LAI and vertical stratification of microclimate.

VAPOR PRESSURE DEFICIT. An analogous reversal of edge response functions from ground level to upper canopy was observed for VPD, with the magnitude of the vertical gradient in VPD declining from edge to interior. At face value, this compression of the vertical VPD profile at the edge is exactly the opposite of that found by Camargo and Kapos (1995) for a tropical rain forest edge in central Amazonia, where VPD was reported to increase more with height near the edge than in interior-forest control areas. However, this discrepancy is almost certainly an artifact of Camargo and Kapos' (1995) spatial measurement interval encompassing only a portion of the horizontal and vertical gradient at the edge. Camargo and Kapos (1995) only sampled up to one-third canopy height (five heights from 1.5 to 10 m in a forest 30 m tall) and did not sample the near-edge zone for

logistical reasons (six edge distances from ca. 12 to 100 m). In our study reported here, if we were to make a direct comparison with Camargo and Kapos' (1995) results over the same restricted spatial interval, we would actually find the equivalent result that the magnitude of the vertical difference in VPD from ground to subcanopy level increased toward the edge (see Figure 2c). This suggests that the horizontal and vertical interval over which measurements are made has a critical influence on conclusions about the vertical stratification of microclimate. It also suggests that midstory attenuation of edge influence on VPD must be somewhat slower than at either ground or upper-canopy levels, resulting in greater depth of edge influence in the subcanopy (although it was beyond the scope of our study to quantify edge extent).

INCIDENT LIGHT. Incident light levels in the interior forest understory were typical of the 2%–5% incident light levels reported for New Zealand native forests (McDonald and Norton 1992), even though our interior sites were only 16 m from a dense closed edge. Moreover, at our interior distance, the strong vertical attenuation of incident light from canopy to ground level was consistent with that found for unfragmented montane *Nothofagus* forests in New Zealand (Turton 1985), with incident light declining to less than 5% of the open-area value within 2 m of the outer canopy edge. Proximity to edge had a dramatic effect on the vertical light profile, with a strong breakdown of vertical stratification within 8 m of the forest edge. Near-edge light environments were more similar to the 5%–20% incident light penetration observed in small forest gaps by McDonald and Norton (1992), regardless of vertical height.

As with air temperature and VPD, there was a significant reversal of edge responses in incident light from ground level to upper canopy, which can only be due to very high LAI in the uppermost layers at the forest edge. This is not due to direct shading of the sensor in the upper canopy but rather to lateral scatter of light being impeded by high foliage density and the edge. Our sensors were placed exactly equal to the outer foliage layer, not above it, and therefore differences

in LAI would affect lateral scatter of light onto the sensor. We did use a sensor with a narrow (30°) receptive angle to counter this type of effect, but it is possible that the semi-opaque Perspex diffuser cube placed over the sensor may have been responsible for diffusing lateral light scatter in high light environments. Canopy structure is known to have a pronounced influence on spatial distribution of light environments within New Zealand forests (Turton 1985, Hollinger 1989, McDonald and Norton 1992), but the direct relationship between edge closure and vertical microclimate profiles has not been quantified. However, at closed forest edges in southwestern Ontario, Canada, Mourelle et al. (2001) found that 80% of the variation in light occlusion from canopy to ground level could be explained by species-specific differences in lateral branch growth and increase in leaf density at the edge. In our study reported here, lateral occlusion appeared to result in variable light penetration across the vertical profile and highly nonlinear edge responses, with attenuation of edge responses being most rapid at ground level and slowest in the subcanopy. This is similar to a study of light penetration into riparian forest remnants in southeastern Australia, where Dignan and Bren (2003) found that 75% of the total light attenuation response at ground level occurred within 3–6 m of the forest edge, compared with 13–41 m at a vertical height of 6.8 m in the subcanopy.

Implications of Edge Closure for Landscape Influence on Patch Microclimate

The degree of edge closure is well recognized as one of the most important factors mediating the magnitude and extent of surrounding landscape influence on understory microclimate (Didham and Lawton 1999). It is surprising that there has been no attempt to extrapolate these findings across the full vertical profile at forest edges, even though vertical LAI profiles at the edge have been shown to influence direct penetration of solar radiation (Mourelle et al. 2001), turbulent wind flow and eddy recirculation patterns (Camargo and Kapos 1995, Laurance 2004, Detto et al.

2008), advective heating as wind moves warm air masses across the forest edge from the adjacent landscape matrix (e.g., Chen et al. 1995), and conductive heat flow within the canopy (Malcolm 1998). The lack of information on vertical microclimate profiles measured across forest edges is a major gap in our knowledge and is especially critical if we want to better understand edge processes. Here we have provided an initial test of the hypothesis that edge effects alter the vertical stratification of forest microclimate, although we fully acknowledge the need to validate these results across a greater number of replicate forest edges and determine the relative influence of aspect, topography, and other factors on vertical edge profiles. In spite of these limitations, our initial results support the hypothesis that edge closure has greatly varying influences on remnant forest microclimate at ground level versus canopy level and therefore that edge responses across vertical strata cannot be inferred from understory measurements alone. Attenuation of edge responses in incident light, VPD, and to a lesser extent air temperature, all appeared to be more rapid in the ground and upper-canopy layers but slower in the midstory subcanopy layers. These findings are consistent with previous evidence for the effects of altered vegetation structure on light attenuation before versus after clear-cutting of adjacent forest in southeastern Australia (Dignan and Bren 2003), where edge penetration was greater in the subcanopy rather than the ground layer. Similarly, they are consistent with the effects of logging and thinning on incident light and leaf trait responses in young plantation stands of black walnut in the United States, where gap-induced changes in incident light were much greater in the subcanopy than in the upper canopy (Gauthier and Jacobs 2010). This all tends to suggest that previous studies of edge effects on forest microclimate conducted at ground level have underestimated the spatial extent of edge influence for organisms in the midstory and subcanopy of forest fragments. It should also be pointed out that in this study we purposely selected a north-facing, closed forest edge where microclimatic edge effects were expected to be high in

magnitude but attenuate rapidly (Didham and Lawton 1999), and the question remains as to the spatial extent of edge influence on vertical stratification of microclimate at open edges. A productive avenue for future investigation would be to test the relative influence of edge effects on vertical stratification across gradients from north- to south-facing edges, and edges in mesic through to semiarid environments. The clear implication is that a full understanding of the influence of edge closure and edge contrast on forest microclimate can only be achieved through appropriate quantification across the full vertical profile.

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