J.Natn.Sci.Foundation Sri Lanka 2011 **39** (4):321-331

RESEARCH ARTICLE

The variation of resource availability within canopy gaps and adjacent understories across elevational gradients of a Sri Lankan rainforest

Sisira Ediriweera[1*], B.M.P. Singhakumara[2] and Mark S. Ashton[3]

[1] *Faculty of Science and Technology, Uva Wellassa University, Badulla.*

[2] *Department of Forestry and Environmental Science, Faculty of Applied Science, University of Sri Jayewardenepura, Gangodawila, Nugegoda.*

[3] *School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut, USA.*

Revised: 05 January 2011 ; Accepted: 17 January 2011

Abstract: Among factors that might help to explain coexistence of tree species is environmental heterogeneity created by physical and biological processes of the forest environment. The differences in resource availability across rainforest landscapes were investigated by measuring the abiotic resources of light, soil nutrients and soil water availability in relation to forest structure.

This study was conducted in canopy gaps and adjacent understories across an elevational gradient from lowland mixed dipterocarp forest (100 m amsl) to submontane mixed dipterocarp forest (1200 m amsl) in southwest Sri Lanka. Middle elevation gap sites (300-700 m amsl) were sub divided into valley, midslope and ridge topographic positions. Eighteen canopy openings caused by tree falls were randomly selected across the elevation gradient. Plots were demarcated in gap centers and in adjacent understories and measurements were taken of forest structure (basal area, canopy height, tree canopy projection area), shade (light sensors- photosynthetic photon flux density or PPFD), and soil nutrients (pH, Al, K, N, P, Mg and Ca) across all sites. Surface soil moisture was measured at bi- weekly intervals for five years across the middle elevation site only.

Stand basal area, mean canopy height, gap size and canopy area index (a surrogate for leaf area index) all declined with increase in elevation. As expected, understory PPFD decreased with increases in canopy height, basal area and canopy area index. The size of canopy opening decreased with increase in elevation. Valley sites had significantly greater levels of mean soil water contents compared to midslope and ridge sites. K and Ca in gap and adjacent forest understories increased with increase in elevation. pH increased and Al decreased with elevation but only for forest understory conditions. Results suggest strong differentiation in soil and light resources with elevation that appear to relate to size of disturbance, stature of the forest, and underlying geology and soil weathering environment. This implies that silvicultural practices need to develop and tailor techniques and treatments that can be applied to the forest that emulate and/or account for change in elevation and topographic position.

Keywords: *Dipterocarpus*, gap dynamics, PPFD, *Shorea*, Sri Lanka.

INTRODUCTION

Many factors have been put forward to explain co-existence of tree species in tropical rain forests. Examples are distinction in life form (Whitmore, 1984), phenological differences (Grubb, 1977), differences in response to kind and scale of disturbance (Connell, 1978), variations in soil resources (Clark & Clark, 1984; Clark *et al*., 1996) and environmental heterogeneity created by physical and biological processes of the forest environment (Brandani *et al*., 1988).

The reproductive phase of a tree is the most active period of sorting for site adaptation and selection. In particular variation in seedling characteristics (growth and growth allocation to stems, roots and leaves, leaf area, and mortality) in response to shade and soil resources may have important implications for the coexistence of shade-tolerant tropical tree species (Hall *et al*., 2002; Bloor & Grubb, 2003; Singhakumara *et al*., 2003).

Accordingly, regeneration of tree species may differ by specializing in particular combinations of light, soil water and nutrients beneath canopy openings and within

* Corresponding author (sisira_ke@yahoo.co.uk)

the forest understory (Gunatilleke *et al*., 1996). The long-term persistence of seedlings under closed forest canopies provides a partial explanation for high levels of tree species in mixed dipterocarp forests of Asia (Delissio *et al*., 2002). Heterogeneity of resource availability within mixed dipterocarp forests also promotes differences in horizontal and vertical tree species distribution, which partially explains the coexistence of tree species (Davies *et al*., 1998).

A number of studies in mixed dipterocarp forests have examined individual plant responses to spatial patchiness in resources; light (Turner, 1990; Brown & Whitmore, 1992; Brown, 1993; Ashton, 1995; Ashton *et al*., 1995; Lee *et al*., 1996); soil nutrients (Burslem *et al*., 1995; Burslem, 1996; Burslem *et al*., 1996; Gunatilleke *et al*., 1996, 1997; Gamage *et al*., 2003; Singhakumara *et al*., 2004); and soil moisture (Ashton, 1992; Ashton *et al*., 2005). These studies have been conducted on potted seedlings in nutrient enriched soils and kept under different shade conditions. In other field studies on natural regeneration of tree species growing within the resource patchiness of stand scale forest environments have also been determined (Brown & Whitmore 1992; Ashton *et al.*, 1995).

Only a few studies have purposefully examined differences in resource availability across mixed dipterocarp forest landscapes by measuring the abiotic variables of light, soil nutrition and soil water availability in relation to forest structure. In this study the differences in environmental heterogeneity of canopy gaps across an elevational gradient – from lowland mixed dipterocarp forest (100 m amsl) to submontane mixed dipterocarp forest (1200 m amsl) – was measured directly. Based on the data, the environmental heterogeneity and the variation of forest structure across the topographic gradient were examined, and the following questions were addressed. Do canopy openings change in size and structure in relation to elevation? Do canopy openings change in relation to topographic position (valley, midslope and ridge at a given elevation range)? How do shade, soil moisture and nutrients change in relation to canopy openings across elevational and topographic gradients?

Site description and species selection

This study was conducted in the wet evergreen mixed dipterocarp rainforests of southwest Sri Lanka (Ashton & Gunatilleke, 1987). The flora of southwest Sri Lanka is localized based on coastal plains, hill ranges that comprise deep valleys and ridges, and mountains with an elevation gradient that occurs within a 30 – 50 km distance (Gunatilleke & Ashton, 1987).

Mixed dipterocarp rain forests are the dominant forest type of Southeast and South Asia (Whitmore, 1984) and comprise an important part of the international hardwood timber trade (Appanah & Weinland, 1993). Several distinctive rain forest communities have been described for an elevation gradient that ascends from moist coastal lowlands to the lower montane hill range of southwest Sri Lanka (Gunatilleke & Ashton, 1987). Tree species belonging to the families Dipterocarpaceae, Bombacaceae, Sapotaceae and Myrtaceae occur across this gradient (Gunatilleke & Gunatilleke, 1985; Gunatilleke & Ashton, 1987). Rainforests of the coastal plain, valleys and lower slopes of up to 300 m elevation comprise the *Dipterocarpus* community (Gunatilleke & Ashton, 1987). The *Mesua-Shorea* community occupy steep upper slopes and mid elevations from 300-900 m and also descends to low elevations on shallow soils over siliceous rocks (Gunatilleke & Ashton, 1987). At this elevation range (300-900 m) eight of the nine *Doona* species (Dipterocarpaceae) can occur (Gunatilleke & Gunatilleke, 1981, 1985) either singly or in combination with other tree species of families that dominate the lower montane rainforests at 900 – 1600 m (Gunatilleke & Ashton, 1987).

The selected study sites ranged across the elevational gradient of southwestern Sri Lanka, and represented the *Dipterocarp* community, the *Mesua-Shorea* community, and the *Shorea gardneri* association. The sites selected were within the Waga Forest Reserve (*Dipterocarp* community, $6^0$55''N, $80^0$10'' E; 125 ±50 m amsl), the western region of the Sinharaja World Heritage Site (*Mesua-Shorea* community, $6^0$45''N, $80^0$30'' E; 580 ± 250 m amsl), and the eastern region of the Sinharaja forest (*S. gardneri* community, $6^0$40''N, $80^0$40'' E; 1200 ± 200 m amsl).

The climate at all three sites is aseasonal and receives precipitation from the southwest (April - July) and northeast monsoons (October - December), with inter-monsoonal convectional rains. The mean annual rainfall fluctuates between 3000-3500 mm at Waga, between 3750 and 6000 mm in the western region of Sinharaja and the eastern end of Sinharaja. The high elevations receive about 3000 mm (Gunatilleke *et al*., 1997). The mean annual temperature at these sites is 26 ^{0}C, 25 ^{0}C and 18 ^{0}C respectively (Ashton, 1992; Gunatilleke *et al*., 1997).

The soil at the low elevation (Waga Forest Reserve) belongs to the Homagama series, derived from quartz schist rocks of the Highland Geological Province. These soils are moderately shallow to moderately deep, well drained and highly vulnerable to soil erosion due to steep slopes and high amounts of quartz sand (Moorman & Panabokke, 1961; Cooray 1967; Mapa *et al*., 1999).

The western region of the Sinharaja forest topography is undulating valley to ridge with differences generally less than 200 m. The soils belong to the Weddagala Series and are derived from the gneissic rocks again of the Highland Geological Province. These soils are deep and well drained in the valleys, skeletal on ridges typified by the presence of an organic dark coloured A horizon at the surface. Ironstone gravel can be observed in the surface soil horizons making them gravely in nature (Moorman & Panabokke, 1961; Cooray 1967; Mapa *et al*., 1999).

The soil of the eastern Sinharaja region belongs to the Malaboda Series derived from feldspar-rich rocks of the Highland Province that break down into fine textured clay-like material. These soils can be deep, well drained, and high in organic matter (Moorman & Panabokke, 1961; Cooray 1967; Mapa *et al*., 1999).

METHODS

***Site selection*:** Eighteen gap sites resulting from natural-disturbances within the forest canopy with the adjacent undisturbed understory were randomly selected from a stratified pool of such gap/understory sites that represented low elevation (Waga Forest Reserve, n=2) mid-elevation [western Sinharaja with valley (n=5), midslope (n=5) and ridge (n=4) topographic positions] and high elevation (eastern Sinharaja, n=2). Pre- existing canopy openings that had been created by recent treefalls (< 8years) were used for this experiment.

***Mapping of forest structure within sites*:** For each site a 20 x 20 m plot (aligned east-west, north-south) was demarcated across the opening of the gap and an adjacent 20 m x 20 m plot was demarcated within the closed canopied rain forest. Trees with >5 cm dbh were stem mapped using X–Y coordinates, and measures of canopy projection in N, S, E, W directions and heights to the top of the crown were measured. Canopy projection and heights were measured using a SUUNTO clinometer (SUUNTO Instruments, Finland) and 50 m distance tape. Species were identified and stem diameters were measured from which species basal areas were calculated. The size of the canopy opening and canopy-covered area were calculated and a Canopy Area Index (CAI) was calculated using the following equation:

CAI = Total canopy projection area of all trees combined over a unit area of ground area (20 x 20) m = 400 m^2/ ground area

***Shade measurements*:** Continuous measurements of photosynthetic photon flux (PPF) were taken at the gap centres and adjacent understory 20 x 20 m plots using data logger (LI-1000, Li Cor Inc, Nebraska, USA) and quantum sensors (LI-190SA). Five sensors were used for each plot – one in the plot centre and four at the corners of a 2 x 2 m grid around the plot centre. Sensors were placed 1 m above the ground. Data logger was programmed to take measurements every 30 s (µmol m^{-2} sec^{-1}) and to store 5 min means. Means were recorded and summed over the day to yield the total daily PPF (mol d^{-1} m^{-2}). Several sunny and overcast days were measured for each plot during the dry (December- March) and wet season (May- July). The minimum and maximum PPF reading for each 5 min interval were also recorded.

***Soil resource measurements*:** Soil moisture measurements were recorded only at mid-elevation sites (western Sinharaja) across the valley, midslope and ridge topographic positions (n=14). Soil moisture was monitored at bi-weekly intervals at 10 cm depth using a soil moisture meter (Delta –T HH2) over a five-year period from June 1998 - June 2003.

Soil samples were taken from all gap and understory plots at all elevations using an ordinary post-hole auger. Five sub samples at 15 cm depths were taken from the four corners and the center of each 20 x 20 m plot. Sub samples were pooled together as a composite soil sample for each plot and used for analysis of nutrients (N, P, K, Al, Ca, Mg) and pH at the Tea Research Institute, Talawakelle.

Each sample was thoroughly mixed, lumps were broken, visible parts like leaves, twigs, roots and gravel were removed, and soil spread on trays at room temperature. The drying process was accelerated using a fan. Well-dried samples were then ground by using a pestle and mortar and passed through a 2 mm sieve followed by a 100 mm sieve.

Available Ca, Mg, K and Al were extracted using $SrCl_2$ and then measured using an atomic absorption spectrometer. Available P was extracted using NH_4F/ HCl solution and measured using an auto analyser. The Kjeldahl method was used for the determination of total N in soil samples.

Ten grams of soil were sifted through a 2 mm sieve, and collected into a flat bottom test tube. This soil was mixed with 25 ml of distilled water, stirred, and kept covered over - night (more than 14 h). The pH of the suspension was read using a pH meter (standardized using buffers of pH=4 and pH=7).

RESULTS

Trends in forest structure and canopy openings

Some obvious trends in forest structure were observed with increase in elevation from 175 to 1050 m amsl (Figure 1). Stand basal area of the forest overstory decreased from 35 to 12 m^2/ha (F value =16.85, n=18), mean canopy height decreased from 23 to 13 m (F=14.47, n=18), CAI decreased from 12 to 3 (F=13.58, n=18), and the size of canopy opening decreased from 260 to 40 m^2 (F=16.16, n=18).

As expected stand basal area and CAI increased with increasing canopy height (F=21.55, N=18; F=20.99, N=18 respectively) (Figure 1). The size of canopy opening as measured by gap area increased with canopy height (F=17.78; n=18).

Trends in ground-level shade with forest and canopy opening structure

Variation of understory PPF showed fairly weak correlation with vegetation structure. However understorey PPF decreased with increase in canopy height (F value=7.69, n=16), with increase in basal area (F=5.39, n=16), and with increase in canopy area index (F=5.52, n=16) (Figure 2).

The size of canopy opening decreased with increase in elevation, while PPF increased (F=12.03, n=16). This means that PPF decreased with increase in gap area (F=5.42, n=16) and decreased with increase in canopy height (F=18.10, n=16).

Variation in soil nutrients with elevation and geology

There were no significant trends observed for measures of pH, and exchangeable Al and Mg, total N, and plant available P in the canopy opening in relation to elevation and/or geology. However, exchangeable K and Ca increased with increase in elevation (F value=18.76, n=18; F=25.38, n=18 respectively). Values doubled from 28 to 60 µg/g for K; and exponentially increased from almost nothing to about 50 µg/g for Ca with increase in elevation and/or geology (Figure 3).

For adjacent forest understories total N, plant available P, and exchangeable Mg again showed no significant trends but pH, and exchangeable K and Ca all significantly increased with elevation and/or geology (F=13.98, n=18; F=12.45, n=18; F=18.20, n=18 respectively) and exchangeable Al decreased with elevation and/or geology (F=16.18, n=18) (Figure 3).

Variation in soil moisture across topographic position and microsite

Over the course of five years (from 1999 to 2003) at the mid-elevation range (valley, mid-slope, ridge) of western Sinharaja, valley sites had significantly greater levels ($p<0.0001$) of mean soil water content (30.46%) compared to values at the mid-slope (27.37%) and ridge sites (26.19%) (Figure 4). Dry season periods (usually between December and April) provided the most dramatic percentage deviations in soil water content by topographic position (ridge>midslope>valley) as compared to the five-year mean for both microsites (understory, gap). This appeared to be more accentuated during an *El Niño* year (1998-1999) in combination with the failure of the northeast monsoons to bring rain in October and November. However, at the onset of the southwest monsoons in May all sites became equally wet.

General trends show that soil water content increased about 40-60% on all microsites with the onset of the southwest monsoons but declined gradually with the weakening of the rains. On ridges, soil water content averaged 39% during the wet season and 16% during the dry season; while valley sites averaged 40% during the wet season and 24% in the dry season. No significant differences in soil water content could be found between canopy gap microsites and adjacent forest understories.

DISCUSSION

Trends in ground-level shade with forest and canopy opening structure

In this study the mean height of canopy trees, stand basal area and CAI all exhibited a downward trend with increase in elevation; as would be expected and reported by many studies that have measured forest structure across elevation gradients (Weaver & Murphy, 1990; Singh *et al*., 1994; Kitayama & Aiba, 2002). While several researchers have examined for effects of topography on a gap regime (Worrall & Harrington, 1988; Hunter & Parker, 1993; Battles *et al*., 1995); the difference in this study is that the decline in canopy opening size (and therefore size of tree fall) occurs with increase in elevation; and this appears to be related to decrease in tree stature. This study is assumed to be the first to demonstrate the direct relationship between tree height and gap size with elevation. Results support findings that the stature of overstory trees effect canopy gap size (Pedersen & Howard, 2004).

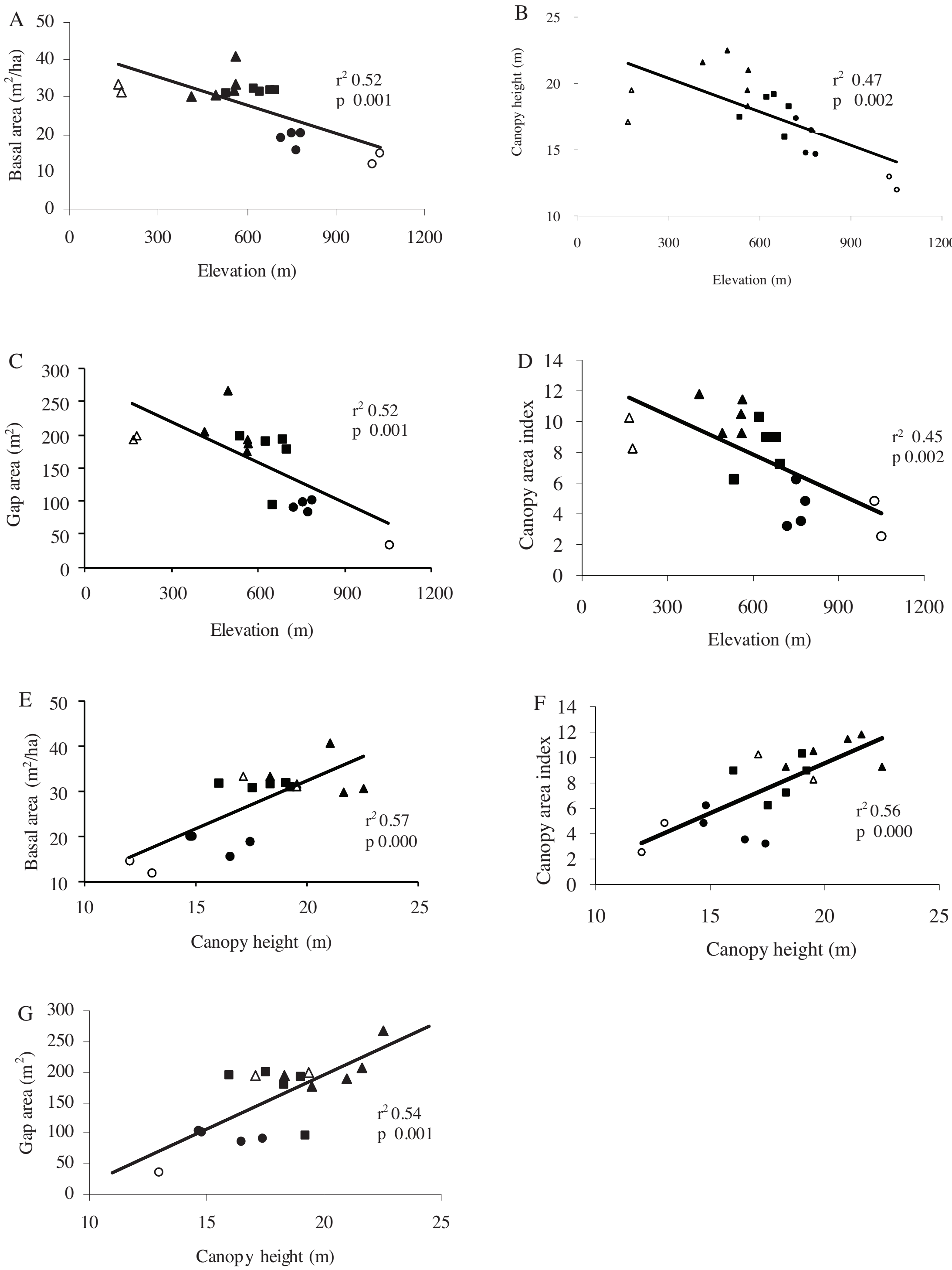

Figure 1: Regression of plot data from rainforests in southwest Sri Lanka. Gap area and canopy heights measured within 20 m x 20 m plots included all trees > 5 cm dbh surrounding the opening > 5 cm dbh. Basal area and canopy area index were calculated from adjacent 20 m x 20 m understory plots where all trees were measured. Symbols denote plots in high (open circles), low (open triangles) and mid elevation sites; valleys (closed triangles), mid slope (closed squares) and ridges (closed circles). Df = 17

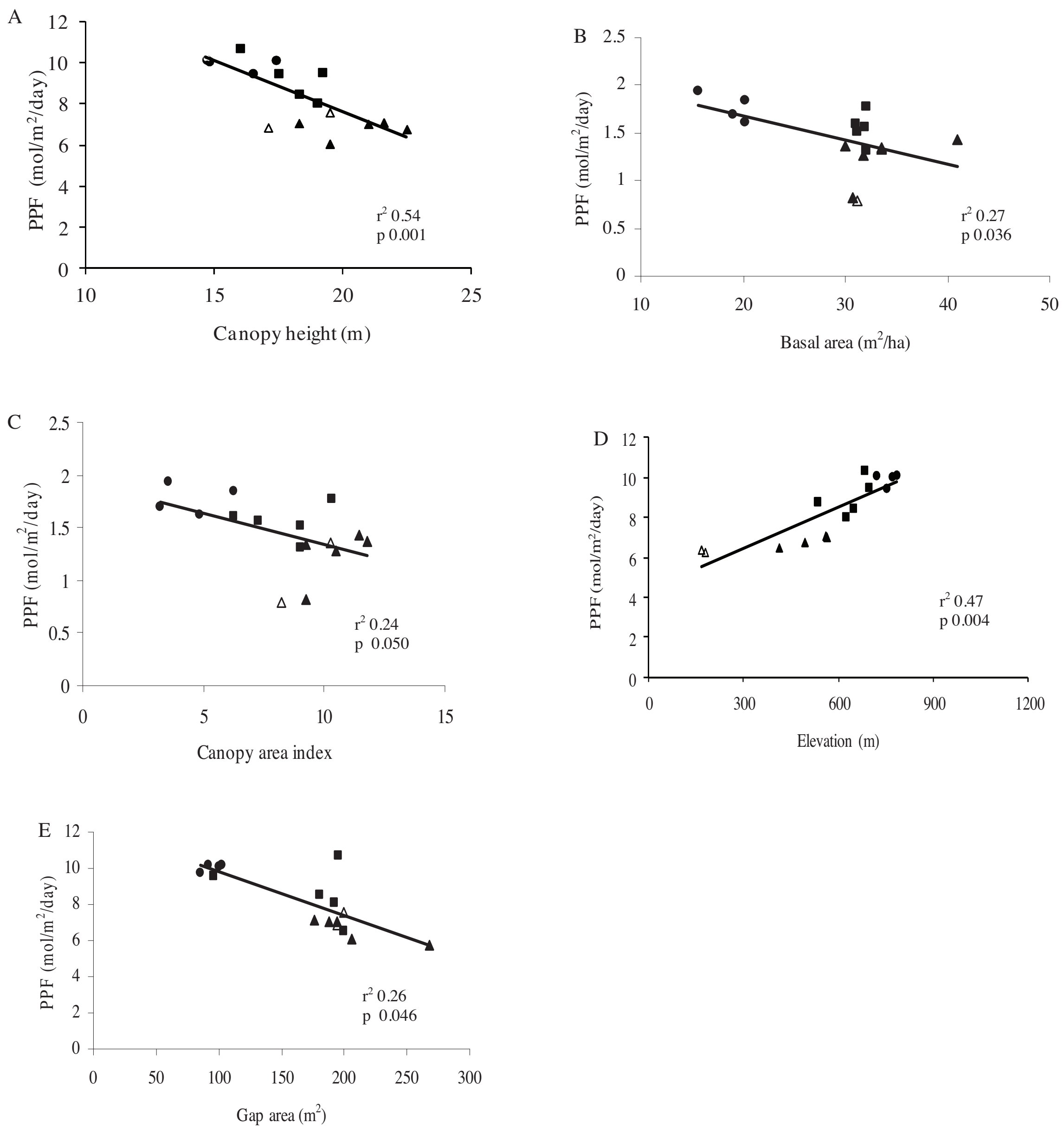

Figure 2: Regression of plot data from rainforests in southwest Sri Lanka. Canopy height and gap area measured within 20 m x 20 m plots included all trees > 5 cm dbh surrounding the opening > 5 cm dbh. Basal area and canopy area index were calculated from adjacent 20 m x 20 m understory plots where all trees were measured. A measurement of PPF was made in May-July 2001 from the centers of each 20 m x 20 m and 20 x 20 m plot. Symbols denote plots in high (open circles), low (open triangles) and mid elevation sites; valleys (closed triangles), mid slope (closed squares) and ridges (closed circles). Df = 15

The nature of the forest canopy is one of the chief determinants of the microhabitat within the forest (Jennings *et al*., 1999). The results of this study show that PPF in forest openings and adjacent understories increase with elevation, even though gap size decreases, suggesting that forest canopy stature plays a more important role in influencing shade conditions at the ground level than the size of tree fall. Previous studies

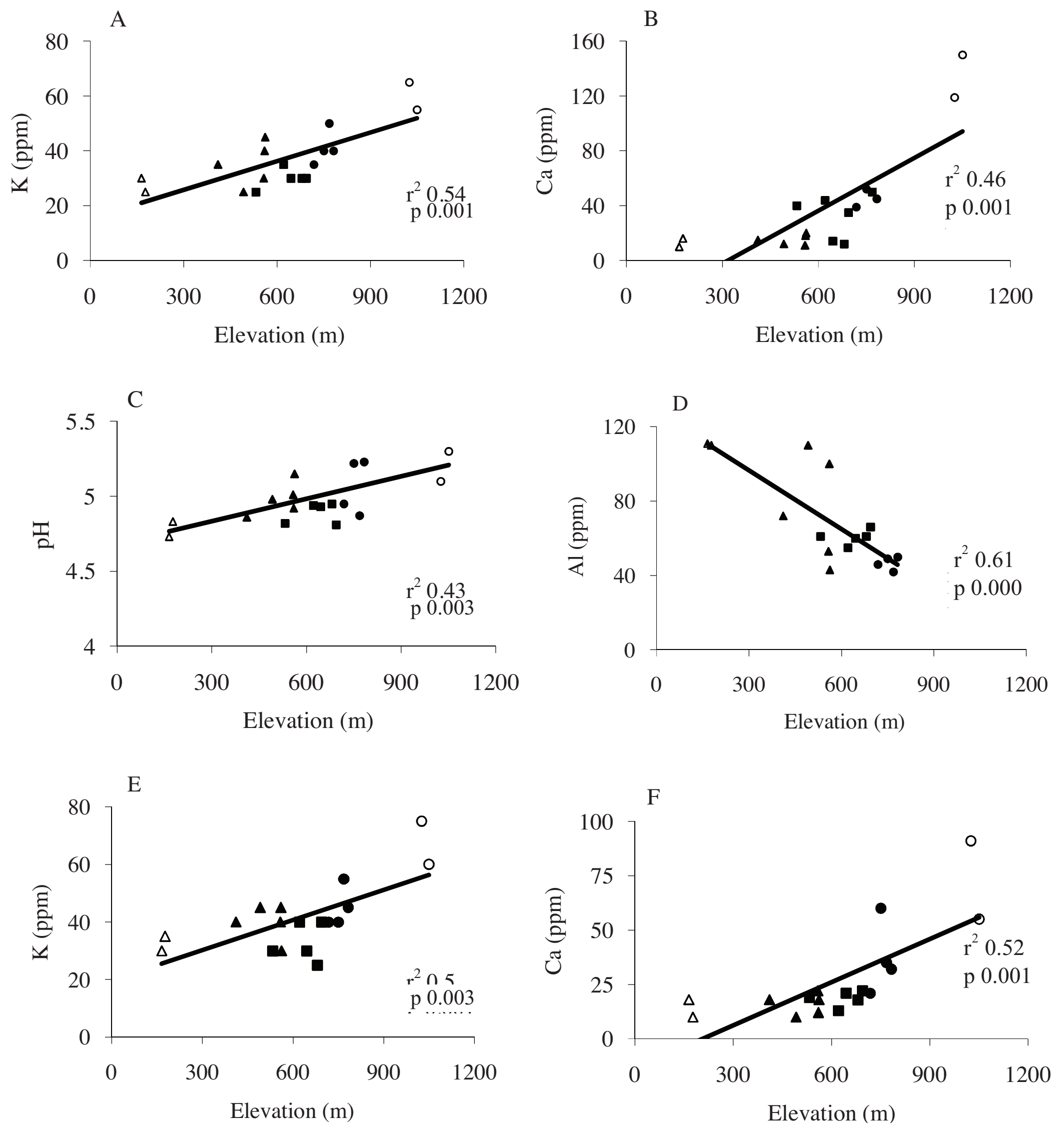

Figure 3: Plot data from rain forest in southwest Sri Lanka with regressions depicting A) gap microsite exchangeable K; B) gap microsite exchangeable Ca; C) gap microsite pH; D) gap microsite exchangeable Al; E) understory microsite exchangeable K; and F) understory microsite exchangeable Ca plotted against elevation. Soils were sampled at 10 – 15 cm depth in the centers of understory plots (20 x 20 m) and gap plots (20 x 20 m). Symbols denote plots Wigh (open circles) elevation sites; ridges of mid-elevation sites (closed darkened circles); mid-slopes of mid-elevation sites (closed squares); valleys of mid-elevation sites (closed triangles); and low elevation sites (open triangles). Df = 17

qhave found the same across more limited gradients of valley to ridge in southern New England (Fladeland *et al*., 2003); but findings contradict some of the first studies done in the same forest where larger gap sizes at valley sites had higher PPF than ridge sites (Ashton, 1992).

The findings of this study complement the work by Nicotra *et al*., (1999) who examined effects of forest developmental age and structure on understory light regime. They showed that though no difference in amounts of light in the understory could be detected between second growth and old-growth forests of Costa Rica, old-growth forests showed higher degrees of variability, due to greater variability in canopy height and stratification. In addition to decrease in forest stature the results of this study suggest that mid-slope and ridges had more lateral

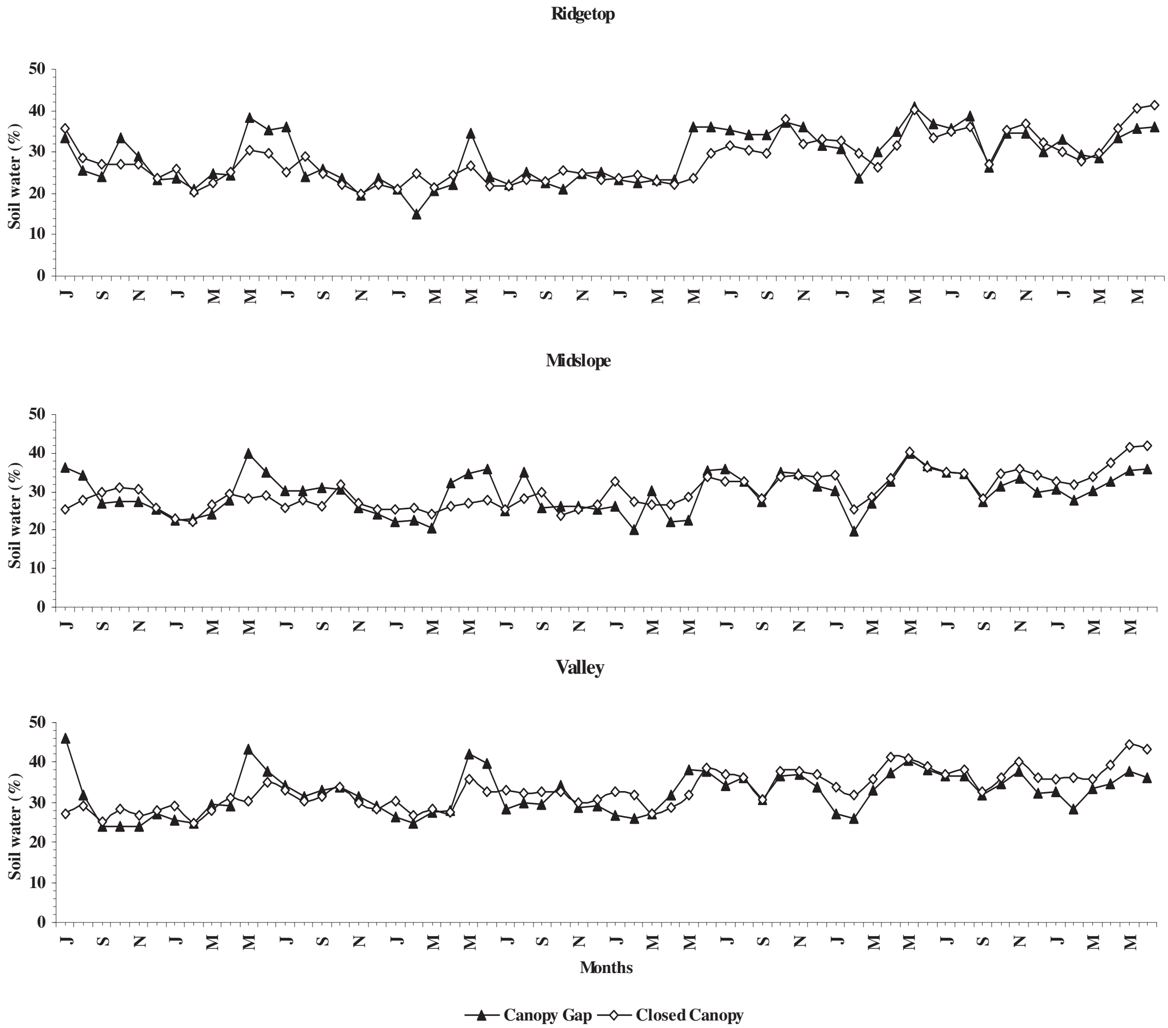

Figure 4: The percentage value of soil water by weight in upper 5 cm for the valley, midslope and ridge top, gaps and understorey sites measured at biweekly intervals during June 1998–June 2003

light penetration owing to the nature of the topography. This study showed a fairly weak relationship between the forest structure and PPF. There is a variety of factors, which may determine the variation of light availability across the topographic positions. Selected naturally opened canopy gaps were not equal in terms of gap size within a particular topographic position. Also it is not surprising since chosen gaps and understory sites were located in different aspects and different slope angles. In a forested hilly terrain, variation in slope angle, aspect and elevation control the light availability on the forest floor (Bale *et al*., 1998). Total average daily PPF of gap and understory of the ridges on sunny days was 9.7 mol m^{-2} day and 1.8 mol m^{-2} day respectively, as compared to 6.1 mol m^{-2} day and 1.1 mol m^{-2} day for valleys.

It has also been shown in a number of studies that sun flecks play an important role in the light resources of temperate and tropical forest understories (Chazdon, 1986; Chazdon & Pearcy, 1991). This study did not explicitly examine the sun fleck phenomena. However, a previous study in the same forest showed that the total daily PPF on sunny days under the forest canopy varied between sites from 0.26 to 0.92 mol m^{-2} day; of which sun flecks contributed to 24–62% (Ashton, 1992). Studies of other forests have shown that sun flecks can represent 40–80% of PPF on clear sunny days in the forest understory, though the duration may be no more than ten minutes (Chazdon & Fetcher, 1984; Chazdon, 1986; Chazdon & Pearcy, 1986; Ashton & Larson, 1996).

Variation in soil nutrients with elevation and geology

Exchangeable K and Ca in gap centers and adjacent forest understories increased with increase in elevation. This can largely be explained by a change in metamorphic geology from rocks that are silaceous at low elevation, gneissic at mid-elevation and rich in feldspars (K, Ca) at high elevation. pH increased and Al decreased with elevation but only for forest understory conditions. Other nutrients (plant exchangeable P, total N and exchangeable Mg), showed no detectable trends with elevation and geology. Trends in pH, and exchangeable Ca and K suggest that soils are less weathered, with higher levels of fertility with increase in elevation and relates well to underlying mineral content of the rock. This corresponds with the soil formations described for this regional elevation gradient by Mapa *et al*., (1999) who, using USDA (1975) soil classifications, describe erodeable and leachable oxisols at the lowest elevation, progressing to less weathered and more fertile ultisols with higher components of organic matter at higher elevations. This would also explain why in understory plots Al increased as a cation with decrease in elevation, with easier substitution for other more leachable cations and its adhesion to clay sesquioxides of oxisols.

Differences in soil nutrient status for exchangeable Ca and K between sites of the elevation gradient are similar to those observed between broad ridge and valley alluvium in lowland evergreen rain forest at Mulu, Sarawak (Proctor *et al*., 1983).

Variation in soil moisture across topographic position and microsite

In tropical rain forests most of the length and mass of tree roots is concentrated in the upper 20 cm of the soil (Jetten, 1994). We ensured that the soil moisture measured in this study was conducted within the same depth of soil ranges.

During the five-year study period of the mid-elevation part of the gradient, surface soil moisture was monitored in gaps and understory at three different topographic positions (valley to ridge). Valley sites had significantly greater levels of mean soil water content as compared to mid-slope and ridge sites during the dry season. This appeared more pronounced during an *El NiNo* year (1998-1999) and resulting failure of the northeast monsoons to bring rain in October and November as compared to other years. This supports the work of Becker *et al*., (1988) who demonstrated similar soil moisture effects across slopes in a Panamanian tropical moist forest during the dry season.

Surface soil water contents were similar for gap and understory sites in all topographic positions despite large differences in vegetation structure and incident contradict Ashton (1992) who found that there was a higher amount of soil water content in the understory than gap. Supporting this study Poorter and Yahashida-Oliver (2000) found similar soil water content in both gap and understorey in a Bolivian moist forest.

Soil moisture can be higher in gaps due to (a) increased input of rain through a higher throughfall (Jetten, 1994) and water drip from gap bordering tree crowns (Geiger, 1965) and (b) slower depletion of soil water reserves through a reduced root density (Ostertag, 1998) and (C) a reduced Leaf Area Index (Jetten, 1994). However, soil moisture content can be lower in gaps due to higher radiation loads, which lead to desiccation of the top soil through evaporation (Brouwer, 1996) and higher transpiration rates of gap plants (Meinzer *et al.*, 1995) or bordering trees, which have their roots extended into the gap. Higher (Becker *et al*., 1988; Jetten, 1994; Veenendaal *et al*., 1996), Ostertag 1998; similar (Vitousek and Denslow, 1986; Poorter & Yahashida-Oliver, 2000), and lower (Ashton, 1992b) soil moisture values have been reported for gaps compared to understorey. Differences may be due to low numbers of replicates, small gap sizes, and high spatial variation in soil texture.

These findings offer new opportunities to investigate the role of environmental heterogeneity on variation of forest structure and species coexistence across mixed dipterocarp forest landscapes.

Acknowledgment

The authors gratefully acknowledge funding by the MacArthur Foundation, J. & J. Ruinen Fund for Research in Tropical Biology (CTFS-AA programme) and Central Research Fund, University Grant Commission, Sri Lanka (CRF/ASP/6/Pr/2000/2003) and logistical support from staff and students from the University of Sri Jayewardenepura and Yale University, USA. Special thanks are due to P. Dias for data analysis and B.W. Gunasoma, Chaminda de Silva, Nimal Dharmasiri and M.A. Gunadasa for collecting the soil moisture measurements.

REFERENCES

1. Appanah S. & Weinland G. (1993). A preliminary analysis of the 50-Ha Pasoh demographics plot: 1. Dipterocarpacaeae, p. 165. Forest Research Institute, Kuala Lumpur, Malaysia.
2. Ashton M.S. (2003). The silviculture of dipterocarp forests

in the Asian wet tropics. *Forestry Chronicle* **79**:263–267.
3. Ashton M.S., Singhakumara B.M.P. & Gamage H.K. (2005). Interaction between light and drought affect performance of tropical tree species that have differing topographic affinities. *Forest Ecology and Management* **207**(1):110 –122.
4. Ashton P.M.S. (1992). Some measurements of the microclimate within a Sri Lankan tropical rainforest. *Agricultural and Forest Meteorology* **59**(3): 217–235.
5. Ashton P.M.S. (1995). Seedling growth of co-occuring *Shorea* species in the simulated light environments of a rain forest. *Forest Ecology and Management* **72**(1): 1–12.
6. Ashton P.M.S., Gunatilleke C.V.S. & Gunatilleke I.A.U.N. (1995). Seedling survival and growth of four Shorea species in a Sri Lankan rain forest. *Journal of Tropical Ecology* **11**(2): 263–279.
7. Ashton P.M.S. & Larson B.C. (1996).Germination and seedling growth of Quercus (section Erythrobalanus) across openings in a mixed-deciduous forest of southern New England, USA. *Forest Ecology and Management* **80**(1): 81– 94.
8. Ashton P.S. & Gunatilleke C.V.S. (1987). New light on the plant geography of Ceylon I. Historical plant geography. *Journal of Biogeography* **14**(4): 249 –285.
9. Battles J.J., Fahey T.J. & Harney E.M.B. (1995). Spatial patterning of a subalpine Abies– Picea forest in the northeastern United States. *Journal of Vegetation Science* **6**(6): 807–814.
10. Becker P., Rabenold P.E., Idol J.R. & Smith A.P. (1988). Water potential gradients for gaps and slope in a Panamanian tropical moist forest's dry season. *Journal of Tropical Ecology* **4**(2):173–184.
11. Bloor J.M. & Grubb P.J. (2003). Growth and mortality in high and low light: Trends among 15 shade-tolerant tropical rain forest tree species. *Journal of Ecology* **91**(1): 77–85.
12. Brandani A., Hartshorn G.S. & Orians G.H. (1988). Internal heterogeniety of gaps and species richness in Costa Rican tropical wet forest. *Journal of Tropical Ecology* **4**(2): 99 –119.
13. Brouwer L.C. (1996). Nutrient cycling in pristine and logged tropical rain forest. A study in Guyana. Tropenbos-Guyana series 1.
14. Brown N.D. (1993). The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. *Journal of Tropical Ecology* **9**(2): 153–168.
15. Brown N.D. & Whitmore T.C. (1992). Do dipterocarp seedlings really partition tropical rain forest gaps ? *Philosophical Transactions of the Royal Society London* **B 335**: 369 –378.
16. Burslem D.F.R.P. (1996). Differential responses to nutrients, shade and drought among tree seedlings of lowland tropical forest in Singapore (ed. M.D. Swaine), pp. 245–266. *The Ecology of Tropical Forest Tree Seedlings*. UNESCO, Parthenon Press, Paris, France.
17. Burslem D.F.R.P., Grubb P.J. & Turner I.M. (1995). Responses to nutrient addition among shade-tolerant tree seedlings of lowland tropical rain forest in Singapore. *Journal of Ecology* **83**(1): 113–122.
18. Burslem D.F.R.P., Grubb P.J. & Turner I.M. (1996). Responses to simulated drought and elevated nutrient supply among shade-tolerant tree seedlings of lowland tropical forest in Singapore. *Biotropica* **28**(4): 636 – 648.
19. Chazdon R.L. (1986). Light variation and carbon gain in rain forest understorey palms. *Journal of Ecology* **74**(4): 995 –1012.
20. Chazdon R.L. & Fetcher N. (1984). Photosynthetic light environments in a low land tropical rain forest in Costa Rica. *Journal of Ecology* **72**(2): 553–564.
21. Chazdon R.L. & Pearcy R.W. (1986). Photosynthetic responses to light variation in rain forest species I. Induction under constant and fluctuating light conditions. *Oecologia* **69**(4): 517–523.
22. Chazdon R.L. & Pearcy R.W. (1991). The importance of sun flecks for Forest understorey plant. *Bioscience* **41**(11): 760 –766.
23. Clark D.A. & Clark D.B. (1984). Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *American Naturalist* **124**(6): 769 –788.
24. Clark D.B., Clark D.A., Rich P.M., Weiss S. & Oberbauer S.F. (1996). Landscape-scale evaluation of understory light and canopy structure: method and application in a neotropical lowland rain forest. *Canadian Journal of Forest Research* **26**(5): 747-757.
25. Connell J.H. (1978). Diversity in tropical rainforests and coral reefs. *Science* **199**: 1302-1310.
26. Cooray PG. (1967). An introduction to the geology of Ceylon. p. 340. National Museum of Ceylon Publication, Colombo.
27. Davies S.J., Palmiotto P.A., Ashton P.S., Lee H.S. & Lafrankie J.V. (1998). Comparative ecology of 11 sympatric species of Macaranga in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology* **86**(4): 662– 673.
28. Delissio L.J., Primack R.B., Hall P. & Lee H.S. (2002). A decade of canopy-tree seedling and growth in two Bornean rain forests: persistence and recovery from supression. *Journal of Tropical Ecology* **18**(5): 645 – 658.
29. Fladeland M.M., Ashton M.S. & Xuhui Lee (2003). Landscape variation in understorey PAR for a mixed deciduous forest in New England, USA. *Agricultural and Forest Meteorology* **118**(1): 137–141.
30. Gamage H.K., Ashton P.M.S. & Singhakumara B.M.P. (2003). Leaf structure of Syzygium spp. (Myrtaceae) in relation to site affinity within a tropical rain forest. *Botanical Jouranl of the Linnean Society* **141**(3): 365–377.
31. Geiger R. (1965). The climate near the ground, p. 611. Harvard University Press, Cambridge, UK.
32. Grubb P.J. (1977). The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biological Review* **52**(1):107–145.
33. Gunatilleke C.V.S. & Ashton P.S. (1987). New light on the plant geography of Ceylon. II. The ecological biogeography of the lowland endemic tree flora. *Journal of Biogeography* **14**(4): 295–327.
34. Gunatilleke C.V.S. & Gunatilleke I.A.U.N. (1981). The

floristic composition of Sinharaja – a rain forest in Sri Lanka with special reference to endemics and dipterocarps. *Malay Forester* **44**: 386 –396.

35. Gunatilleke C.V.S. & Gunatilleke I.A.U.N. (1985). Phytosociology of Sinharaja – a contribution to rain forest conservation in Sri Lanka. *Biodiversity Conservation* **31**(1): 21– 40.
36. Gunatilleke C.V.S, Perera G.A.D., Ashton P.M.S., Ashton P.S. & Gunatilleke I.A.U.N. (1996). Seedling growth of *Shorea* section *Doona* (Dipterocarpaceae) in soils from topographically different sites of Sinharaja rain forest in Sri Lanka. *The ecology of tropical forest tree seedlings* (ed. M.D. Swaine), pp. 245–266. UNESCO, Parthenon Press, Paris, France.
37. Gunatilleke C.V.S, Gunatilleke I.A.U.N., Perera G.A.D., Burslem D.F.R.P., Ashton P.M.S. & Ashton P.S. (1997). Responses to nutrient addition among seedlings of eight closely-related species of *Shorea* in Sri Lanka. *Journal of Ecology* **85**(3): 301–311.
38. Hall J.S., Medjibe V. Berlyn G.P. & Ashton P.M.S. (2002). Seedling growth of three co-occurring Entandrophragma species (Meliaceae) under simulated light environments: implications for forest management in Central Africa. *Forest Ecology and Management* **167**(1): 1–10.
39. Hunter J.C. & Parker V.T. (1993). The disturbance regime of an old growth forest in coastal California. *Journal of Vegetation Science* **4**(1): 19–24.
40. Jennings S.B., Brown N.D. & Sheil D. (1999). Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry* **72** (1): 61–73.
41. Jetten V.G. (1994). Modeling the effect of logging on the water balance of a tropical rain forest. A study in Guyana. *Tropenbos Series 6*. The Tropenbos Foundation, Wageningen, Germany.
42. Kitayama K. & Aiba S.I. (2002). Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology* **90**(1): 37–51.
43. Lee D.W., Baskaran K. Mansor M., Mohamad H. & Yap S.K. (1996). Irradiance and spectral quality affect Asian tropical rain forest tree seedling development. *Ecology* **77**(2): 568–580.
44. Mapa Z.R.B., Somasiri S. & Nagarajah S. (1999). Soils of the wet zone of Sri Lanka: morphology, characterization and classification. *Special publication*, p. 184. Soil Science Society of Sri Lanka, P.O. Box 10, Peradeniya.
45. Meinzer F.C., Goldstein G., Jackson P., Holbrook N.M., Gutierrez V.M. & Cavalier J. (1995). Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of boundary layer and hydraulic properties. *Oecologia* **101**(4): 514 –522
46. Moorman F.R. & Panabokke C.R.(1961). Soils of Ceylon. *Government Press* **117**: 4 – 65.
47. Nicotra A.B., Chazdon R.L. & Iriarte S.V.B. (1999). Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* **80**(6): 1908–1926.
48. Ostertag R. (1998). Belowground effects of canopy gaps in a tropical wet forest. *Ecology* **79**(4): 1294 –1304.
49. Pedersen B.S. & Howard J.L. (2004). The influence of canopy gaps on overstory tree and forest growth rates in a mature mixed-age, mixed-species forest. *Forest Ecology and Management* **196**(2): 351–366.
50. Pooter L. & Hayashida-Oliver Y. (2000). Effect of seasonal drought on gap and understory seedlings in a Bolivian moist forest. *Journal of Tropical Ecology* **16**(4): 481– 498.
51. Proctor J., Anderson J.M. & Vallack H.W. (1983). Comparative study on forests, soil and litterfall at four altitudes on Gunung Mulu, Sarawak. *The Malaysian Forester* **46**: 60 –76.
52. Singhakumara B.M.P., Gamage H.K. & Ashton M.S. (2003). Comparative growth of four Syzygium species within simulated shade environments of a Sri Lankan rain forest. *Forest Ecology and Management* **174**(1): 511–520.
53. Turner I.M. (1990). The seedling survivorship and growth of three Shorea species in a Malaysian tropical rain forest. *Journal of Tropical Ecology* **6**(4): 469 – 477.
54. Veenendaal E.M., Swaine M.D., Agyeman V.K., Abebrese I.K. & Mullins C.E. (1996). Differences in plant and soil water relations in and around a forest gap in West Africa may influence seedling establishment and survival. *Journal of Ecology* **84**(1): 83–90.
55. Vitousek P.M. & Denslow J.S. (1986). Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *Journal of Ecology* **74**(4): 167–1178.
56. Weaver P.L. & Murphy P.G., (1990). Forest structure and productivity in Puerto Rico, Luquillo Mountains. *Biotropica* **22**(1): 69–82.
57. Whitmore T.C. (1984). *Tropical Rain Forests of the Far East*, 2nd edition, p. 352. Clarendon Press, Oxford. UK.
58. Worrall J.J. & Harrington T.C., (1988). Etiology of canopy gaps in spruce–fir forests at Crawford Notch, New Hampshire. *Canadian Journal of Forestry* Research **18**(2): 1463–1469.