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# LIGHT ENVIRONMENTS IN TEMPERATE NEW ZEALAND PODOCARP RAINFORESTS

**Summary:** Light environments in two lowland New Zealand podocarp rainforests are described using data from quantum sensors. Mean daily total photosynthetic photon flux density (PPFD) in the forest understorey varies from 2.6-5.2% incident PPFD in summer and 1.0-2.5% in autumn, and in gaps from 5.0-16.6% in summer and 6.3-8.3% in autumn. Pronounced differences in understorey PPFD occur between clear and overcast days. Overcast days tend to have a lower proportion of 2-minute periods with very low mean PPFD than clear days. In summer, 37.7-91.7% of PPFD occurs as sunflecks, but these only occur for 4.0-27.9% of the time. Most sunflecks are short duration (42.2-72.7% less than 4 minutes in summer) but some are very long (>32 minutes). Overall, light environments are similar to those found in other forests, both in New Zealand and elsewhere. However, canopy structure has a pronounced influence on spatial distribution of light environments within a forest, and differences in the size and frequency of canopy disturbances are a contributing factor to the floristic differences between the two forests studied.

**Keywords:** Light environment; gaps; photosynthetic photon flux density; species coexistence; Podocarpaceae; temperate rainforest; New Zealand.

## Introduction

Disturbance and resultant changes in forest interior microenvironments are considered critical for the coexistence of many tree species within forest ecosystems (Denslow, 1985). The importance of natural disturbance in creating opportunities for the growth and establishment of future canopy trees has been widely documented in forest ecosystems including those in New Zealand (e.g., Ogden, 1985). The creation of gaps in the forest canopy results in many changes in the forest understorey microenvironment, the most obvious being in the quality and quantity of light (Chazdon, 1988; Canham *et al.,* 1990).

Studies quantifying forest light environments have concentrated in particular on differences in light environments between canopy gaps and undisturbed forests (e.g., Chazdon and Fetcher, 1984; Lowman, 1986; Torquebiau, 1988; Barton, Fetcher and Redhead, 1989; Canham *et al.,* 1990). Both diffuse (filtered) and direct beam (sunfleck) radiation are important. Most of these studies have been undertaken in tropical, subtropical or northern temperate forests, with little information published on light environments in southern temperate forests.

New Zealand rainforests, although temperate, have been likened to tropical rainforests (Dawson and Sneddon, 1969). In particular, they are dominated by evergreen trees, especialIy podocarps, and are often structuralIy complex. Only a limited number of studies have examined light environments in New Zealand forests (Bieleski, 1959; Turton, 1984; Hollinger, 1987; Van Gardingen, 1987) and except for Bieleski (1959) have been restricted to forests dominated by angiosperm trees in the genus *Nothofagus*. No studies have been published on light environments in podocarp dominated forests.

In this study we describe light environments in two New Zealand podocarp dominated rainforests in order to address the following questions:

(i) Are light environments in New Zealand podocarp forests comparable to those measured in other forests, both in New Zealand and elsewhere?
(ii) What role does canopy structure have in influencing the spatial and temporal distribution of light in the study forests?

## Materials and methods

The study was undertaken in two adjacent areas of lowland rainforest on the west coast of South Island (Harihari Ecological District, Whataroa Ecological Region). Saltwater Forest (43°08' S, 170°25' E) is at about 80 m a.s.1. and Mt Hercules Scenic Reserve (43°10' S, 170°28' E) at about 345 m a.s.1. Prevailing westerly winds and close proximity to the coast result in a wet equable climate. Mean annual rainfall at Harihari, 10 km to the northeast, is 3789 mm (1965-1980 normals). Mean annual temperature at Harihari is 11. 1°C, with a January mean of 15.4 °C and a July mean of 6.0°C. Sunshine is recorded 43% of the possible time at Hokitika, 60 km to the northeast. Both areas are located on glacial outwash surfaces pre-dating (at Mt Hercules) and concurrent (at Saltwater Forest) with the final advance of the last glaciation. Soils are strongly influenced by the high rainfall and are predominantly gleyed.

Saltwater Forest is dominated by *Dacrydium cupressinum* Lamb. which forms the canopy at 30-35 m. *Prumnopitys ferruginea* (D. Don) Laubenf., *Lagarostrobos colensoi* (Hook.) Quinn, *Weinmannia racemosa* Linn. f., and *Quintinia acutifolia* Kirk are present in the subcanopy. Regeneration of this forest appears to occur in even-aged patches, often up to several hectares in area, created after disturbance of the previous canopy. The forest canopy at Mt Hercules is dominated by *Dacrydium cupressinum, Prumnopitys ferruginea, Podocarpus hallii* Kirk, and *Metrosideros umbellata* Cav; *Weinmannia racemosa* and *Quintinia acutifolia* dominate the subcanopy, and with *Elaeocarpus dentatus* (J.R. et G. Forst.) Vahl, occasionally occur in the canopy. In contrast to Saltwater Forest, regeneration appears to be by the windthrow of a single tree or small group of trees.

Three 30 x 30 m plots were subjectively established in similar landscape positions at Saltwater Forest to sample homogeneous stands of increasing age: SF1 is a recently disturbed forest with a few residual trees from the previous canopy and abundant sapling and pole sized regeneration (measured tree ages range from 45-107 years and density is 277 *Dacrydium cupressinum* trees (>10 cm dbh) $ha^{-1}$ excluding residual trees from the previous canopy). SF2 is a closed canopy forest with a dense canopy of narrow crowned trees (175-297 years, 755 trees $ha^{-1}$). SF3 is a mature forest with large spreading canopy trees (448-628 years, 155 trees $ha^{-1}$).

At Mt Hercules four sites were subjectively chosen representing undisturbed closed canopy forest (MHF); a large gap (425 $m^2$) less than 2 years old created by the windthrow of a single canopy *Prumnopitys ferruginea* tree (MHG1); a small gap (75$m^2$) less than 2 years old created by the windthrow of a single subcanopy *Quintinia acutifolia* tree (MHG2); and an old gap *(c.* 500 $m^2$) 50-60 years old created by the windthrow of a single canopy *Metrosideros umbellata* tree, but now with regenerating forest (MHG3). Variable sized plots were located at each site; 15 x 20 m (MHG2), 20 x 20 m (MHF and MHG3), 20 x 40 m (MHG1).

Photosynthetically active photon flux densities (PPFD) were measured using quantum sensors (Li190SB, Li-Cor Inc, Nebraska, U.S.A.) placed about 0.9 m above the ground. Measurement at this height was necessary to ensure that sensors were located above forest floor ferns. In Saltwater Forest six quantum sensors were located at each plot in a stratified random manner so that each plot quarter contained at least one sensor. The same layout was used in the closed canopy (MHF) and old gap (MHG3) plots at Mt Hercules, except four quantum sensors were used. Four and six quantum sensors were positioned about the fallen tree at its base, mid-trunk, crown, and to the side of the upper trunk in the small (MHG2) and large (MHG1) Mt Hercules gaps respectively. At control sites adjacent to the Saltwater Forest and Mt Hercules study sites, one sensor was located in an unobscured position in the middle of a forest clearing. Microloggers (CR21X, Campbell Scientific Inc, Utah, U.S.A.) were programmed to measure PPFD at 5-second intervals, with 2-minute mean flux densities recorded. Data for periods when the sun was less than 10° above the horizon were excluded as quantum sensors are less accurate then (Li-Cor, 1981).

Microloggers ran at all plots *within* each study site, and at its control site, simultaneously. However, it was not possible to monitor PPFD at both Mt Hercules and Saltwater Forest simultaneously. Data loggers were run at the two sites during consecutive nine day periods in both summer (January/February) and autumn (April) 1988.

Hemispherical canopy photographs were taken at each sensor location, and analysed using the method of Chan *et al*. (1986) to provide estimates of total canopy cover above each quantum sensor.

# Results

Light data are presented as mean total daily PPFD for assessing general trends, and as frequency distributions of 2-minute PPFD readings and sunfleck durations 'for looking in more detail at differences in light environment between sites. Forest light environments are contrasted between summer and autumn, and between high incident PPFD (clear sky) and low incident PPFD (overcast sky) days.

Data for six sensors (out of 76) were excluded from the analysis because of negative PPFD measurements caused by moisture on the electrical circuitry. Data for some days were also lost because of memory overwrite; a minimum of five days' data was analysed for anyone sensor and most were analysed for the full nine days in each measurement period.

Mean total daily PPFD at Saltwater Forest and Mt Hercules at control site sensors was 36.6 and 46.2 mol $m^{-2}$ respectively in summer, and 19.1 and 20.4 mol $m^{-2}$ in autumn (Table 1). Mean total daily PPFD for individual sensors dropped as low as 0.01 mol m$^{-2}$ for sensors at the Saltwater Forest and Mt Hercules closed canopy plots (SF2, MHF) in autumn. In Saltwater Forest, the recently disturbed plot (SA) received significantly more PPFD than the other two plots (SF2 and SF3) in summer and autumn, but these two were not significantly different from each other. At Mt Hercules, the large gap (MHG1) received significantly more PPFD than the other gap (MHG2, MHG3) or the closed canopy (MHF) plots in summer, but these three were not significantly different from each other. In autumn the large gap (MHGI) received significantly more PPFD than the old gap (MHG3) and closed canopy (MHF) plots, but was not significantly different from the small gap (MHG2).

The relative difference between forest interior PPFD and incident PPFD was greatest in autumn at both sites (Table 1), when forest interior PPFD ranged from 0.9-6.6% (Saltwater Forest) and 1.1-8.1 % (Mt Hercules) incident PPFD. In summer the range was 2.7-16.0% (Saltwater Forest) and 2.6-16.7% (Mt Hercules) incident PPFD. Autumn forest interior PPFD was 15.8-56.2% that received in summer. Autumn incident PPFD was 52.2% (Saltwater Forest) and 44.2% (Mt Hercules) that recorded in summer.

Considerable spatial variability in mean total daily PPFD occurred between sensors within each site reflecting differences in overhead canopy conditions. However, at Saltwater Forest at least, there was generally a good association between canopy cover (CC) and mean PPFD over all sensors (Summer, PPFD = -0.340(%CC) + 31.729; n = 15, $r^2$ = 0.614, $F$ = 20.70, $f$< 0.00l: Autumn, PPFD = -0.083(%CC) + 7.518; n = 18, $r^2$ = 0.837, $F$ = 76.91, $f$ < 0.001). The overall association was less strong at Mt Hercules (Summer, PPFD = -0.365(%CC) + 34.109; n = 17, $r^2$ = 0.551, $F$ = 18.38, $f$ < 0.001; Autumn, PPFD = -0.045(%CC) + 4.855; n = 16, $r^2$ = 0.242, $F$ = 4.40, $f$ = 0.053). Spearman rank correlation coefficients calculated between sensors within sites (Table 2) showed that variations in PPFD measurements for each sensor were more similar between sensors during overcast days than during clear days, except for MHF during autumn.

Frequency distributions of 2-minute mean PPFD readings calculated over all sensors and all days at each site for each season summarise overall between-site differences in light environments (Fig. 1). At both Saltwater Forest and Mt Hercules the majority of incident 2-minute means were over 100 $\mu$mol m$^{-2}$ s$^{-1}$ in both summer and autumn, although no means over 1000 $\mu$mol m$^{-2}$ s$^{-1}$ were recorded in autumn. In contrast, the majority of gap and forest understorey 2-minute means were below 100 $\mu$mol m$^{-2}$ s$^{-1}$, especially in autumn. At Saltwater Forest the proportion of 2-minute means in lower PPFD classes was greatest in the closed canopy plot (SF2), with all PPFD readings below 25 $\mu$mol m$^{-2}$ s$^{-1}$ in autumn, and 70% below 25 $\mu$mol m$^{-2}$ s$^{-1}$ in summer (Fig. 1a,b). A similar pattern occurred at the mature plot (SF3), but 2-minute readings at the recently disturbed plot (SFl) were not as strongly skewed to low values, with some readings above 50 $\mu$mol m$^{-2}$ s$^{-1}$, even in autumn, and some above 1000 $\mu$mol m$^{-2}$ s$^{-1}$ in summer. A similar pattern occurred at Mt Hercules with the closed canopy plot (MHF) having 2-minute PPFD readings strongly skewed to low values (Fig. 1c,d). The three gap sites showed a progressive increase in the frequency of lower PPFD readings from MHG1 - MHG3. In summer, some 2-minute PPFD readings at the large gap (MHG1), were in excess of 1000 $\mu$mol m$^{-2}$ s$^{-1}$, and in autumn a few readings over 100 $\mu$mol m$^{-2}$ s$^{-1}$ were made. All sites show the expected decrease in PPFD between summer and autumn.

Table 1: *Mean total daily PPFD (mol m$^{-2}$.d$^{-1}$) and standard deviations for all sites during summer (January/February) and autumn (April)* 1988. *Mean values not followed by the same letter are significantly different* (p < *0.05) based on a one-way analysis of variance.*

| Site | Summer PPFD | | Autumn PPFD | |
|---|---|---|---|---|
| | $\bar{x}$ | sd | $\bar{x}$ | sd |
| SF open | 36.6 | 18.5 | 19.1 | 5.4 |
| SF1 | 5.8 a | 3.1 | 1.3 a | 1.3 |
| SF2 | 1.0 b | 0.8 | 0.2 b | 0.1 |
| SF3 | 1.9 b | 1.6 | 0.3 b | 0.2 |
| | | | | |
| MHopen | 46.2 | 14.9 | 20.4 | 4.7 |
| MHF | 1.2 b | 1.0 | 0.2 b | 0.2 |
| MHGI | 7.7 a | 3.6 | 1.7 a | 0.7 |
| MHG2 | 2.3 b | 0.6 | 1.3 ab | 0.4 |
| MHG3 | 1.9 b | 0.7 | 0.5 b | 0.1 |

Table 2: *Mean Spearman rank correlations between all pairs of sensors within each site for one clear day and one overcast day in summer (January/February) and autumn (April)* 1988

| Site | Summer | | Autumn | |
|---|---|---|---|---|
| | clear | overcast | clear | overcast |
| SF1 | 0.232 | 0.697 | 0.070 | 0.949 |
| SF2 | 0.119 | 0.602 | 0.058 | 0.968 |
| SF3 | 0.123 | 0.994 | 0.081 | 0.929 |
| | | | | |
| MHF | 0.298 | 0.710 | 0.689 | 0.319 |
| MHG1 | 0.166 | 0.845 | 0.417 | 0.946 |
| MHG2 | 0.169 | 0.890 | 0.090 | 0.807 |
| MHG3 | 0.053 | 0.814 | 0.506 | 0.850 |

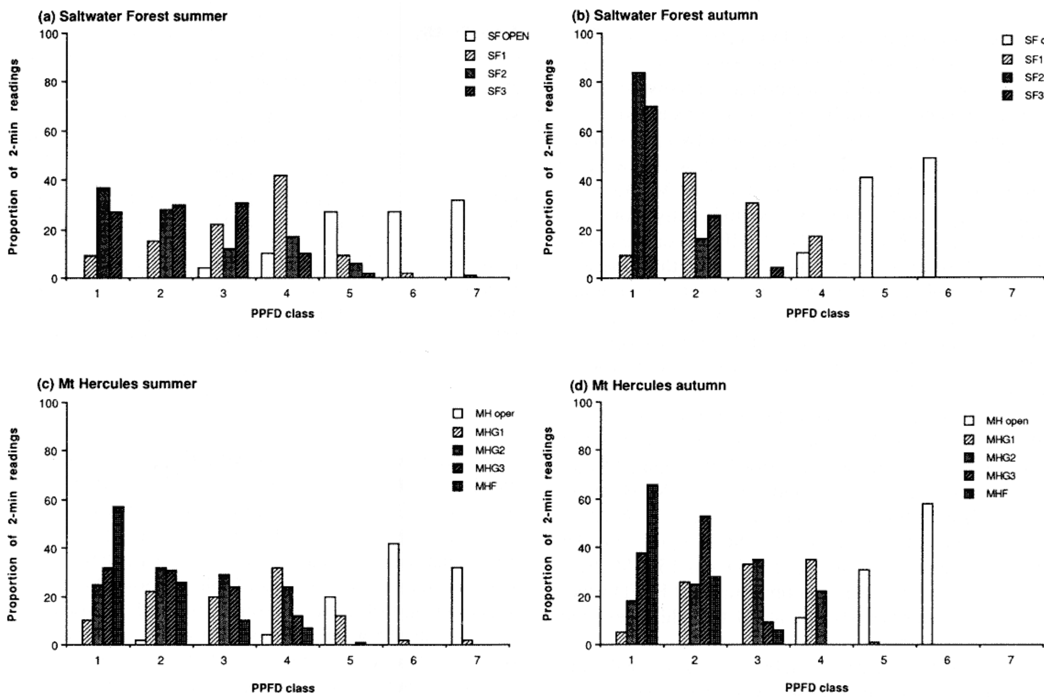


Figure 1: *Proportion of 2-minute average PPFD readings in different intensity classes for all days and all sensors at each site in summer (January/February) and autumn (April)* 1988 *at Saltwater Forest (a,b) and Mt Hercules (c,d). PPFD classes (µmol $m^{-2}$ $s^{-1}$): 1, <9.9; 2,10-24.9; 3, 25-49.9; 4, 50-99.9; 5,100-499.9;* 6, *500-999.9;* 7, *>1000.*

Frequency distributions of 2-minute mean PPFD readings calculated over all sensors for one clear day and one overcast day are presented in Table 3. Some general patterns emerge from these data:

(i) Overcast days tend to have a smaller proportion of very low 2-minute mean PPFD readings than do clear days, especially in autumn (e.g., SF2).
(ii) A greater proportion of high 2-minute mean PPFD readings occurs on clear days, particularly in autumn.
(iii) 2-minute mean PPFD readings in the two recent Mt Hercules gaps (MHGl, MHG2) show a broader PPFD distribution on overcast days than on clear days, with peak PPFD generally higher on overcast days. This difference is less obvious in autumn.

Much of the PPFD reaching the forest floor arrives as sunflecks (Table 4), although the duration of sunflecks varies between sites and seasons (Table 5). Several points are evident from the sunfleck data:

(i) The amount of PPFD recorded during sunflecks was disproportionate to the duration of the sunflecks, with sunflecks contributing much (37.7-91.7%) of the PPFD recorded in summer at all plots while occurring for only 4-27.9% of the time. A similar pattern is evident in autumn.
(ii) Sunflecks appear to be most prominent at plots with open canopies (SFl, MHGl, MHG2) and least prominent at plots with high canopy cover (SF2, MHG3). This difference was greatest in autumn, with the closed canopy Mt Hercules plot (MHF) receiving no sunflecks at all.
(iii) Although most sunflecks were short duration (42.2-72.7% less than 4 minutes in summer), some were very long (> 32 minutes). Plots with the longest duration sunflecks had the lowest canopy cover (e.g., the large Mt Hercules gap, MHG1, where 23.4% and 14.8% of sunfleck events lasted more than 16 minutes in summer and autumn respectively).

Table 3: *Proportion of 2-minute average PPFD readings in different intensity classes for one clear day and one overcast day in summer (January/February) and autumn (April)* 1988. *PPFD classes* (*µmol $m^{-2}$ $s^{-1}$*): 1. <9.9; *2, 10-24.9;* 3, 25-49.9; *4,50-99.9; 5,100-499.9;* 6, *500-999.9* ; 7,. *>1000.*

| | PPFD CLASS 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| **Saltwater Forest** | | | | | | | |
| *Summer* | | | | | | | |
| SF1 - clear | 6.8 | 17.8 | 26.0 | 21.4 | 19.5 | 4.5 | 4.0 |
| SF1 - overcast | 5.4 | 12.6 | 30.4 | 28.6 | 22.5 | 0.4 | 0.1 |
| SF2 - clear | 39.2 | 43.2 | 9.4 | 4.2 | 3.6 | 0.4 | 0.0 |
| SF2 - overcast | 37.1 | 40.2 | 16.9 | 4.7 | 1.1 | 0.0 | 0.0 |
| SF3 - clear | 30.7 | 26.3 | 19.1 | 9.0 | 11.0 | 2.3 | 1.6 |
| SF3 - overcast | 44.3 | 32.6 | 18.0 | 5.1 | 0.0 | 0.0 | 0.0 |
| *Autumn* | | | | | | | |
| SF1 - clear | 22.3 | 43.0 | 20.8 | 6.8 | 6.0 | 1.1 | 0.0 |
| SF1 - overcast | 6.4 | 23.0 | 44.1 | 26.5 | 0.0 | 0.0 | 0.0 |
| SF2 - clear | 97.7 | 1.7 | 0.4 | 0.1 | 0.1 | 0.0 | 0.0 |
| SF2 - overcast | 66.9 | 33.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| SF3 - clear | 86.3 | 8.6 | 2.7 | 1.7 | 0.7 | 0.0 | 0.0 |
| SF3 - overcast | 54.5 | 38.2 | 7.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| **Mt Hercules** | | | | | | | |
| *Summer* | | | | | | | |
| MHF - clear | 63.9 | 14.8 | 6.5 | 5.7 | 7.7 | 0.8 | 0.6 |
| MHF - overcast | 69.5 | 20.7 | 8.6 | 0.8 | 0.2 | 0.1 | 0.1 |
| MHG1 - clear | 9.6 | 38.1 | 21.9 | 7.4 | 8.9 | 3.5 | 10.6 |
| MHG1 - overcast | 4.8 | 23.4 | 9.2 | 20.9 | 30.8 | 0.7 | 0.2 |
| MHG2 - clear | 37.7 | 36.4 | 9.1 | 5.9 | 5.8 | 1.5 | 3.6 |
| MHG2 - overcast | 22.5 | 23.4 | 21.9 | 25.6 | 6.6 | 0.0 | 0.0 |
| MHG3 - clear | 32.3 | 43.2 | 9.1 | 6.0 | 7.0 | 1.6 | 0.8 |
| MHG3 - overcast | 40.0 | 24.0 | 24.8 | 10.3 | 0.9 | 0.0 | 0.0 |
| *Autumn* | | | | | | | |
| MHF - clear | 80.7 | 19.1 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| MHF - overcast | 52.9 | 46.9 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| MHG1 - clear | 7.9 | 26.6 | 24.9 | 25.0 | 14.9 | 0.3 | 0.4 |
| MHG1 - overcast | 1.6 | 24.3 | 52.7 | 21.2 | 0.2 | 0.0 | 0.0 |
| MHG2 - clear | 38.9 | 20.1 | 23.8 | 12.1 | 4.8 | 0.3 | 0.0 |
| MHG2 - overcast | 4.9 | 50.9 | 37.5 | 6.7 | 0.0 | 0.0 | 0.0 |
| MHG3 - clear | 38.4 | 40.9 | 18.8 | 1.4 | 0.5 | 0.0 | 0.0 |
| MHG3 - overcast | 22.1 | 77.3 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 |

Table 4: *Contribution of sun flecks (PPFD >* 100 *µmol $m^{-2}$ $s^{-1}$) to total daily PPFD (% total) and total sun fleck duration (% day) on one clear day at each site in each season.*

| | Total daily PPFD (%) | Duration (%day) | Total daily PPFD (%) | Duration (%day) |
|---|---|---|---|---|
| | *Summer* | | *Autumn* | |
| SF1 | 84.5 | 27.9 | 52.3 | 7.1 |
| SF2 | 37.7 | 4.0 | 5.6 | 0.1 |
| SF3 | 78.4 | 14.9 | 20.2 | 0.7 |
| MHF | 73.1 | 8.9 | 0 | 0 |
| MHG1 | 91.7 | 24.9 | 50.6 | 15.6 |
| MHG2 | 84.2 | 10.9 | 38.6 | 5.0 |
| MHG3 | 69.4 | 9.4 | 3.2 | 0.3 |

Table 5: *Proportion of sun fleck events in different duration Classes for Saltwater Forest and Mt Hercules for one clear day at each site in each season. Sun flecks are defined as 2-minute average PPFD readings above 100 µmol $m^{-2}$ $s^{-1}$. n = Number classes for Saltwater Forest and Mt Hercules for one clear day of events.*

| | n | Sunfleck duration (minutes) 0-1.9 | 2-3.9 | 4-7.9 | 8-15.9 | 16-31.9 | >32 |
|---|---|---|---|---|---|---|---|
| *Summer* | | | | | | | |
| SF1 | 175 | 26.7 | 21.3 | 24.0 | 12.0 | 8.0 | 8.0 |
| SF2 | 29 | 34.5 | 27.6 | 10.3 | 20.7 | 6.9 | 0 |
| SF3 | 64 | 37.4 | 26.6 | 15.6 | 11.0 | 6.3 | 3.1 |
| MHF | 44 | 41.1 | 13.6 | 29.5 | 13.6 | 2.2 | 0 |
| MHG1 | 64 | 26.6 | 15.6 | 21.9 | 12.5 | 7.8 | 15.6 |
| MHG2 | 35 | 37.1 | 28.6 | 5.7 | 14.3 | 11.4 | 2.9 |
| MHG3 | 55 | 38.2 | 34.5 | 18.2 | 7.3 | 0 | 1.8 |
| *Autumn* | | | | | | | |
| SF1 | 41 | 36.5 | 22.0 | 29.3 | 9.8 | 2.4 | 0 |
| SF2 | 1 | 100.0 | 0 | 0 | 0 | 0 | 0 |
| SF3 | 4 | 50.0 | 25.0 | 0 | 25.0 | 0 | 0 |
| MHF | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| MHG1 | 54 | 33.3 | 22.2 | 16.7 | 13.0 | 7.4 | 7.4 |
| MHG2 | 20 | 30.0 | 30.0 | 25.0 | 15.0 | 0 | 0 |
| MHG3 | 2 | 50.0 | 50.0 | 0 | 0 | 0 | 0 |

# Discussion

**Comparison with other forests**

Only limited data are available for detailed comparison of PPFD measurements in this study with those in other natural New Zealand forests. Hollinger (1987) recorded a mean total daily PPFD of 0.7 mol $m^{-2}$ under a *Nothofagus truncata* canopy. This value, 1.9% of incident PPFD (measured March-April), is comparable with the values found here for closed canopy forest sites (0.9-1.6% in autumn). Van Gardingen (1987), using chemical light metering, measured forest interior PPFD values of around 5% incident PPFD with little seasonal variation in a mixed *Nothofagus fusca - Nothofagus menziesii* forest. Bieleski (1959) studied light environments in a *Leptospermum* shrubland near Auckland and measured light intensities 1-40% that of incident light, with considerable spatial variability.

Understorey PPFD values measured here are similar to those estimated for four temperate North American forests using hemispherical canopy photographs (Canham *et al.* 1990). Mean transmission of diffuse plus direct-beam PPFD during the growing season ranged from 1.3-5.2% incident PPFD. New Zealand podocarp forest light environments are also similar to the very low values measured In tropical rainforests. For example, Chazdon and Fetcher (1984) measured understorey PPFD of 1-2% incident PPFD in both the wet and dry season in Costa Rican forests, and

Canham *et al*. (1990) estimated a mean ttansmission of 0.5% for another Costa Rican rainforest using hemispherical canopy photographs. Torquebiau (1988) measured understorey PPFD of 0.6-0.8% incident PPFD at ground level in two Indonesian rainforests. In Australian montane tropical rainforests, Turton (1990) measured daily total PPFD of 0.41 % and 1.23% of incident in heavily and lightly shaded understoreys.

PPFD in the large and small Mt Hercules gaps MHG1, MHG2) and at the recently disturbed Saltwater Forest plot (SF1) range from 4.9-15.8% of incident PPFD in summer and from 6.3-8.3% of incident in autumn. These are lower than those recorded by Van Gardingen (1987) for a 65 $m^2$ gap in mixed *Nothofagus fusca - Nothofagus menziesii* forest, where gap PPFD ranged from about 15% of incident PPFD in winter to 25% incident PPFD in summer. However, the results obtained here are comparable to those recorded in small forest gaps in tropical rainforests; 6.0% in a 150 $m^2$ gap (Turton, 1990), and 6.2-11.1 % in three gaps 71-96 $m^2$ (Barton, Fetcher and Redhead, 1989). The reasons for the much higher values obtained by Van Gardingen (1987) are unclear, although the use of chemical light meters rather than quantum sensors may in part explain this.

These data suggest that evergreen rainforests experience similar overall light environments despite pronounced differences in structure and floristics. Certainly the success of species such as *Sambucus nigra* (Roxburgh, 1991) and *Tradescantia fluminensis* (Esler, 1988) in invading closed canopy indigenous New Zealand forests suggests that New Zealand forest interior light environments are not substantially different from light environments in the natural forests for these species.

**Effects of canopy structure on light distribution**

Breaks in forest canopies (gaps) allow direct beam radiation to reach the forest floor, substantially increasing light levels. Direct beam radiation can also reach the forest floor through closed canopies, but the spatial and temporal duration of these events is usually very brief (Chazdon, 1988). Gap creation is therefore a key factor influencing forest interior light environments. As tree species within a forest often differ in their specific light requirements for regeneration, the nature of disturbance to the canopy will have a significant influence on the spatial and temporal heterogeneity of forest interior light environments, and hence on future canopy composition.

The pronounced differences between gap and understorey light environments observed in forests elsewhere (e.g., Chazdon and Fetcher, 1984; Canham *et al.,* 1990) are also evident in the two forests studied here. Light environments in the forest understorey are not only characterised by less total light (Table 1), but also by differences in the way the light is received. Sunflecks, for example, make a smaller contribution to total PPFD and occur for shorter durations in the forest understorey than in canopy gaps (Tables 4 and 5). This is particularly evident in autumn when sunflecks are virtually absent in the forest understorey, presumably because gaps in the overhead canopy foliage are too small for direct beam radiation to reach the forest floor at low solar angles. In contrast, the large gap at Mt Hercules (MHG1) and the open canopied site at Saltwater Forest (SF1) experience light environments more similar to those in the open. At these sites sunflecks play a dominant role in the light environment (Table 4), especially in summer when both sites receive prolonged periods of direct beam radiation (Table 5).

Sunflecks are considered to have profound effects on ecological processes in forest understoreys where they can contribute more than 50% of total daily PPFD (Chazdon, 1988; Pearcy, 1988). In the south Westland podocarp forests, sunflecks contributed 37.7-91.7% of total daily PPFD in summer and 0-52.3% in autumn (Table 4). These levels are similar to those recorded in temperate and tropical forests outside New Zealand (Chazdon, 1988; Canham *et al.,* 1990), and are comparable to that recorded by Hollinger (1987) for a *Nothofagus truncata* forest (20% contribution in March/ April). Sunflecks are thought to play a key role in the growth of understorey plants, with photosynthesis during sunflecks accounting for 30-60% of daily carbon gain (Chazdon, 1988). The importance of sunflecks for seedling growth was clearly shown by Pearcy (1983) who found a strong positive correlation between seedling relative growth rates and potential daily sunfleck duration in an Hawaiian rainforest. Gaps in particular enhance the intensity and duration of sunflecks in rainforests (e.g., Tables 4 and 5).

The influence of canopy structure is also dependent on the nature of incident radiation. The pronounced differences observed here between clear and overcast days (Table 3) are similar to those found elsewhere. For example, Lowman (1986), working in tropical and temperate evergreen rainforests in Australia, found marked reductions in both sunfleck (direct beam radiation) and diffuse radiation between clear and overcast days. Differences in diffuse and direct radiation are likely to contribute to observed differences in understorey and gap light environments during clear and overcast days (Chazdon and Fetcher, 1984). In particular, overcast days tend to be characterised by a smaller proportion of very low 2-minute mean PPFD readings than do clear days (Table 3). This is particularly evident in autumn at both Saltwater Forest and Mt Hercules, and presumably occurs because of the low solar angle during clear days, with diffuse flux making up the majority of total PPFD recorded. In summer, the sun is higher in the sky and direct beam radiation is more important, and the difference between clear and overcast days is not as evident.

Light environments are very low in the closed canopy podocarp forests studied here, and elevated light environments associated with gaps are therefore likely to be critical for the growth of seedlings and saplings of canopy trees. In Saltwater Forest, McDonald (1989) recorded podocarp seedling and sapling (>0.25 m tall and < 5 cm diameter at 1.3 m) densities of 30211 $ha^{-1}$ in recently disturbed plot (SF1), compared to densities of 711 and 419 $ha^{-1}$ in the closed canopy (SF2) and mature (SF3) plots respectively. The two recent gaps on Mt Hercules (MHG1 and MHG2) were too young for any appreciable seedling recruitment to have occurred <2 years old), but podocarp seedlings and saplings (especially *Dacrydium cupressinum)* are abundant in the older Mt Hercules gap (MHG3), growing under a canopy of young even-aged *Weinmannia racemosa* and *Quintinia acutifolia* (D.A. Norton and J. Ogden, unpublished data). For example, the frequency of *Dacrydium cupressinum* saplings (> 1 m tall and < 5 cm diameter at 1.3 m) was 667 $ha^{-1}$ in the older gap (MHG3) compared to 188 $ha^{-1}$ in 2410 x 10 m quadrats located through adjacent forest.

**Conclusion**

Light environments were generally similar in the two forests studied despite differences in their disturbance regimes, although no comparable information was collected on the spatial distribution of light environments. The two forests are, however, very different floristically, with Saltwater Forest being dominated by a virtually monospecific canopy of *Dacrydium cupressinum* while Mt Hercules has a mixed canopy including both podocarp and angiosperm trees. In both forests, disturbance to the forest canopy results in elevated forest interior light environments which provide opportunities for establishment and growth of new canopy trees. Differences in disturbance frequency and the size of disturbed areas occur between Saltwater Forest and Mt Hercules (Six Dijkstra, Mead and James, 1985; James, 1987; D.A. Norton and J. Ogden, unpublished data) and are likely to result in differences in the spatial distribution of light within these two forests. These differences may be a contributing factor to the floristic differences between Saltwater Forest and Mt Hercules. The smaller. more frequent, gaps that occur on Mt Hercules are likely to result in a greater spatial diversity in light environments and provide a wider range of regeneration sites, thus favouring the coexistence of several species in the canopy. In contrast, the generally larger, less frequent gaps in Saltwater Forest result in less spatial diversity of light environments and favour the canopy dominance of one species, *Dacrydium cupressinum*. It can be concluded that the spatial and temporal heterogeneity in light is both a product of and a contributing factor in spatial species diversity in forest ecosystems.

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## References

Barton, A.M.; Fetcher, N.; Redhead, S. 1989. The relationship between treefall gap size and light flux in a neotropical rain forest in Costa Rica. *Journal of Tropical Ecology 5*: 437-439.

Bieleski, R.L. 1959. Factors affecting growth and distribution ofkauri *(Agathis australis* Salisb.). I. Effect of light on the establishment of kauri and of *Phyllocladus trichomanoides* D. Don. *Australian Journal of Botany 7*: 252-267.

Canham, C.D.; Denslow, J.S.; Platt, W.J.; Runkle, J.R.; Spies, T.A.; White, P.S. 1990. Light regimes beneath closed canopies and tree-falI gaps in temperate and tropical forests. *Canadian Journal of Forest Research 20:* 620-631.

Chan, S.S.; McCreight, R.W.; Walstad, J.D.; Spies, T.A. 1986. Evaluating forest vegetation cover with computerised analysis of fisheye photographs. *Forest Science 32*: 1085-1091.

Chazdon, R.L. 1988. Sunflecks and their importance to forest understorey plants. *Advances in Ecological Research 18*: 1-63.

Chazdon, R.L.; Fetcher, N. 1984. Photosynthetic light environments in a tropical rain forest in Costa Rica. *Journal of Ecology 72*: 553-564.

Dawson, J.W.; Sneddon, B.V. 1969. The New Zealand lowland rain forest. A comparison with tropical rain forest. *Pacific Science 23*: 131-147.

Denslow, J.S. 1985. Disturbance-mediated coexistence of species. *In:* Pickett, S.T.A.; White, P.S. (Editors), *The ecology of natural disturbance and patch dynamics,* pp. 307-323. Academic Press, San Diego, U.S.A. 472 pp.

Esler, A.E. 1988. The naturalisation of plants in urban Auckland, New Zealand. 6. Alien plants as weeds. *New Zealand Journal of Botany 26*: 585-618.

Hollinger, D.Y. 1987. Photosynthesis and stomatal conductance patterns of two fern species from different forest understoreys. *Journal of Ecology 75*: 925-935.

James, I.L. 1987. *Silvicultural management of the rimu forests of south Westland*. Forest Research Institute, Bulletin No. 121, New Zealand Forest Service, Wellington, N.Z. 32 pp.

Li-Cor 1981. *Li-190SB quantum sensor instruction manual*. Li-Cor Inc., Lincoln, Nebraska, U.S.A. 8 pp.

Lowman, M.D. 1986. Light interception and its relation to structural differences in three Australian rainforest canopies. *Australian Journal of Ecology 11*: 163-170.

McDonald, D. 1989 (unpublished). *Seedling/sapling light environment in different regeneration stages of lowland podocarp forest. south Westland. New Zealand*. M.For.Sc. thesis, University of Canterbury, Christchurch, N.Z. 168 pp.

Ogden, J. 1985. An introduction to plant demography with special reference to New Zealand trees. *New Zealand Journal of Botany 23*: 751-772.

Pearcy, R.W. 1983. The light environment and growth of C3 and C4 species in the understorey of a Hawaiian forest. *Oecologia 58*: 26-32.

Pearcy, R. W. 1988. Photosynthetic utilisation of lightflecks by understorey plants. *Australian Journal of Plant Physiology 15*: 223-238.

Roxburgh, J. 1991 (unpublished). *The relationship between the light and regeneration ecology of Himalayan honeysuckle* (Leycesteria formosa) *and elder* (Sambucus nigra) *and their distribution*. M.Sc. thesis, University of Canterbury, Christchurch, N.Z 119 pp.

Six Dijkstra, H.G.; Mead, D.J.; James, I.L. 1985. Forest architecture in terrace rimu forest, south Westland, and its implications for management. *New Zealand Journal of Forestry Science 15*: 3-22.

Torquebiau, E.F. 1988. Photosynthetically active radiation environment, patch dynamics and architecture in a tropical rainforest in Sumatra. *Australian Journal of Plant Physiology 15*: 327-42.

Turton, S.M. 1984. The relative distribution of photosynthetically active radiation within four tree canopies, Craigieburn Range, New Zealand. *Australian Forestry Research 15:* 383-394.

Turton, S.M. 1990. Light environments within montane tropical rainforest, Mt Bellenden Ker, north Queensland. *Australian Journal of Ecology 15*: 35-42.

Van Gardingen, P.R. 1987 (unpublished). *Environmental and stomatal physiology of* Nothofagus *seedlings*. Ph.D. thesis, University of Canterbury, Christchurch, N.Z. 96 pp.