

Solar radiation transmission in and around canopy gaps in an uneven-aged *Nothofagus betuloides* forest

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Abstract The transmission of direct, diffuse and global solar radiation in and around canopy gaps occurring in an uneven-aged, evergreen *Nothofagus betuloides* forest during the growing season (October 2006–March 2007) was estimated by means of hemispherical photographs. The transmission of solar radiation into the forest was affected not only by a high level of horizontal and vertical heterogeneity of the forest canopy, but also by low angles of the sun's path. The below-canopy direct solar radiation appeared to be variable in space and time. On average, the highest amount of transmitted direct solar radiation was estimated below the undisturbed canopy at the southeast of the gap centre. The transmitted diffuse and global solar radiation above the forest floor exhibited lower variability and, on average, both were higher at the centre of the canopy gaps. Canopy structure and stand parameters were also measured to explain the variation in the below-canopy solar radiation in the forest. The model that best fit the transmitted below-canopy direct solar radiation was a growth model, using plant area index with an ellipsoidal angle distribution as the independent variable ($R^2=0.263$). Both diffuse and global solar radiation were very

sensitive to canopy openness, and for both cases a quadratic model provided the best fit for these data ($R^2=0.963$ and 0.833 , respectively). As much as 75% and 73% of the variation in the diffuse and global solar radiation, respectively, were explained by a combination of stand parameters, namely basal area, crown projection, crown volume, stem volume, and average equivalent crown radius.

Keywords *Nothofagus betuloides* · Uneven-aged forest · Hemispherical photographs · Below-canopy solar radiation transmission · Tierra del Fuego

Definitions

BA	Basal area ($\text{m}^2 \text{ha}^{-1}$)
CP	Crown area projection (m^2)
CP	Average crown area projection per plot (m^2)
C_L	Crown length (m)
CO	Canopy openness (%)
C_R	Average equivalent crown radius per plot (m)
C_{SA}	Crown surface area (m^2)
C_V	Crown volume (m^3)
D	Stocking density (trees ha^{-1})
DBH	Diameter at breast height (cm)
DIF	Transmitted diffuse solar radiation during the growing season (%)
DIR	Transmitted direct solar radiation during the growing season (%)
GC	Gap centre
GF	Gap fraction (%)
GLO	Transmitted global solar radiation during the growing season (%)
L_e-60	Plant area index calculated using the mean tilt angle of the foliage integrated over zenith angles from $0-60^\circ$ ($\text{m}^2 \text{m}^{-2}$)

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L_c -75	As above, but integrated over zenith angles from 0–75° ($m^2 m^{-2}$)
L_c -E	Plant area index employing an ellipsoidal angle distribution ($m^2 m^{-2}$)
NGE	Northwestern gap edge
NUC	Northwestern undisturbed canopy
R	Equivalent crown radius (m)
SGE	Southeastern gap edge
SUC	Southeastern undisturbed canopy
S_v	Stem volume ($m^3 ha^{-1}$)

Introduction

Forest ecosystems are frequently subjected to small-scale canopy disturbance (Spies et al. 1990; Oliver and Larson 1996). The severity of a canopy disturbance influences canopy closure, stand structure, regeneration dynamics, species composition, and species diversity (Connell 1978; Canham et al. 1994; Oliver and Larson 1996). Numerous studies have shown that resources such as light, water, and soil nutrients required for plant growth are modified by canopy gaps (e.g. Canham and Marks 1985; de Freitas and Enright 1995). It is possible to find a gradient of site conditions from the centre of a disturbed forest canopy to the undisturbed surrounding forest (Ricklefs 1977; Denslow 1980).

Above and within forests, chemical, physical, and physiological processes are driven by the components of solar radiation (Anderson 1964a; Barnes et al. 1998; Holst and Mayer 2005). Knowledge of the effects of solar radiation on forest understorey is important to gain deeper insight into forest dynamics. Solar radiation affects plant regeneration patterns such as germination, establishment, growth, and survival (Grant 1997). Latitude, time of day, atmospheric clarity, and altitude can all affect the total amount of solar radiation reaching a forest canopy (Hutchison and Matt 1977; Barnes et al. 1998). The forest canopy itself is an exceedingly complex, three-dimensional structure that changes with time (Anderson 1964b). Its irregular surface modifies reflection, transmission, and absorption of solar radiation (Grant 1997; Geiger et al. 2003). Only a small percentage of the incident radiation reaches the forest floor (Barnes et al. 1998). Even in tropical forests with no pronounced seasonal variation in stand structure, the below-canopy changes in light throughout the year will differ from those occurring in an open area (Anderson 1964b; Rich et al. 1993). Therefore, measuring direct solar radiation beneath a forest canopy is complicated due to the highly irregular distribution of radiation in space and time (Reifsnnyder et al. 1971/1972; Geiger et al. 2003) and the highly variable distribution of canopy gaps

(Hutchison and Matt 1977; Barnes et al. 1998; Geiger et al. 2003). In contrast, the penetration of diffuse solar radiation is less variable, as it depends on the level of sky brightness, and the number, size and spatial distribution of canopy openings, the canopy geometry, and the spatial distribution and optical characteristics of the forest biomass. Thus, within a forest, diffuse solar radiation is more uniform in space and time than either direct or global solar radiation (Hutchison and Matt 1977; Geiger et al. 2003).

Seasonal changes in below-canopy solar radiation have been reported for deciduous (Hutchison and Matt 1977; Baldocchi et al. 1984; Caldentey et al. 1999/2000; Mayer et al. 2002; Holst and Mayer 2005; Holst et al. 2005) and coniferous (Weiss 2000; Hardy et al. 2004) forests. The seasonal changes in the below-canopy solar radiation regime in coniferous forest are driven by solar angle and cloudiness (Weiss 2000), although seasonal differences have been observed because of the timing of needle flush and needle cast (Chen 1996; Lieffers et al. 1999). In addition, canopy phenology and leaf pigmentation influence the solar radiation regime below the canopy of deciduous forests (Hutchison and Matt 1977; Holst and Mayer 2005).

Several attempts have been made to estimate the below-canopy solar radiation from stand parameters (Comeau and Heineman 2003; Geiger et al. 2003). Individually or in combination, basal area, stocking density, tree height, crown dimensions, canopy cover, and leaf area index have been correlated with the availability of solar radiation in coniferous forests (Sampson and Smith 1993; Vales and Bunnell 1988; Hale 2003; Sonohat et al. 2004) and in broadleaved forests (Comeau 2001; Pinno et al. 2001; Comeau and Heineman 2003; Piboule et al. 2005; Comeau et al. 2006). For example, it was shown that the availability of solar radiation in the understorey of a homogeneous, even-aged forest may differ drastically from that of a heterogeneous, uneven-aged forest with the same leaf area (van Pelt and Franklin 2000; Piboule et al. 2005). The canopy of a heterogeneous, uneven-aged forest is characterised by a multi-layered vertical distribution of biomass and an irregular horizontal distribution of canopy openings of different sizes (Rebertus and Veblen 1993; Franklin and van Pelt 2004).

As a result of the apparent complexity of below-canopy radiation regimes, there are still gaps in our knowledge of (1) the effects of canopy gaps on the below-canopy solar radiation regime, and (2) whether the spatial variation of the solar radiation regime is affected by the canopy structure and stand parameters in an uneven-aged *Nothofagus betuloides* forest. Since the amount of solar radiation transmitted into the forest has a great effect on forest dynamics (Grant 1997), efforts have been made to characterize below-canopy solar radiation availability on the basis of stand attributes in order to assess the competitive

environment in which the understorey is growing (Comeau and Heineman 2003). Furthermore, a deeper understanding of stand attributes during different stages of stand development would allow the use of the below-canopy solar radiation regime as a predictive forest management tool (Lieffers et al. 1999).

The purpose of this study was (1) to analyse the effects of the forest canopy and canopy gaps on transmission of solar radiation to the floor of a *N. betuloides* forest, and (2) to evaluate whether canopy structure and stand parameters explain the variation in below-canopy solar radiation in this forest. The evergreen *N. betuloides* is one of the endemic forest species characteristic of the Chilean and Argentinean sub-Antarctic forest. It grows from 40°31'S to 55°31'S (Rodríguez and Quezada 2003), and from sea level near the southern limit of its distribution to altitudes of 1,200 m a.s.l. near the northern limit of its distribution (Veblen et al. 1996). *N. betuloides* exhibits a high ecological amplitude. It can germinate in very shady environments (Veblen et al. 1996; Promis 2009). There are indications that, for all South American *Nothofagus* species, seedling establishment occurs best under moderately high light levels. However, *N. betuloides* appears to be more shade-tolerant than other *Nothofagus* species (Veblen et al. 1996; Promis 2009).

Materials and methods

Study area

The study area is located in an old-growth, uneven-aged evergreen *N. betuloides* forest [20 ha, with a stocking density (D) of 1,362 trees ha⁻¹, and a basal area (BA) of 105 m² ha⁻¹] with no direct evidence of human impact. The

forest appears to be closely related to the evergreen *N. betuloides* forest described by Veblen et al. (1983). A thick layer of partially decomposed organic matter covers the forest soil. The species diversity of the shrub layer is poor, but there is a very pronounced layer of abundant epiphytic ferns, mosses and liverworts, particularly on the slowly decaying tree trunks that lie on the forest floor. The forest is located at the 'Estancia Olguita,' on the southeastern side of the Río Cónдор (53°59'S, 69°58'W), which flows along the southwestern Chilean side of Tierra del Fuego (Fig. 1).

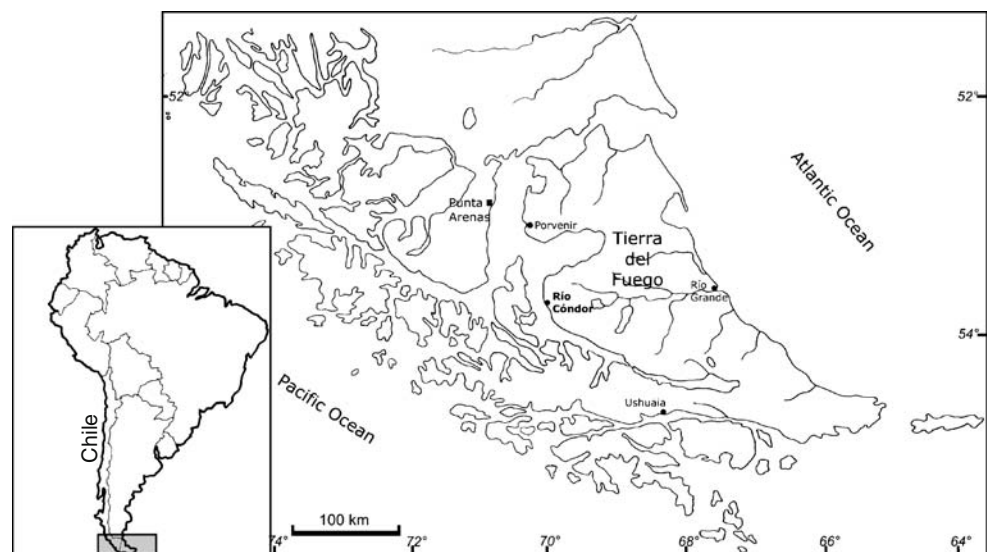
The climate of the study area is confined to the northern antiboreal sub-zone of Tierra del Fuego, with a mean air temperature between 9.0 and 9.5°C in the warmest month of the year, and air temperature remaining above 0.0°C in the coldest month. The mean annual rainfall is around 500–600 mm, but can reach up to 900 mm. The wind direction is commonly west to southwest and more persistent and stronger in spring and summer, with average wind speeds of 14–22 km h⁻¹. However, the monthly maximum wind speed may exceed 100 km h⁻¹ (Tuhkanen 1992).

Below-canopy solar radiation assessment

Hemispherical photographs were used to indirectly estimate the amount of transmitted solar radiation in the forest. Other than for deeply shaded environments, hemispherical photography is a suitable technique with which to analyse canopy structure and below-canopy solar radiation environments (Canham et al. 1990; Rich et al. 1993; Wagner 1994; Roxburgh and Kelly 1995; Wagner 1996; Wright et al. 1998; Clearwater et al. 1999; Machado and Reich 1999; Engelbrecht and Herz 2001; Bartemucci et al. 2006; Collet and Chenost 2006).

Thirteen canopy gaps (≥ 20 m²) were selected from a study of canopy gaps (average size of 51 m²) and disturbance

Fig. 1 Map of South America and Tierra del Fuego showing the location of the forest studied on the Río Cónдор



dynamics in the *N. betuloides* forest (Promis 2009). The size of the selected canopy gaps ranged from 21 to 92 m², with an average size of 47±6.3 m² (average ± SE). A ‘gap’ was defined as the horizontal projection of a canopy opening to the forest floor (Runkle 1982), and was considered closed if the vegetation growing below the opening in the canopy was more than 2 m in height (Promis 2009).

Photographs were taken during the summer of 2006 along southeasterly to northwesterly transects of five location points running from areas beneath the undisturbed canopy to the centre of the canopy gaps (Fig. 2). One hemispherical photograph was taken at the centre (GC), one at the southeast edge (SGE), and one at the northwest edge (NGE) of each selected gap. In addition, photographs were taken below the undisturbed canopy to the southeast (SUC) and to the northwest (NUC) of GC at a distance of half the height of the highest tree in the vicinity of the gap (26±0.9 m) (measured from the tree base).

All hemispherical photographs were taken with a Nikon Coolpix 990 digital camera (Nikon, Tokyo, Japan) fitted with a Nikon FC-E8 fisheye converter. The camera was mounted on a tripod at a height of approximately 1.3 m above the ground. The camera and lens were levelled with the aid of a spirit level and oriented to magnetic north. The digital images were processed according to Brunner (2002). This included the manual setting of a threshold value to separate canopy and sky elements into a binary black and white image. All images were analysed using HemiView Version 2.1 (Delta-T Devices, Cambridge, UK). The lens distortion was corrected using the Coolpix 900 option (Hale and Edwards 2002). The hemispherical photographs were divid-

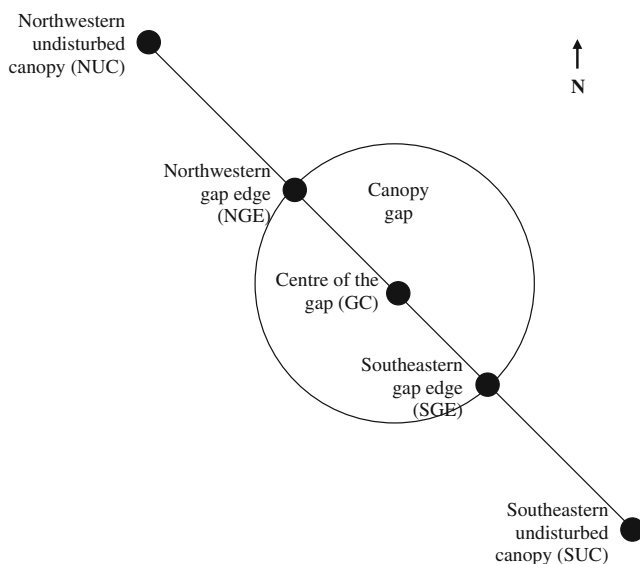


Fig. 2 Layout of the transects in the canopy gaps from which hemispherical photographs were taken. The circular shape of the canopy gap does not reflect reality, as all gaps analysed had different shapes

ed into 16 azimuth and 9 zenith regions (144 sky regions in total) in order to determine whether the below-canopy diffuse solar radiation originates from different sky regions in areas beneath the disturbed and undisturbed canopy.

Cosine-corrected transmitted direct (DIR), diffuse (DIF), and global (GLO) solar radiation below the forest canopy were estimated over the course of a growing season (October 2006–March 2007). A cosine-correction allowed comparison with meteorological data (Anderson 1964b; Rich 1990; Brunner 1998). Due to the lack of meteorological stations in Tierra del Fuego, the length of the growing season was calculated on the basis of monthly mean air temperature values in excess of 5°C (Tuhkanen 1992).

The universal overcast sky (UOC) model (Steven and Unsworth 1980) was used to estimate the intensity of the spatial distribution of DIF. The UOC model assumes that the diffuse solar radiation above the forest canopy is the same from all sky directions. Although at any given time diffuse solar radiation can be very anisotropic due to cloudiness variations and diurnal differences in the position of the bright circumsolar region on clear days (Canham et al. 1994), it was assumed that the total diffuse solar radiation is isotropic over the sky hemisphere over the whole growing season. The relative proportion of direct to diffuse solar radiation was set at 0.5; this was done because in the vegetation period (October–March) the mean monthly cloudiness of southern Patagonia [Meteorological stations: ‘Jorge C. Scythe’ in Punta Arenas (53°08’S; 70°53’W; 6 m a.s.l.), and Río Grande (53°80’S; 67°78’W; 9 m a.s.l.) and Río Olivia (54°82’S; 68°30’W) in Tierra del Fuego] ranges between 5.0 and 6.4 oktas (Butorovic 2003, 2004, 2005; Santana 2006, 2007; SMN 2007).

HemiView is able to estimate potential direct solar radiation for each day over the course of a year (Rich et al. 1999). It was used to estimate the hourly mean values of DIR for each canopy gap over the research period.

Transmitted global solar radiation (GLO) is defined by HemiView as the sum of the transmitted direct (DIR) and diffuse (DIF) solar radiation, which does not include radiation reflected off obscured sky directions (Rich et al. 1999).

Canopy structure and stand parameter assessment

Gap fraction (GF), canopy openness (CO), and plant area index (L_e) were estimated from hemispherical photographs. GF is the vertically projected canopy area per unit ground area. CO is a sine-weighted measure (Frazer et al. 1999) that represents the proportion of the image not obstructed by canopy (Hale and Edwards 2002). L_e is the sum of all elements of the canopy blocking out light (stems, twigs, leaves), as hemispherical photographs do not distinguish between opaque objects (stems) and photosynthetic tissue (Holst et al. 2004).

L_e was estimated using HemiView and Gap Light Analyzer Version 2.0 (Frazer et al. 1999). Both programmes use methods based on the determination of gap fraction in the canopy and inversion procedures (Norman and Campbell 1989). HemiView incorporates an inversion algorithm of canopy transmission employing an ellipsoidal leaf angle distribution parameter to estimate the plant area index (L_e -E). This means that the leaf elements are distributed in the same proportions as the surface of an ellipsoid of revolution (Wood 2001). Gap Light Analyzer uses the mean tilt angle of the foliage to estimate L_e . The mean tilt angle is calculated by a polynomial derived for a uniform leaf azimuth distribution and a constant leaf normal angle (Welles and Norman 1991; Frazer et al. 1999). This technique is similar to that used by the LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, NE). Gap Light Analyzer was used to estimate L_e over the two zenith angle ranges 0–60° (L_e -60) and 0–75° (L_e -75).

Stand parameter measurements were made at 26 stand parameter measurement plots (15×15 m) during the summer of 2007 (Table 1). In each plot, the diameter at breast height (DBH) for all trees with DBH≥5 cm was recorded, and D , BA and the stem volume (S_V) per hectare were estimated. The centres of the 26 plots (13 at GC, and 13 at NUC) were located at the same points from which the hemispherical photographs were taken. The crown projection to the ground of each tree was also visually estimated. Crown radii were measured in the four cardinal directions. The edge of the crown was determined with the aid of a clinometer, and the radii measured. For each crown quarter, the crown projected to the ground (CP) was calculated using the formula of an ellipse, and all four quarters were then summed. S_V was calculated from a species-specific allometric regression based on DBH and the dominant height of the trees in the plot (Promis et al. 2007).

In order to reconstruct the crown shape of each tree, the equivalent crown radius (R) was estimated. R is defined as the radius of a circle whose area is equal to the CP projected to the ground (Piboule et al. 2005). The crown surface area (C_{SA}) and the crown volume (C_V) were then computed, assuming that the crown has a parabolic shape:

$$C_{SA} = \frac{\pi \times R}{6 \times C_L} \times (R^2 + 4 \times C_L^2)^{1.5} - R^3 \tag{1}$$

$$C_V = \pi \times \frac{R^2 \times C_L}{2} \tag{2}$$

where C_L (m) is the crown length. C_L is defined as the distance between the treetop and the base of the tree crown, excluding epicormic shoots.

A regression analysis was performed to find a relationship between C_L and DBH. From a sub-sample of 70 trees, the total height [22.1±3.6 m (average ± SD)], C_L (5.5±1.7 m), and DBH (48.3±18.3 m) were measured. Although significant, the best relationship was a power function, which showed large variation ($n=70$; $R^2=0.147$; RMSE=0.295; $P<0.01$), indicating a high variability of C_L among the trees in this old-growth forest.

$$C_L = 1.707 \times DBH^{0.296} \tag{3}$$

Statistical and regression analysis

The non-parametric Kruskal-Wallis H-test and a post-hoc Mann-Whitney U-test were used to analyse the variation in the transmitted, cosine-corrected solar radiation between areas beneath the disturbed and the undisturbed canopy. A regression analysis was performed to test the strength of the

Table 1 Stand parameters estimated at the 26 stand parameter measurement plots. Thirteen plots were located at the gap centre (GC) of the canopy gaps and thirteen plots were located at the northwestern undisturbed canopy plot locations (NUC). D Stocking density, BA basal area

GC			NUC		
Plot	D (trees ha ⁻¹)	BA (m ² ha ⁻¹)	Plot	D (trees ha ⁻¹)	Basal area (m ² ha ⁻¹)
1	2,356	106	14	1,778	109
2	2,044	50	15	1,956	74
3	1,911	118	16	1,111	99
4	1,111	66	17	800	122
5	756	104	18	1,244	124
6	711	86	19	1,289	156
7	1,111	97	20	711	129
8	622	93	21	1,733	170
9	1,289	58	22	978	88
10	578	80	23	533	83
11	622	36	24	1,200	65
12	889	56	25	1,156	98
13	1,378	32	26	2,578	100

relationship between the transmitted solar radiations above the forest floor, canopy structure, and stand parameters. The CURVEFIT algorithm in SPSS 15.0 for Windows (SPSS, Cary, NC) was used. Linear functions, logarithmic functions, inverse functions, quadratic functions, compound functions, power functions, Schumacher's equation, growth and exponential functions were tested with the independent variables DIR, DIF, GLO, $\ln(\text{DIR})$, $\ln(\text{DIF})$, and $\ln(\text{GLO})$ calculated from the hemispherical photographs. The independent variables recorded at the stand parameter measurement plots that were tested were BA, CP, CO, C_{SA} , C_V , D , GF, L_c-60 , L_c-75 , L_c-E , and S_V . For the regression analysis, the goodness-of-fit was calculated using the coefficient of determination (R^2), the root mean square error (RMSE), and the significance of the P -value (Sokal and Rohlf 2000). When the hemispherical photographs were used to fit the regression models, 65 observations (five hemispherical photographs taken along the transects of the 13 canopy gaps) of CO, GF, L_c-60 , L_c-75 , and L_c-E were available; 26 observations were used to build the regression models if the explanatory variables were calculated from the stand parameter measurement plots (BA, CP, C_{SA} , C_V , D , and S_V). In addition, the non-linear regression procedure of SPSS 15.0, employing a Levenberg-Marquardt algorithm, was used to evaluate the relationship between solar radiation transmission with a combination of canopy structure and stand parameters obtained from stand measurements.

Results

Transmission of solar radiation

During the growing season (October 2006–March 2007), the transmitted direct solar radiation below the canopy ranged between 3.5 and 22.2 % of above-canopy DIR. The highest

amount of DIR [$10.6 \pm 3.2\%$ (average \pm SD)] was recorded at SUC. This value did not differ significantly ($n=13$, $P>0.05$) from mean transmitted DIR calculated at GC ($9.1 \pm 4.4\%$) and SGE ($8.7 \pm 3.9\%$). Although DIR was higher at SGE, the deviation from DIR calculated at NUC ($8.1 \pm 3.3\%$) was not significant. The lowest transmission was computed at NGE ($5.9 \pm 3.1\%$). In this case the difference from the values obtained for all other locations (GC, SGE, SUC, and NUC) was statistically significant (Table 2).

The hourly mean values of DIR differed between all five locations (GC, SGE, NGE, SUC and NUC) (Fig. 3). Hourly maximum DIR occurred at noon at two locations (GC and SGE) in the disturbed canopy (Fig. 3a, b). At NGE, maximum DIR transmission was more variable. It occurred at 1200 hours local time (LT) in October, at 0900 hours LT in December, and at 1100 hours LT in February (Fig. 3c). Except in October, greatest DIR values were almost always observed between 1300 hours and 1400 hours LT beneath the undisturbed canopy (Fig. 3d, e).

DIF above the forest floor ranged from 4.4 to 28.0% of above-canopy DIF (Table 2). The highest DIF-value ($13.9 \pm 4.8\%$) was calculated at GC. This value did not differ significantly ($n=13$, $P>0.05$) from the mean value calculated at SGE ($12.5 \pm 2.2\%$). Although DIF was higher at SGE than at NGE ($11.1 \pm 2.7\%$), the difference was not significant. Lowest DIF values were calculated at SUC and NUC ($9.0 \pm 1.6\%$; $8.5 \pm 2.1\%$), but did not differ significantly ($n=13$, $P>0.05$).

The highest proportion of DIF in the canopy gaps originated from the 10–30° range of zenith angles. On average, 43% at GC, 46% at SGE, and 44% at NGE originated from this range of zenith angles. Beneath the undisturbed canopy, largest DIF values (47% at SUC and 43% at NUC) were observed within the 30–50° range of zenith angles (Fig. 4).

The below-canopy global solar radiation values ranged from 4.5 to 25.8% of above-canopy GLO (Table 2). There was no significant difference ($n=13$, $P>0.05$) between mean

Table 2 Descriptive statistics of the cosine-corrected transmitted direct (DIR), diffuse (DIF), and global (GLO) solar radiation at the centre of the canopy gaps (GC), the southeastern gap edge (SGE), the northwestern gap edge (NGE), and below the southeastern undisturbed canopy (SUC) and the northwestern undisturbed canopy

Cosine-corrected transmitted solar radiation		GC	SGE	NGE	SUC	NUC
DIR	Mean	9.1 ab	8.7 ab	5.9 c	10.6 a	8.1 b
	SD	4.4	3.9	3.1	3.2	3.3
	Range	4.9–22.2	4.2–18.5	3.5–13.3	6.0–15.7	4.1–17.3
DIF	Mean	13.9 a	12.5 ab	11.1 b	9.0 c	8.5 c
	SD	4.8	2.2	2.7	1.6	2.1
	Range	8.9–28.0	8.7–17.3	5.0–17.5	5.4–11.5	4.4–11.8
GLO	Mean	12.1 a	11.1 ab	9.2 bc	9.6 abc	8.3 c
	SD	4.5	2.7	2.5	1.7	1.9
	Range	8.3–25.8	7.2–17.8	4.5–13.5	6.6–11.9	4.7–11.8

(NUC). Locations with the same letter (a, b, c) for the same transmitted solar radiation variable are not significantly different (Kruskal-Wallis H-test and a post-hoc Mann-Whitney U-test, $n=13$, $P>0.05$). SD Standard deviation

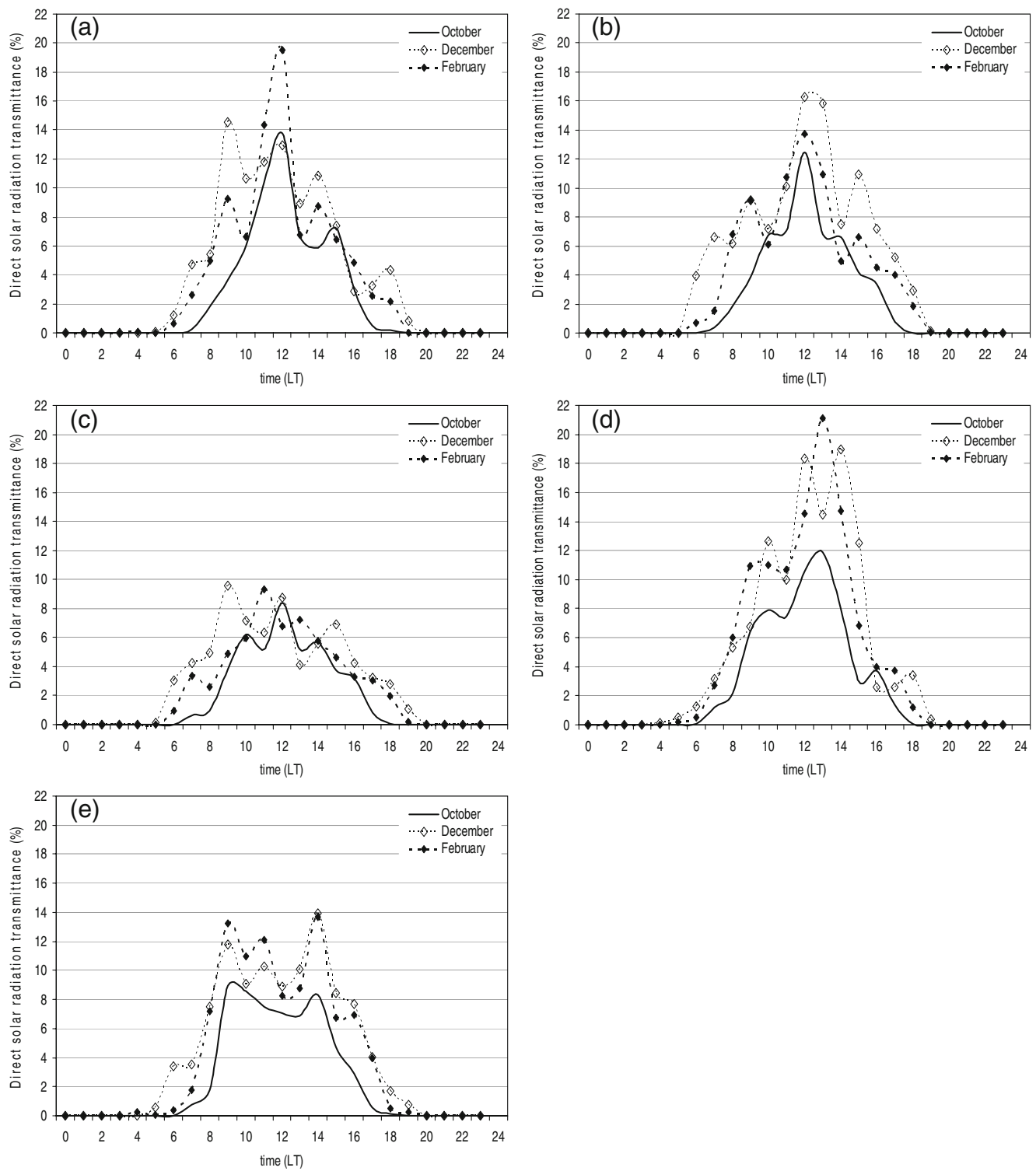


Fig. 3 Hourly mean values of transmitted direct (DIR) solar radiation for three months (October, December, and February) at (a) the gap centre (GC), (b) the southeastern gap edge (SGE), (c) the northwestern

gap edge (NGE), and below the (d) southeastern (SUC), and (e) northwestern (NUC) undisturbed canopy. *LT* Local time

GLO at GC ($12.1 \pm 4.5\%$) and SGE (11.1 ± 2.7). In contrast, there was a statistically significant difference between GLO at GC and below-canopy GLO at NGE ($9.2 \pm 2.5\%$). However, GLO values recorded at the two edges of the

gaps did not differ. The lowest estimates of GLO were found at SUC and NUC ($9.6 \pm 1.7\%$ and $8.3 \pm 1.9\%$).

Models fitted through regression analysis (Table 3, model 4, and Fig. 5a) suggested that L_e -E, although with a low

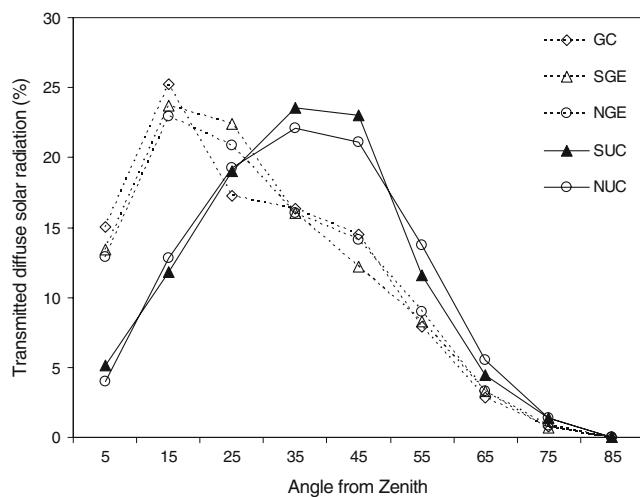


Fig. 4 Average distribution of transmitted diffuse (DIF) solar radiation at GC, SGE, NGE, SUC, and NUC. DIF was estimated from 10° bands of zenith angle of the sky hemisphere

coefficient of determination ($R^2=0.263$), is the variable that explains the largest proportion of the variance of below-canopy DIR. Other variables explaining more than 20% of the variation of below-canopy DIR were CO ($R^2=0.221$) and L_e-60 ($R^2=0.219$).

The best regression model fitted for the estimation of below-canopy DIF (Table 4, model 11, and Fig. 5b) used CO ($R^2=0.963$) as predictor variable. Further significant predictor variables explaining more than 20% of the variation of DIF were GF ($R^2=0.839$), R_e-60 ($R^2=0.479$), R_e-75 ($R^2=0.396$), CP ($R^2=0.266$), the average equivalent crown radius per plot (R_R) ($R^2=0.265$), BA ($R^2=0.256$), R_V ($R^2=0.245$), and R_V ($R^2=0.215$).

When the simple stand parameters were used alone, BA, CP, C_V , C_R , and S_V were poor predictors of the variation in DIF (Table 4). However, when the aforementioned, readily measured canopy structure and stand parameters are combined, they can explain 75% of the variation in DIF (Fig. 6), without showing great differences from the observed values.

For the prediction of below-canopy GLO, CO ($R^2=0.833$) fitted the best regression model (Table 5, model 23, and

Fig. 5c). The other predictor variables explaining more than 20% of the variation of GLO were GF ($R^2=0.638$), L_e-60 ($R^2=0.536$), L_e-75 ($R^2=0.434$), and C_R ($R^2=0.296$). Nonetheless, when only stand parameters (BA, CP, S_V , and C_R) were combined, a model explaining 73% of the variation in the global solar radiation was developed (Fig. 7).

Discussion

The transmission of DIR into forests is a function of above-canopy DIR, stand characteristics, and the number, size, and spatial distribution of canopy openings (Anderson 1964a; Reifsnnyder 1971/1972; Hutchison and Matt 1977). In a canopy gap, the solar radiation regime is affected by gap size, gap shape, gap orientation (Brokaw 1985), and height of the surrounding trees (Lieffers et al. 1999). Moreover, at high latitudes in the southern hemisphere, an occasional opening of the canopy low on the horizon increases DIR transmission. Therefore, of the parameters estimated in the canopy gaps here, DIR showed the largest variation. From the canopy structure describing variables tested (CO, GF, L_e-60 , L_e-75 , and L_e-E), L_e-E explained the largest part of below-canopy DIR-variation. No functional relationship could be established between DIR and the tested stand parameters. This corresponds to the findings of Gray et al. (2002).

In contrast to similar studies carried out in the northern hemisphere (Canham et al. 1990; Bazzaz 1996; Gray et al. 2002), the southern edges of the canopy gaps received more direct solar radiation than the northern edges, which has also been observed by Heinemann and Kitzberger (2006) in *Nothofagus pumilio* forests. Due to the changing angle of solar elevation throughout the year (Geiger et al. 2003), the diurnal DIR-pattern within the canopy gaps were also reversed as mentioned by Bazzaz (1996). On average over the growing season, the southeastern gap edge received maximum DIR at noon. At the northwestern gap edge, maximum DIR was between 1 (in February) and 3 (in December) hours later. The effect of the canopy gaps on the below-canopy solar radiation extended to the areas below

Table 3 Regression models fitted for the estimation of the transmitted direct (DIR) solar radiation into the *Nothofagus betuloides* forest. b_0 , b_1 , b_2 Model coefficients, R^2 coefficient of determination, RMSE root mean square error, N number of observations

No.	Model	b_0	b_1	b_2	R^2	RMSE	P -value	N
4	$\ln(y) = \exp(b_0 + b_1 L_e - E)$	1.06	-0.10	-	0.263	0.187	0.000**	65
5	$\ln(y) = b_0 + b_1 \ln(L_e - 60) + b_2$	-0.86	6.66	-3.53	0.219	0.385	0.001**	65
6	$\ln(y) = \exp(b_0 + b_1 L_e - 75)$	1.48	-0.26	-	0.159	0.200	0.001**	65
7	$y = b_0 + b_1 CO + b_2 CO^2$	9.29	-0.82	0.09	0.221	3.420	0.000**	65
8	$y = b_0 + b_1 / \ln(C_R)$	6.36	0.98	-	0.175	3.501	0.030*	26

* $P>0.05$, ** $P>0.01$

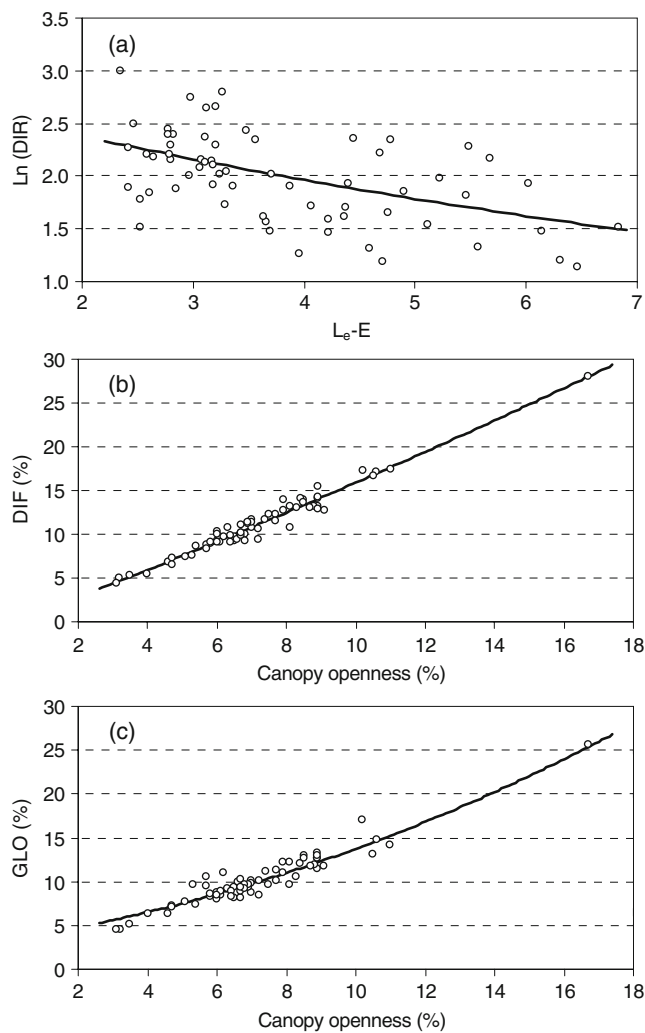


Fig. 5 Scatter plots of the best relationships between (a) transmitted DIR during the growing season (October 2006–March 2007) and plant area index, employing an ellipsoidal leaf angle distribution (L_c -E) (see Table 3, model 4); (b) transmitted DIF during the growing season and canopy openness (see Table 4, model 11), (c) transmitted GLO during the growing season and canopy openness (see Table 5, model 23)

the undisturbed canopy and, on average, the highest DIR was recorded at SUC.

The below-canopy values of DIF exhibited less variability than below-canopy DIR-values. The highest DIF-values were found in the canopy gaps rather than below the undisturbed canopy. The reason for this is that the transmission of diffuse light depends mainly on sky brightness and canopy openings (Anderson 1964b; Reifsnnyder 1971/1972; Hutchison and Matt 1977). Thus, the contribution of DIF to the overall below-canopy light regime decreases with increasing distance from the centre of a canopy gap (Canham et al. 1990). Furthermore, the greater proportion of below-canopy DIF originated from two bands of the sky, between 10–30° of the zenith angles in canopy gaps, and between 30–50° of the zenith angles beneath undisturbed canopies. Similar patterns have been observed in temperate and tropical forests (Canham et al. 1990). Eleven variables describing the canopy structure and stand parameters (L_c -60, L_c -75, CO, GF, BA, CP, C_{SA} , C_V , S_V , C_R and CP) exhibited a significant functional relationship with DIF. The best regression model fitted for predicting below-canopy DIF used either CO or GF. Battaglia et al. (2002) report similar relationships for a *Pinus palustris* forest.

Through the regression analysis, each independent variable of stand parameters alone (BA, CP, C_{SA} , C_V , S_V , C_R and CP) explained between 15% and 27% of the variation in DIF. Nonetheless, in single species stands, or within even-aged mixed stands with homogeneous canopy architecture, simple stand architecture parameters such as basal area, stocking density, canopy cover, age, etc., have been used successfully in predictions, especially for transmitted diffuse solar radiation (Vales and Bunnell 1988; Comeau 2001; Hale 2001, 2003; Pinno et al. 2001; Comeau and Heineman 2003; Sonohat et al. 2004; Comeau et al. 2006). However, a strong relationship was obtained when BA, CP, C_V , C_R and S_V were used as independent variables, thus 75% of the variation in DIF could be explained (Fig. 6).

Table 4 Regression models fitted for the estimation of the transmitted diffuse (DIF) solar radiation into the *Nothofagus betuloides* forest. b_0 , b_1 , b_2 Model coefficients, R^2 coefficient of determination, RMSE root mean square error, N number of observations

No.	Model	b_0	b_1	b_2	R^2	RMSE	P-value	N
9	$y = b_0 + b_1 \ln(L_c - 60) + b_2 \ln(L_c - 60)^2$	82.66	-106.06	37.87	0.479	2.646	0.000**	65
10	$\ln(y) = \exp(b_0 + b_1 L_c - 75)$	1.66	-0.26	-	0.396	0.110	0.000**	65
11	$y = b_0 + b_1 CO + b_2 CO^2$	-0.25	1.50	0.01	0.963	0.707	0.000**	65
12	$y = b_0 + b_1 GF + b_2 GF^2$	4.79	0.36	0.01	0.839	1.469	0.000**	65
13	$\ln(y) = b_0 + b_1 \ln(BA)$	4.49	-0.48	-	0.256	0.340	0.007**	65
14	$\ln(y) = b_0 + b_1 \ln(CP)$	5.15	-0.48	-	0.266	0.338	0.006**	26
15	$\ln(y) = \exp(b_0 + b_1 / \ln(C_{SA}))$	-0.86	10.9	-	0.183	0.157	0.026*	26
16	$\ln(y) = b_0 + b_1 C_V + b_2 C_V^2$	3.01	-0.002	0.00	0.245	0.350	0.035*	26
17	$y = b_0 + b_1 / S_V$	6.79	3581.58	-	0.215	4.242	0.015*	26
18	$y = b_0 + b_1 / \ln(C_R)$	7.84	1.50	-	0.265	4.106	0.006**	26
19	$y = b_0 + b_1 / \ln(CP)$	2.25	22.53	-	0.146	4.425	0.049*	26

* $P > 0.05$, ** $P > 0.01$

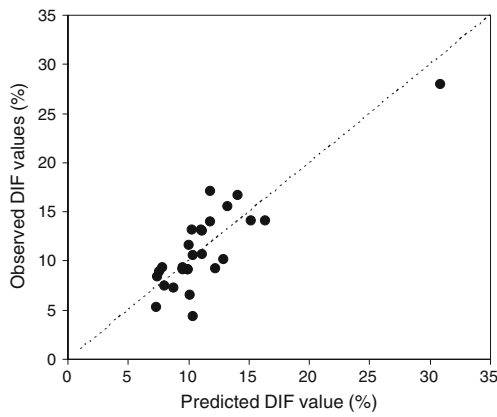


Fig. 6 Comparison between the observed and the predicted transmitted DIF during the growing season (October 2006–March 2007). Predicted values were calculated using the model $DIF = 206.60 - 11.98 \ln(BA) - 13.98 \ln(CP) + 0.03 C_V - 8.22E-06 C_V^2 \exp(-7.84 + 1.31 / \ln(C_R)) - 501.37 / \ln(S_V)$ ($n=26$; $R^2=0.749$; $RMSE=2.751$; $P<0.001$). The dashed line represents a 1:1 reference, where predicted values of DIF during the growing season would equal DIF-values determined from hemispherical photographs

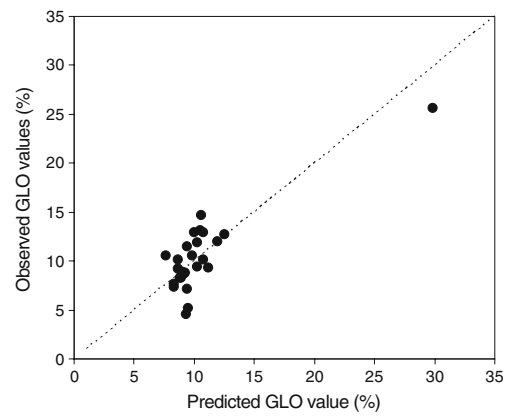


Fig. 7 Comparison between observed and predicted transmitted GLO during the growing season (October 2006–March 2007). Predicted values were calculated using the model $GLO = -11.67 + 7.23 \ln(BA) + 122.95 \ln(CP) + \exp(-10.79 + 1.66 / \ln(C_R)) - 1310.80 / \ln(S_V)$ ($n=26$; $R^2=0.734$; $RMSE=2.213$; $P<0.001$). The dashed line represents a 1:1 reference, where the predicted values of GLO during the growing season would be equal to the GLO-values determined from the hemispherical photographs

The variables that explain the variation in the below-canopy GLO best were CO (83 %) and GF (64%) (Table 5). Canopy architecture and stand parameters (BA, CP, S_V , C_R) explained between 16% and 54% of the variation in GLO (Table 5). However, the heterogeneity of the spatial distribution of structures, which is a distinct feature of old, uneven-aged forests (Franklin and van Pelt 2004), also influences the heterogeneity of the transmission of global solar radiation below the canopy. Therefore, when BA, CP, S_V , and C_R were used as independent variables, 73% of the variation in below-canopy global solar radiation was explained through a regression analysis (Fig. 7).

In general, the below-canopy DIR- and DIF-values found in this study were lower than those estimated in forests of *N. betuloides* mixed with deciduous *N. pumilio* during spring and summer (Veblen 1979; Veblen et al. 1979, 1980). These differences may result from differing forest composition, forest structure, times at which the solar radiation transmission was estimated (Gray et al. 2002) or the differing forest locations. Nonetheless, the general pattern in below-canopy

solar radiation observed in this *N. betuloides* forest over the course of the growing season in canopy gaps and beneath closed canopies was also found in other forests (Denslow 1980; Canham et al. 1990; de Freitas and Enright 1995; Gray et al. 2002; Heinemann and Kitzberger 2006).

Conclusions

The transmission of solar radiation onto the floor of a *N. betuloides* forest is characterised by a high degree of spatial and temporal variability. Although canopy gaps appear to increase the amount of solar radiation reaching the forest floor, a higher below-canopy DIR was found below the undisturbed canopy to the southeast of the gap centre, at a distance from the gap edge of half the height of the highest tree in the vicinity of the gap.

Canopy structure and stand parameters explain, at least in part, the variation in the below-canopy solar radiation regime. The best predictors of the below-canopy DIF and GLO are CO

Table 5 Regression models fitted for the estimation of the transmitted global (GLO) solar radiation into the *Nothofagus betuloides* forest. b_0 , b_1 , b_2 Model coefficients, R^2 coefficient of determination, $RMSE$ root mean square error, N number of observations

No.	Model	b_0	b_1	b_2	R^2	RMSE	P -value	N
20	$y = b_0 + b_1 / \ln(L_e - E)$	4.78	6.58	-	0.137	2.889	0.002**	65
21	$\ln(y) = \exp(b_0 + b_1 L_e - 60)$	1.56	-0.23	-	0.536	0.087	0.000**	65
22	$\ln(y) = \exp(b_0 + b_1 L_e - 75)$	1.58	-0.25	-	0.434	0.096	0.000**	65
23	$y = b_0 + b_1 CO + b_2 CO^2$	3.36	0.62	0.04	0.833	1.281	0.000**	65
24	$y = b_0 + b_1 GF + b_2 GF^2$	8.02	-0.11	0.02	0.638	1.885	0.000**	65
25	$\ln(y) = b_0 + b_1 / \ln(BA)$	0.97	5.77	-	0.162	0.301	0.037*	26
26	$\ln(y) = b_0 + b_1 / \ln(CP)$	0.52	10.13	-	0.166	0.300	0.035*	26
27	$y = b_0 + b_1 / S_V$	7.09	2544.68	-	0.161	3.600	0.038*	26
28	$y = b_0 + b_1 / \ln(C_R)$	7.29	1.30	-	0.296	3.299	0.003**	26

* $P>0.05$, ** $P>0.01$

and GF, indicating a sensitivity to canopy openings in this forest. The models fitted for the readily estimated canopy architecture and stand parameters showed a poor correlation with the transmitted solar radiation into the forest. However, by combining BA, CP, C_v , and S_v , a large amount of the variability of the below-canopy DIF and GLO can be explained.

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