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# Transmissivity of solar radiation within a *Picea sitchensis* stand under various sky conditions

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Abstract

We tested the hypothesis that diffuse radiation from cloudy and overcast skies penetrates the canopy more effectively than direct radiation from clear skies. We compared the flux density and spectral properties of direct and diffuse radiation (around solar noon ( $\pm 1$  h)) above, within and below a forest stand under sunny, cloudy and overcast conditions in a thinned Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forest (28 years old, with an leaf area index of approximately 5.2). We recorded vertical profiles of radiation penetration (from 350 to 1050 nm), and we also explored the horizontal pattern of radiation along a 115 m transect.

We showed that in “clear sky” conditions, the photosynthetically-active radiation in the lower parts of the canopy was substantially attenuated, more so than under cloudy and overcast skies. It was particularly depleted in the blue part of the spectrum, but only slightly blue-depleted when the sky was overcast or cloudy. Moreover, the red far-red ratio under clear skies fell to values less than 0.3 but only to 0.6 under cloudy or overcast skies. Near the ground, the light climate was strongly influenced by the thinning pattern (carried out in accordance with standard forestry management practice).

1 Introduction

The solar radiation reaching the Earth’s surface is influenced by the absorption, transmission and reflection of light by the aerosol and water vapour constituents of the atmosphere. The extent of cloud cover affects the intensity and proportions of “direct” and “diffuse” radiation reaching the Earth’s surface. While diffuse radiation is thought to enhance photosynthesis of terrestrial vegetation (Gu et al., 1999, 2002; Urban et al., 2007; Dengel and Grace, 2010), direct solar radiation can cause saturation of photosynthesis at the top of the canopy and possibly photo-inhibition (Powles, 1984; Krause, 1988; Long et al., 1994). Furthermore, unsaturated photosynthesis during

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direct solar radiation is possibly occurring within the canopy and under-storey region as a result of shading (Kanniah et al., 2012). Urban et al. (2007, 2012) hypothesised that optimal photosynthetic activity of the canopy is achieved under diffuse radiation (cloudy) conditions, when scattered light penetrates throughout the canopy, illuminating all the leaves to some extent and providing a more uniform distribution of light between the leaves. However, the spectral properties of the diffuse component inside the canopy have only been investigated in a Norway spruce (*Picea abies* [L.] Karst) – European beech (*Fagus sylvatica* L.) forest stand in Southern Germany (Leuchner et al., 2007; Hertel et al., 2011) and a Norway spruce stand by Navratil et al. (2007) and Urban et al. (2007, 2012) in the Czech Republic. No measurements are known from higher latitudes.

The vertical profile of irradiance through a plant canopy is often approximated by the Beer–Lambert equation of light extinction first introduced by Monsi and Saeki (1953), and subsequently serving as the base of many canopy transmission studies (Grace and Woolhouse, 1973; Norman and Jarvis, 1974; Lewandowska et al., 1977; Hale, 2003; Sonohat et al., 2004). However, the equation does not describe the complexity of the radiation field to which the photosynthesising elements are exposed, neither the spatial, angular, nor the temporal distribution, because forest canopies are dynamic and far from homogenous (Gholz et al., 1991; Smith et al., 1991). The diffuse radiation inside a forest canopy includes the fraction scattered by the foliage itself as well as radiation transmitted through the leaves and through the many gaps in the foliage (Muller, 1971; Grant, 1997). Sunflecks – their size, shape, duration and spectral distribution – depend on the orientation and inclination of woody and photosynthesising elements within the forest canopy as well as the position of the sun in the sky (Federer and Tanner, 1966; Norman and Jarvis, 1974; Pearcy, 1990; Chazdon and Pearcy, 1991; Grant, 1997). The way plants respond to sunflecks may vary, and in some shade plants this may be crucial to effective gas exchange and photosynthetic production (Sellers, 1985; Leakey et al., 2003). Indicators for light quality, in contrary to light quantity, specified for example as blue light and red far-red ratio effects are prime

factors in plant functionality. Blue light may have important implications for stomatal control, causing stomatal opening (Morison and Jarvis, 1983) while the red far-red ratio is known to influence photomorphogenesis, heating regulation, as well as stem elongation and chlorophyll synthesis (Gates, 1965; Smith, 1982; Wherley et al., 2005; Casal, 2013).

The observation that diffuse light is utilised in canopy photosynthesis more effectively than direct sunlight (Urban et al., 2007; Dengel and Grace, 2010) poses a number of questions to be addressed in the present work. They are (a) to what extent is it true that light is distributed more evenly throughout the Sitka spruce (LAI of 5.2) forest canopy under cloudy conditions, (b) to what extent are spectral differences important (measurements were carried out around solar noon ( $\pm 1$  h)), (c) and how important are the gaps especially the gaps arising from management interventions.

## 2 Materials and methods

### 2.1 Site description

Measurements were carried out at Griffin forest (Clement et al., 2003; Clement, 2004) in Central Scotland (56°37' N, 3°48' W; 380 m a.s.l.). This Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forest was planted between 1979 and 1983 and row-thinned in 2004 by removing every 5th row of trees. In addition, trees have been felled selectively resulting in a total of 30 % of the forest stand being removed. The planting distance is around 2 m, with approximately 11 m from any mid-thinning line to the next. The mean diameter at breast height (DBH) at the time of measurements were 37 cm, mean canopy height 18.5 m and with an estimated leaf area index (LAI) of approximately  $5.2 \text{ m}^2 \text{ m}^{-2}$ . All meteorological and micrometeorological measurements are carried out on a walk-up scaffolding tower of 22 m height. Below the forest canopy a 115 m-long transect, crossing 10 sections of 1 thinned and 4 planted rows and with a North–South alignment, was established in order to measure below canopy radiation (Fig. 1).

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## 2.2 Methods

### 2.2.1 Spectral flux density

Spectral distribution and flux density were measured using two spectroradiometers (GER1500, Spectra Vista, New York, USA), fitted with cosine corrected diffusers (MacArthur et al., 2012), permitting comparison of the spectral flux density (irradiant energy; units:  $\text{W m}^{-2} \text{nm}^{-1}$ ) in the canopy with simultaneously measured spectral flux density above the canopy at 22 m height. The spectral resolution of the GER1500 is 3 nm, measuring 512 channels between 350 and 1050 nm, although the post-processing methods interpolate data to 1 nm intervals (Walker and MacLellan, 2009).

All spectral measurements were carried out around solar noon ( $\pm 1$  h) during the summer of 2008. Tower and forest floor (transect) scans were carried out back-to-back within less than 10 min of each other. One complete set of measurements including the vertical and horizontal measurements took around one hour. Vertical profiles of radiation penetrating the canopy were made by taking three measurements at 1 m intervals 1.5 m from the tower (south facing, opposite side of the artificial gap created during the tower installation), while the scans recorded for evaluation of the horizontal transect were measured at 1 m height with 2.5 m intervals. Each measurement represents an average of 10 internally averaged scans. Measurements were carried out under (i) clear sky conditions, (ii) cloudy conditions (we selected conditions with altostratus clouds to guarantee minimal changes in cloudiness over the measurement period) and (iii) on a completely overcast day. In all cases light conditions above the forest canopy did not change significantly over the measuring period. To facilitate comparison, data were normalised to the range 0–1.

### 2.2.2 Leaf area index

The vertical distribution of leaf area index (LAI) was estimated from hemispherical images taken every 2 m down the tower using a Nikon digital camera (Coolpix 4500,

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Nikon Corporation, Tokyo, Japan) with a fish eye lens attachment (Fish-eye converter FC-E8, Nikon Corporation, Tokyo, Japan). Images were acquired following the protocols established by Chen et al. (1997) and van Gardingen et al. (1999), and were processed with the scientific image processing software Gap Light Analyzer (GLA) (Forest Renewal BC, Frazer et al., 1999). When calculating LAI from hemispherical images in coniferous forests a correction value, known as the clumping index (van Gardingen et al., 1999), is necessary to account for structural aspects of the canopy. The necessary clumping index value has been calculated from several transect measurements, using a TRAC (Tracing the Radiation and Architecture of Canopies, – Leblanc et al. (2002) (3rd Wave Engineering, Nepean, Canada) in Griffin forest during the growing season 2007 and 2008 and was found to be 0.98. A detailed explanation on the use of this instrument is given in Sect. 2.2.4.

### 2.2.3 Photosynthetic photon flux density and transmissivity at various wavelengths

Values of photosynthetic photon flux density (PPFD) were calculated by adjusting irradiant energy ( $\text{Wm}^{-2}\text{nm}^{-1}$ ) to quanta ( $\mu\text{molm}^{-2}\text{s}^{-1}$ ) and integrating from 400–700 nm (Combes et al., 2000) (Eq. 1):

$$\text{PPFD} = \int_{\lambda=400}^{\lambda=700} E h \nu (\delta \lambda) \quad (1)$$

where the limits of wavelength ( $\lambda$ ) were 400 and 700 nm.  $E$  is the spectral irradiance,  $h$  is the Planck constant and  $\nu$  is frequency, given by  $1/\lambda$ . The wavelength increments used for the numerical integration were 1 nm. Blue light was calculated in the same manner where the limits of wavelength were 430 and 470 nm, and were chosen to be within the margins of the blue light (400–500) which evokes stomatal opening (Kuiper, 1964; Mansfield and Meidner, 1966; Zeiger and Field, 1982; Karlsson, 1986).

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The transmissivity of PPFD was calculated as the quotient of PPFD at the height  $h$  and the simultaneous measured PPFD at 22 m (top of tower), while the transmissivity of blue light was calculated as the quotient of blue light at the height  $h$  and the simultaneously recorded blue part of the irradiance spectrum at 22 m. Hereafter the blue transmissivity of the two diffuse conditions and the blue light transmissivity on the clear day can be visually compared. For an indication of possible photomorphogenetic response, light quality may also be stated as the red far-red (R:FR) ratio of incident radiation and expressed as follows (Heyward, 1984; Holmes and Smith, 1977):

$$R : FR = \frac{\int_{655 \text{ nm}}^{665 \text{ nm}} E_{\lambda} d\lambda}{\int_{725 \text{ nm}}^{735 \text{ nm}} E_{\lambda} d\lambda} \quad (2)$$

where  $E_{\lambda}$  is the spectral irradiance. Holmes and Smith (1977) note that red far-red ratio remains more or less constant over the year and during the day, whereas within the canopy it is additionally dependent on the interaction of the incident light with phytoelements.

## 2.2.4 Below-canopy spectral flux density and PPFD

Spectral flux density measurements were carried out below the Sitka spruce canopy simultaneously with measurements above the forest canopy. High resolution below-canopy photosynthentic photon flux density was measured with a mobile handheld TRAC (Tracing Radiation and the Architecture of Canopies – Leblanc et al. (2002) (3rd Wave Engineering, Nepean, Canada), recording continuously at 32 Hz along the same transect, resulting in a high resolution dataset of total incident (global) and diffuse (through the use of a shading strip) PPFD values. In addition the TRAC software also estimated LAI, the fraction of absorbed photosynthetically active radiation ( $fAPAR$ ), gap fraction, gap dimension and the clumping factor. These measurements

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were carried out routinely throughout the year. Those carried out within the frame of the current study were undertaken immediately after the spectral flux density measurements at solar noon. The TRAC sensor was manually moved along the same transect as used for the spectral irradiance measurements. The standard walking pace along the transect was  $0.3\text{ m s}^{-1}$  (while continuously recording), following markers at 5 m intervals to ensure a consistent high-resolution data set. As data were recorded at 32 Hz not all segments have the identical number of data points. Raw data were logged internally inside the instrument and downloaded after each run before converting and processing them using its own TRAC software. Exact details on theory description, the calculations of gap fraction and dimension, as well as the clumping factor can be found in Chen and Cihlar (1995), Leblanc et al. (2002) and Leblanc (2008).

### 3 Results

Figure 1 illustrates the schematics of the forest, along with visual impressions on canopy structure and fish-eye photographs of the canopy and sky. This forest structure is typical of many commercial coniferous plantations. All above-canopy irradiance spectra display the expected features (Fig. 2a, c): they have their peak spectral irradiances in the blue region at around 480 nm; both oxygen absorption bands are clearly seen (687 and 761 nm), as are the water absorption bands at around 730 and 940 nm. Below the forest canopy, there is a shift in maximum energy from the visible region to the far-red and infrared region (Fig. 2b). Figure 2d visualises the spectral/energy change that occurs once radiation penetrates the forest canopy. An abrupt shift is observed at the height where the canopy is closed, with a sunfleck becoming visible at the heights of around 11 m above ground level. Hereafter the majority of the energy shifts to the red far-red and into the infrared region. Once radiation reaches the forest floor which is illuminated partly by sunflecks and by large open parts of the canopy this shift reverses to similar distributions as seen above and close to the top of the canopy. Figure 2e and f represents the spectral flux





density recorded in cloudy and overcast conditions, respectively. Here, under both sky conditions, high energy levels within the blue region of the spectra remain conserved much lower/deeper into the canopy, with overcast conditions showing a more even distribution. Within the canopy (around 8 m.a.g.l.) some important differences can be noted between the sky types. Under both cloudy and overcast conditions there is relatively more blue radiation. Much less of the incoming radiation is in the photosynthetically -active part of the spectrum (400–700 nm) in the case of the clear sky compared with the cloudy/overcast conditions.

The spectra were re-expressed as quanta and numerically integrated between 400 and 700 nm to yield values of PPFD (Eq. 1). Above the canopy on top of the 22 m tall tower PPFD was approximately  $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$  on the clear day,  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  under cloudy conditions and  $400 \mu\text{mol m}^{-2} \text{s}^{-1}$  when overcast. The mean and cumulative LAI (Fig. 3a) and PPFD distributions (Fig. 3b) down the vertical profile, and the transmissivity values associated with PPFD (Fig. 3c) and blue light (Fig. 3d) are shown as attenuation curves in Fig. 3 respectively. The attenuation of direct radiation (“clear”) is abrupt in the top-most part of the canopy (14–15 m) (Fig. 3b and c). The canopy is inhomogenous and at around 11 m.a.g.l. the sensor encountered a large sunfleck, which has produced a very high signal. Under cloudy and overcast conditions the curves are relatively smooth, showing gradual attenuation on passing through the canopy (Fig. 3b and c). These data may also be presented as a classical Beer–Lambert log-plot (Fig. 4), wherein the slope may be used to yield the attenuation coefficient ( $k$ ). The classical Beer–Lambert approach applied to diffuse conditions (Fig. 4 – solid grey and black line) yields  $k$  values of 0.79 and 0.86 respectively. However, under clear sky conditions this approach is unreliable due to the inhomogeneous vertical distribution of foliage, and the presence of a large gap. Overall, the result shows that under sunny conditions a very high fraction of PPFD is absorbed or reflected at the top of the canopy, and therefore much less remains after a leaf area index of 1.5 (in the main canopy).

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Figure 3d shows the profile of blue-light irradiance. In clear conditions, it is attenuated substantially, but only slightly attenuated in cloudy or overcast conditions. Close to ground level, blue light increases which we attribute to lateral illumination within the trunk space.

In clear conditions, there was a region of the canopy with a very low red far-red ratio, usually indicative of deep shade (Fig. 3e – black line). However, there was considerable spatial variation. In large gaps the clear-sky red far-red ratio is high, reaching near above canopy values visible in Fig. 3e. Usually, however, the red far-red ratio is lower, below 0.75.

The horizontal heterogeneity at the forest floor was surveyed, first by using the spectroradiometer (Fig. 5) and then with the TRAC device (Fig. 6). The spectral flux density, illustrated in Fig. 5 shows clearly the thinning lines. Figure 5a represents a standard irradiance spectrum below the canopy on a clear day (midday), while Fig. 5b presents the spectrum below the canopy under overcast conditions. There are distinctive differences within the photosynthetically active part of the spectrum, with higher energy levels in the photosynthetically active part of the spectrum under overcast conditions. Figure 5c and d illustrates the spectral flux density along the entire 115 m long transect (2.5 m measurement interval) for the clear and overcast day, respectively (cloudy conditions not shown here). Under both conditions the thinning lines become visible, though the irradiance levels shift (also Fig. 6), depending on light regime. Under clear conditions distinctive sunflecks are visible with high energy (similar to above canopy levels) in the photosynthetically active part of the spectrum. Under overcast conditions high energy levels within the photosynthetically active part of the spectrum are sustained and more evenly distributed along the forest floor. Energy levels within the far-red and infrared regions remain high under both conditions.

In clear-sky conditions the huge variation caused by sunflecks is seen (Fig. 6a), often reaching photon flux values of several hundred  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , superimposed on a background that varies systematically with the presence of thinning rows, from a minimum of about 3 to a maximum of about  $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Overcast conditions

(Fig. 6b) show highly regular behaviour, closely resembling the “background” values shown in Fig. 6a, although about 50 % higher.

## 4 Discussion

The study introduced here carried out in the Griffin forest is the first to report both the vertical and an extensive horizontal transect through a forest plantation.

### 4.1 Spectral effects

The spectral distribution of radiation is very important for plant growth and morphogenesis (Endler, 1993; Escobar-Gutiérrez et al., 2009). The spectral distribution of incoming solar radiation was similar under all three sky conditions. However, substantially more energy in the photosynthetically active wavebands penetrated the canopy in the case of diffuse skies. There was significantly more blue light within the canopy under cloudy skies possibly a result of multiple reflections and scattering involving the waxy abaxial surfaces of needles (Jeffree et al., 1971; Reicosky and Hanover, 1978; Cape and Percy, 1993). Blue-enrichment may have important implications for stomatal control of photosynthesis and water use. For Scots pine and Sitka spruce, Morison and Jarvis (1983) reported that blue wavelengths are more effective in causing stomatal opening than red wavelengths. Smith (1982) reported that at low PPFD stomata open only in response to blue light, red light being ineffective; thus, if this is a general result, we may conclude that the conditions of diffuse radiation in the present case are especially conducive to stomatal opening in the lower regions of the canopy, where PPFD is low in all three conditions.

Within the canopy there is a very high proportion of near infrared under all three sky conditions. This is not surprising, as leaves generally transmit as much as 50 % of incident radiation at this waveband and reflect much of the remaining (Middleton and Walter-Shea, 1995; Middleton et al., 1997; Knapp and Carter, 1998; Combes et



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al., 2000; Carter and Knapp, 2001). On the other hand, in the chlorophyll-absorbing region of the red, leaves transmit rather little energy; therefore, the ratio of red to far red is dictated by the presence of leaves. This aspect of light quality has received much attention. The decline in the red far-red ratio has long been known and has been linked in numerous studies to aspects of photomorphogenesis (see reviews by Federer and Tanner, 1966; Smith, 1982; Woodward, 1983; Morgan et al., 1985; Endler, 1993).

Smith (1982) indicates that the blue-absorbing photoreceptor present in plants acts to measure light quantity and that the pigment phytochrome can act to detect the red far-red ratio as an indicator of light quality. This ratio also regulates important aspects of plant growth including stem elongation (Smith, 1982; Corre, 1983; Ballare et al., 1991; Franklin and Whitelam, 2005; Pecot et al., 2005; Wherley et al., 2005).

Ritchie (1997) reported the ability of *Pseudotsuga menziesii* seedlings to detect the presence of nearby trees via changes in light quality and the ability to adjust their growth allometry. In particular, most researchers (see above) find that low red far-red ratio increases stem elongation, but also many other factors: growth rate, shape and in the present case this may have implications for the adjustment to light and competition, and the optimisation of branch location in the canopy. Furthermore, Kasperbauer (1971, 1987) showed that row spacing and orientation (in tobacco plants) are also important regarding light quality. Wherley et al. (2005) reported that high red far-red ratio promoted greater chlorophyll production in turfgrass by influencing phytochrome equilibrium. Leuchner et al. (2007) and Hertel et al. (2011) indicate that a reduction of the red far-red ratio is a strong indicator for competition in Norway spruce. In the present study, we have found that the red far-red ratio in the canopy is much lower under clear skies (Hertel et al., 2011), indicating a lower photomorphogenical “light quality” (sensu Smith, 1982) than under diffuse conditions.

## 4.2 Contrasting light attenuation under cloudy vs. clear skies

It is evident that there are profound differences in the transmissivity of solar radiation under the different sky conditions. The most important of these differences is the extent

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to which the direct sunlight is absorbed or reflected near the top of the canopy, shown by the attenuation patterns. This energy is therefore not available for photosynthesis lower down in the canopy. It is also shown, quite independently, by the extent to which the diffuse irradiation is relatively higher at the forest floor and by the distribution of ground-level data between transmission classes (data not shown here). The same phenomenon was shown by Morgan et al. (1985) for pine canopies and by Leuchner et al. (2005); Navratil et al. (2007) and Urban et al. (2007, 2012) for Norway spruce.

The vertical profile under sunny conditions demonstrated only a poor fit to the Beer–Lambert Law because of inhomogeneity. However, there was marked variation in the attenuation coefficient  $k$ , as was also shown by Norman and Jarvis (1974) and Lewandowska et al. (1977), who obtained similar  $k$  values to those reported here for the same species. Smith (1993) also states that a single extinction coefficient using the Beer's Law model cannot be used effectively to predict the light penetration in Douglas fir (*Pseudotsuga menziesii*). We presume that the explanation of this variation lies in the variable structure as one proceeds from the top to the bottom of the canopy: near the top the leaves are densely crowded on the stems, whereas near the bottom leaves are thin, sparse and attenuation is dominated by braches and stems (Norman and Jarvis, 1974; Schulze et al., 1977; Ford, 1982; Leverenz et al., 1982; Stenberg et al., 1998).

### 4.3 Gaps and sunflecks determine spatial patterns

There are two types of gaps that can occur in forest stands, firstly, natural gaps as the result of the clumping of leaves and stems i.e. the structure and orientation of the coniferous shoot and the needles they hold (Norman and Jarvis, 1974; Leverenz et al., 1982). The second type of gap is artificial, created through forest management (planting design and thinning regime).

Under clear skies the occurrences of gaps in the crown, which are sometimes short-lived (seconds to minutes) and wind-dependent (Federer and Tanner, 1966; Percy, 1990; Chazdon and Percy, 1991), are spots where the direct radiation beam, or some fraction of it, penetrates into the canopy (Fig. 1, lower schematics), sometimes as far

as the forest floor (Stenberg, 1995). They create highly illuminated areas where the incident light can in extremis reach higher values than above the canopy itself due to lateral illumination in the trunk space and a high proportion of scattering of radiation on the surrounding branches (Muller, 1971). Sunfleck spectra are similar to incident radiation (Endler, 1993; Combes et al., 2000; Leuchner et al., 2012) and may also be areas with transient higher temperatures, which in some cases may have physiological significance. Sunflecks also have red far-red ratios (Fig. 3e) close to those measured above the canopy (Reitmayer et al., 2001; Leuchner et al., 2012).

At the forest floor a complex spatial pattern of sunflecks is generally seen. The intensity of the sunflecks shows that almost always they contain substantial penumbral components (Stenberg, 1995). They appear not in the thinning lines but below the trees themselves: under clear sky conditions there is a lateral shift in the total penetrated radiation (Figs. 1 and 5a) compared with the diffuse skies (Figs. 4c, d and 5a, b). This phenomenon is visible because the tree planting lines in this forest happen to be oriented East–West, and at the prevailing solar angles the beam must pass through a large thickness of canopy in order to reach the ground. However, under overcast conditions solar radiation distribution follows the thinning pattern which highest radiation values recorded inside the thinning lines.

As these measurements were carried out around solar noon in summer, the path through the canopy was minimal and radiation values below the canopy are likely to be near their maximum. This high insolation distribution does not remain constant during the day due to the planting orientation and thinning pattern. These radiation distributions do of course change over the course of a clear day with highest values within the thinning lines early and later in the day, respectively (Reifsnyder, 1989; Leuchner et al., 2012). An aspect not investigated within the frame of the current study is the below canopy vegetation, which is also influenced by the type of forest management. At this site, the below canopy vegetation is much more pronounced in the thinning lines than below the canopy itself, as it is visible in the sidewise taken hemispherical image in Fig. 1.

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## 4.4 Implications for CO<sub>2</sub> exchange under such conditions

As shown in many studies (Gu et al., 1999, 2002; Urban et al., 2007, 2012; Dengel and Grace, 2010) diffuse radiation enhances photosynthesis in terrestrial vegetation. Urban et al. (2007, 2012) and Dengel and Grace (2010) hypothesised that optimal photosynthetic activity of the canopy is achieved under diffuse radiation (cloudy and overcast) conditions, when scattered light penetrates throughout the canopy, illuminating all the leaves to some extent and providing a more uniform distribution of light between the leaves.

Leverenz and Jarvis (1979, 1980) determined light response curves of this *Picea* species under controlled conditions and found light-saturation at around  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , a value which is often exceeded at the top of the canopy. Similar over-saturation values are visible in the current study. If the uppermost level of a canopy is experiencing an over-saturation of light and also encountering the highest shoot temperatures in the forest, it is possible that stress responses such as closure of stomata may occur (in this species stomata tend to close at high leaf-to-air vapour pressure difference (Grace et al., 1975; Neilson and Jarvis, 1975; Alton et al, 2007). Other stress responses such as photoinhibition are also possible (Powles, 1984; Krause, 1988; Long et al., 1994). Thus, along the sunfleck-pathway, such effects may contribute to under-activity of photosynthesis in relation to the level of incident radiation (Pearcy, 1990; Kanniah et al., 2012).

Given the poor penetration of direct radiation into the canopy, and the possible stress effects of PPFD values in excess of  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , we can now ask: what influence do sky conditions have on the photosynthesis of the canopy? In an earlier study on a very similar canopy we showed that light was used more efficiently under diffuse irradiance (see Fig. 7, taken from Dengel and Grace, 2010). In that study we found the quantum efficiency under direct radiation to be 28.6, but 41.0/50.1 under cloudy and overcast conditions, respectively. Moreover, tree ring analysis showed that

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diffuse radiation does not only influence gas exchange in the short-term (hourly, daily, monthly), but also influences long-term forest growth (Dengel et al., 2009).

*Author contributions.* S. Dengel has designed, carried out the experiment, processed the data and written the manuscript. J. Grace has contributed to the design of the experiment, the data interpretation and actively contributed to the manuscript writing. A. MacArthur has taken part in the training and experiment itself and has contributed to the data processing and manuscript writing.

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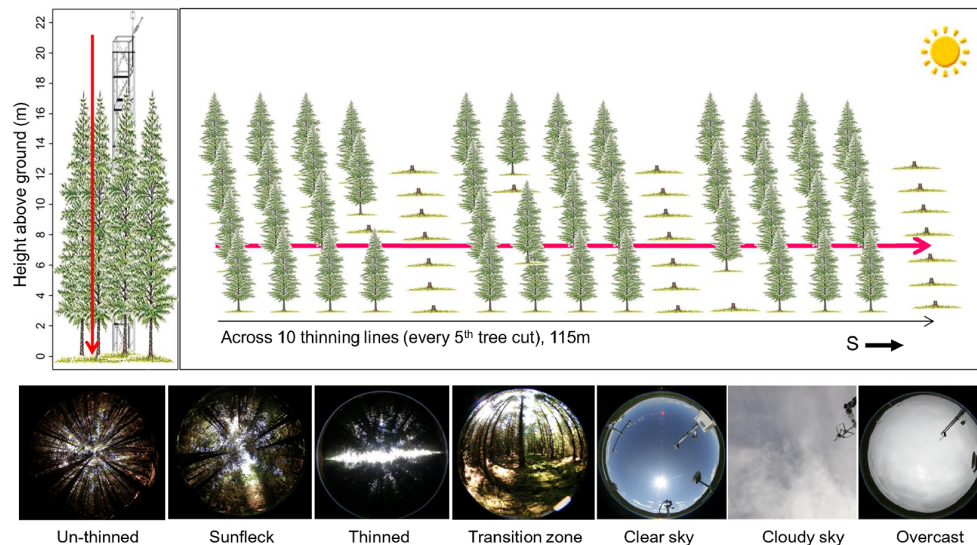
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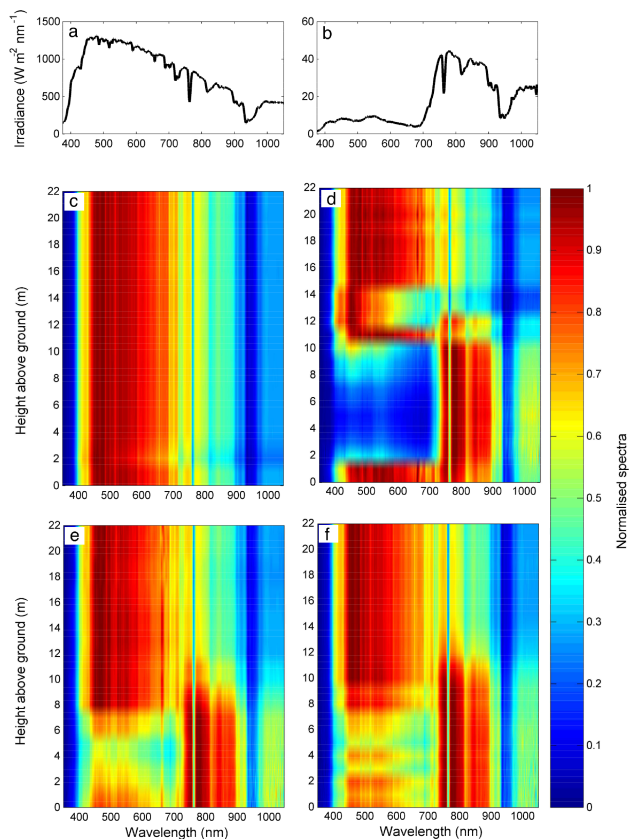
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**Figure 1.** Schematics of the Griffin forest planting and tree distribution properties, showing the thinning lines (the stumps are illustrated). Also shown are hemispherical images taken in the un-thinned as well as thinned area of the forest.

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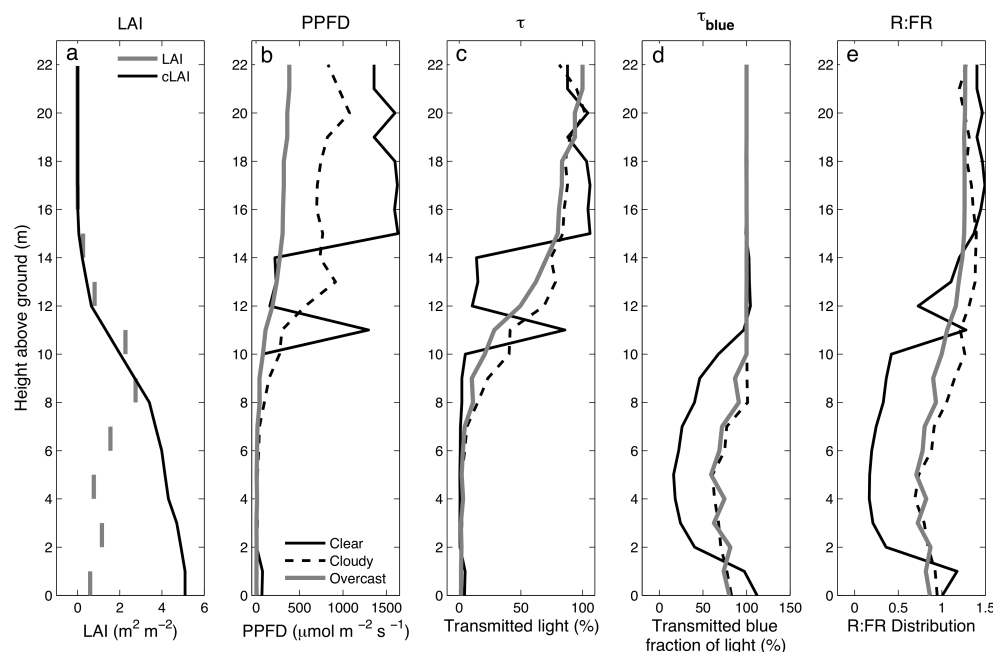



**Figure 2.** (a) The spectrum of solar irradiance above the canopy on a clear day; (b) spectrum below the canopy on a clear day; (c) visualisation of (a); (d) vertical profile on a clear day; (e) vertical profile on a cloudy day; (f) vertical profile on an overcast day. For the visualisations the data are normalised on a scale from 0 to 1.



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**Figure 3.** (a) Vertical distribution of leaf area index (LAI) and cumulative leaf area index (cLAI); (b) vertical distribution of photosynthetic flux density (PPFD) on a clear day (black line), cloudy day (pecked black line), overcast day (grey line); (c) the same as b but normalised as transmissivity; (d) transmissivity of blue light; (e) vertical profile of the red far-red ratio (R : FR).

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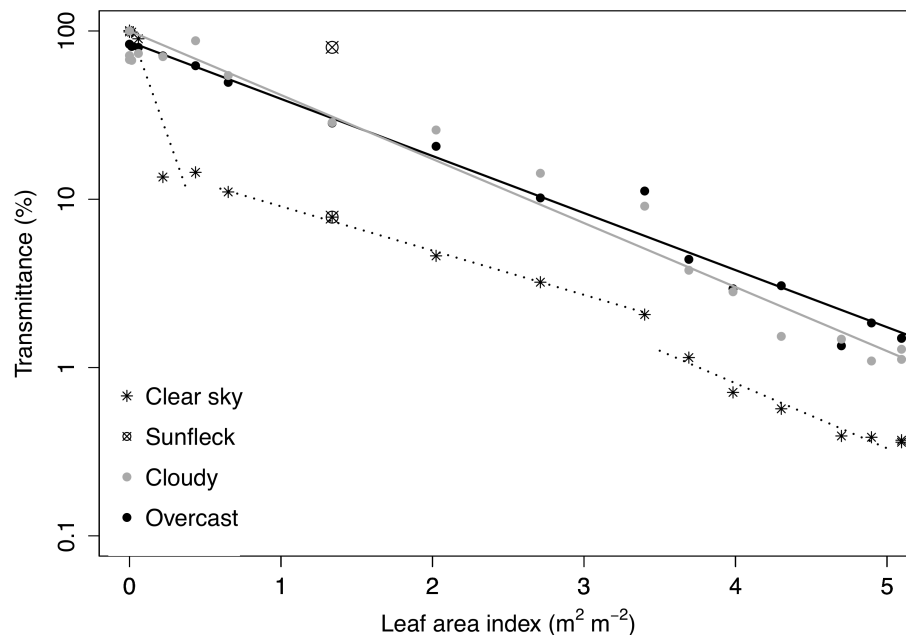
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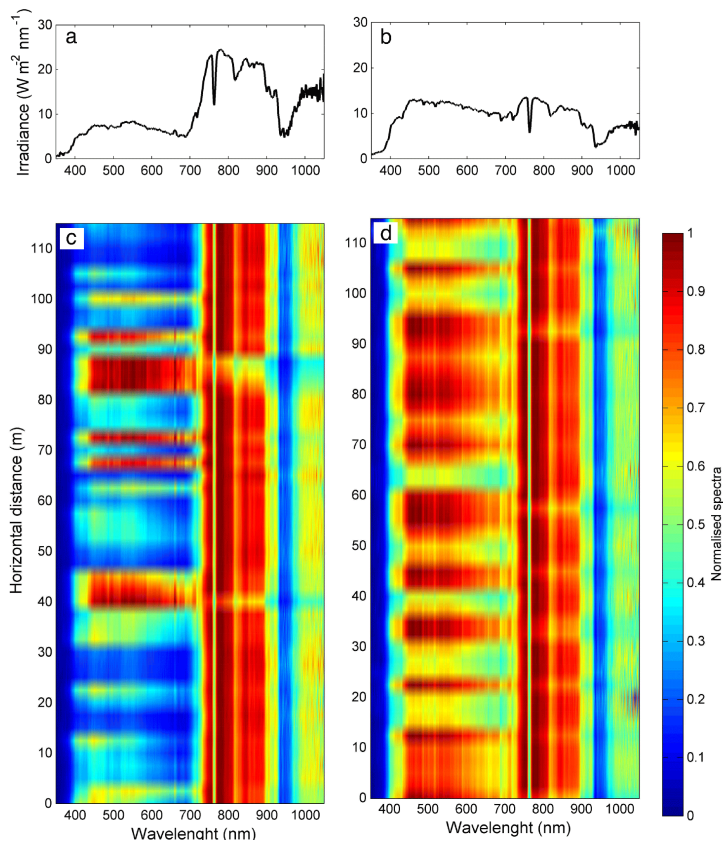
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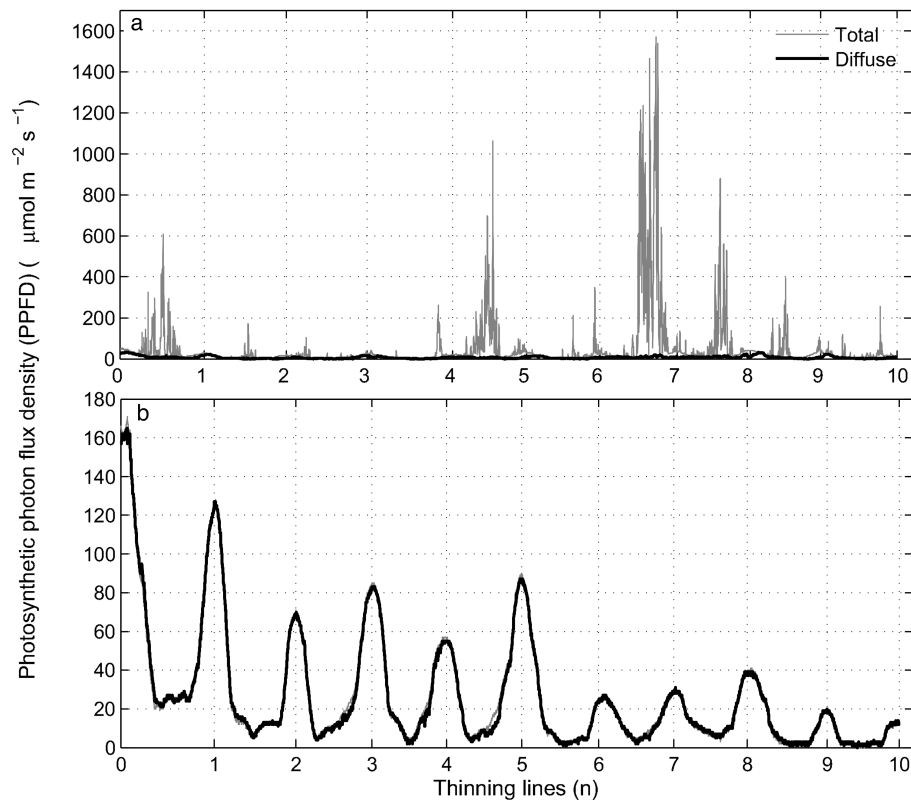
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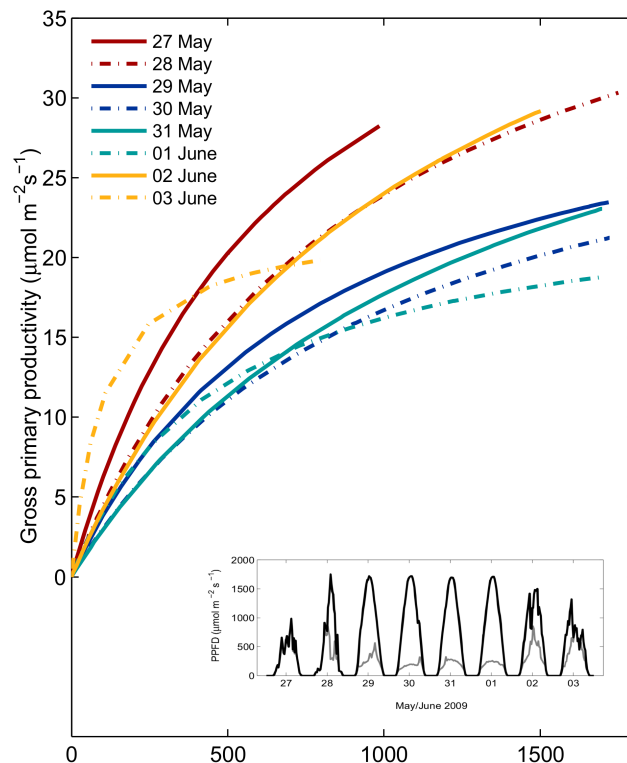
**Figure 4.** Transmissivity and attenuation curves according to the Monsi and Saeki (1953) method. Transmissivity and light attenuation through the forest canopy after applying the Beer–Lambert attenuation law. Stars and dotted lines represent clear sky, grey solid circles and line represent cloudy and solid black circles and line represent the overcast conditions.



**Figure 5.** (a) Typical spectrum at the forest floor on a clear day; (b) typical spectrum below the forest canopy on an overcast day; (c, d) are normalised spectra on the 115m transect for a clear and an overcast day, respectively.



**Figure 6.** Photosynthetic photon flux density (PPFD) distribution below the forest canopy under clear sky (a) and under overcast (b) conditions. Total (global) PPFD is marked as a solid grey line while diffuse PPFD measured simultaneously (using a shading strip) is marked as a solid black line. Thinning lines are every 11 m.



**Figure 7.** Light use efficiency (LUE) curves for eight consecutive days from Dengel and Grace (2010, Fig. 2). These show the day-to-day changes in light use efficiency when sky conditions change from overcast to cloudy to clear sky conditions. After four consecutive clear days (lowest light use efficiency) these are followed again by a cloudy and an overcast day. The scales represent the gross primary productivity (GPP) estimated for these days together with the corresponding photosynthetic photon flux density (PPFD). The insert is a modified reproduction from Dengel and Grace (2010), representing global radiation in black and diffuse radiation in grey.