1   <u>Cover Letter</u>

2   Response of the authors to the reviewer's comments

3   <u>Manuscript:</u> Transmissivity of solar radiation within a Picea sitchensis stand under various sky conditions

4   Sigrid Dengel (corresponding author)

5   The authors would like to thank the referees for their valuable remarks, constructive comments, and

6   careful corrections which helped to increase the overall quality of the manuscript.

7   All changes are marked in bold red throughout the revised manuscript.

8

9   Anonymous Referee #1

10   General comments

11   The manuscript by Dengel et al. describes measurements of the vertical and horizontal distribution of solar

12   radiation in a Sitka spruce plantation in Scotland under three different sky conditions in summer. Besides

13   the PPFD also the spectral distribution of incoming and transmitted radiation is investigated. Data sets

14   including spectral properties in forest stands are quite rare and thus valuable to get a better understanding

15   of the light climate in forests. The manuscript addresses this information gap in a technically well written

16   manner, but several major issues especially on the methodological side need to be clarified before

17   publication in Biogeosciences.

18   The main issue is that, as the authors state correctly, solar radiation distribution is very heterogeneous both

19   vertically and horizontally. Solar angle and biomass distribution play an important role as well as seasonal

20   properties of leaves. To address this large spatiotemporal variability a high spatial and temporal resolution

21   is crucial as well as a high sample size. Regarding the presented data it is not clear if measurements were

22   only performed on one day for each sky condition. If so, the general statements of the paper are not

23   appropriate since they only describe a snapshot at this time. A much larger dataset would be needed to

24   describe the high variability and to derive k-values etc.

25

Reviewer # 1 detailed comments	Response	Author's reasoning , comments
Introduction: - Some information on why Sitka spruce is an important species and worth investigating would be helpful.	Dealt with	We have now added a few sentences on why Sitka spruce is important. It is the most frequently planted commercial tree species in the UK and Ireland and very valued for its fast growth and high timber quality.
- 3828-8ff: The research questions stated here are not really what the paper is about. The paper shows a data set of measurements and does not address questions b) and c) in detail.	Dealt with	Thank you very much for pointing this out. We have now modified the objectives b and c and have improved the wording making the research questions much clearer.

Materials and Methods: - General: more information on the methodology needed: how many days, what days, what was the solar angle, what clearness index, what aerosol optical density (if available).	Dealt with	More information has now been provided, including number of days, solar angle and clearness index.
- For description of the light climate, especially in coniferous stands, a spherical approach would better describe the plant relevant radiation, but mostly cosine-corrected sensors such as in this study are used. This is especially relevant in higher latitudes such as Scotland with quite low solar angles throughout the year where this effect can play a large role. Some discussion about that issue would be informative.	Dealt with	We agree. Spherical sensors have never caught on in forest or crop science, perhaps because results would not be comparable with other papers. This point is now mentioned in the discussion. End of section 4.2.
- 3829-8: The instrument has 512 channels with resolution of 3 nm. That should cover a spectrum of 1536 nm, but only 700 nm (350 – 1050 nm) are measured. Please clarify the discrepancy.	Dealt with	We have now explained that the sensor doesn't work well at high wavelengths as the values become too noisy and also not relevant to the current study.
- 3829-10: Solar noon: what sun angle? What days?	Dealt with	We have now also included this information.
- 3829-11: Tower and forest floor scans were carried out back-to-back: In 3829-6 it is stated that above and below canopy measurements are done simultaneously, here it seems they were performed one after another.	Dealt with	The tower is used for the vertical scans and a transect along the forest floor is used for the horizontal evaluation which have been carried out back to back.
- 3829-16: was the influence of the tower and the tower gap somehow tested and quantified?	Dealt with	All measurements were carried out along the southern side of the tower where they are not influenced by the tower structure (shading) or by the artificial gap created during the tower setup. This information has now also been explained in the main text.

- 3829-19ff: A quantification of the definitions needs to be done, e.g., by fractional cloud cover and clearness index.	Dealt with	No cloud cover in eights estimations were carried out. We estimated the clearness index which is now also included in the main text.
- 3829-23: The normalization is a good and reasonable way for comparison of the different sky conditions. But also absolute values might be of large importance as also stated later in the discussion with the saturation of light. There might be more in the data than can be seen in the normalized values.	Dealt with	We agree. Therefore we have included more figures where irradiance is used as energy, using its corresponding units of mW/m2/nm.
- 3829-25ff: Was there an influence of the tower and the gap on the LAI measurements?	Dealt with	This should not be the case as we have measured away from the tower and on the opposite direction from the artificial gaps. This way the measurements were carried out along the same vertical path as the spectral measurements. Images were "halved" and mirrored in order to estimate the vertical distribution of LAI in the canopy. A sentence has now been included in the main text explaining this procedure a bit in more detail.
- 3830-22: Why was the band 430-470nm chosen as blue? This seems a bit of an arbitrary value.	Dealt with	We chose these wavelengths as they are those within "blue" light that evoke stomatal opening (see several citations within text). We have rephrased the original sentence to avoid any further confusion.
- 3831-14ff: Did the authors compare the measurements by the two different systems? Was there a high agreement? The caption contains the word "spectral", but it seems that the TRAC is not measuring spectrally but only the GER1500?	Dealt with	No, we did not compare the PAR measurements as the GER1500 is measuring as a one point measurement while the TRAC is measuring continuously at 32Hz. In order to give reliable comparison values one would need to carry out measurements with the GER1500 instrument at a higher resolution than 2.5m. We have now deleted the sentence that is misleading in this section and also modified the subtitle to include PPFD only.
- 3831-15f: Rather belongs into chapter 2.2.1	Dealt with	We have removed the information on spectral flux density below the canopy from this section so that it remains as a stand-alone section on below canopy PPFD.
- 3832-1: Here it is stated that measurements were done routinely throughout the year. Is	Dealt with	Those measurements will be reported elsewhere. We have removed the sentence informing the reader about the regular measurement and modified the sentence to

this data shown somewhere? When was it measured? Which data is used for which results in this manuscript? This needs to be clarified.		include only those measurements carried out as part of this study.
Results: - 3832-19: The shift is not from the visible (380-780 nm) to the far-red/infrared region, but at 700nm which still is in the visible region.	Dealt with	This sentence has now been modified to clarify this issue.
- 3832-23: The mean canopy height is 18.5m, but effects start only at 11m. This can happen when only a profile in one location is taken. Thus it cannot be generalized, because if the profile is taken right next to the stem of the trees, it would look completely different. Thus a higher sample number is needed if general conclusions want to be drawn.	Dealt with	At 11 m above canopy we encountered a sunfleck, while the canopy is closing at around 14-15 m above ground. This effect is well visible in all figures related to the vertical measurements.
- 3833-6: The statement that much less of PAR is entering the canopy under clear sky compared to overcast and cloudy only holds for normalized values. But in absolute terms it might still be larger as can be seen in Fig. 3.	Dealt with	PAR is larger within the canopy in clear conditions only in regions surrounding sunflecks or along the forest floor. We have included a further figure in Fig. 3 showing from 5 m above the ground downwards to show this effect.
- 3833-11: approximately 1600 umol/m2/s; why is the real value not given? If only one measurement is considered, the information that can be gained from these plots is very limited.	Dealt with	We reported approximate values as all measurements were carried out within 2 hours. This means small changes in exact PAR can occur. Furthermore all instruments measuring PAR at that location showed similar values around 1600 umol/m2/s. The probability that measurements can be taken again in exact location (time and space) under exact the same solar radiation intensity is rather small. Therefore we limited the data used in the current study to show a snapshot showing 3 distinctive sky conditions and a difference in PAR of approx. 600 umol/m2/s.
- 3833-22ff and Fig. 4: The relationships and k-values cannot be derived from one	Dealt with	We do agree. We are not generalising this, we just show what an effect these three conditions are having on estimating an attenuation coefficient.

measurement only, many measurements at different solar angles are needed for that.		We have extended some of the sentences to make this clearer.
Discussion: - 3835-11: I would rather suggest that the laterally incoming diffuse radiation that makes up a much higher fraction under overcast conditions is responsible for the blue enhancement.	Dealt with	We have added a further sentence stating that the directional properties of direct versus diffuse radiation may also have a role in explaining this difference in blue light distribution.
- 3835-19: No generalization can be made, if data are only from one day.	Dealt with	The sentences has been corrected. By "this" we meant Smith's results. "this" has been replaced to read correctly "If Smith's results…" Generalisation cannot be made from one measurement only, we do agree.
- 3835-22 – 3836-6: This information is not really new.		We do not claim it to be.
- 3836-7 – 3836-22: This paragraph would fit better in the introduction part. In the discussion only the relevant aspects regarding the direct results of the authors should be included.	Dealt with	This paragraph has now been moved to the introduction section and modified accordingly.
- 3836-22: Not possible from one day of data.		This was found for both cloudy and overcast days, in Norway spruce and also described in Smith's review.
- 3837-8: Derivation of k-values from one measurement profile not possible. - 3837-25ff: Exactly that is why a high number of samples with high spatiotemporal resolution are needed.	Dealt with	We have not tried to standardise the light extinction coefficient, we have illustrated how one is estimating the value and what a difference a change in sky condition it makes.
- 3839-1ff: The entire chapter seems to have nothing to do with the results presented. Were CO2 exchange or photosynthesis rates measured on the sampling days?		Yes, CO_2 exchange measurements were carried out but due to power loss, corrections applied to the data, quality control and low turbulence gaps up to half a day do exist on those days. We decided to avoid showing incomplete data and have therefore included data from the only other Sitka spruce forest (250km away - same species, same age, plantation and very similar CO2 exchange and less gaps in the data). By including these measurements we represent the bigger picture of how forests react to changes in sky

		conditions. The instruments used here (GER-1500, TRAC, laptops and photo camera) were running of their internal batteries.
- In the discussion a lot of general conclusions are stated that cannot be drawn from the underlying data set.		We have not generalised our results but have stated in several places that if other published results are general we may conclude that ours are as well.
- The research questions from the introduction are not well answered in the discussion.	Dealt with	We have reformulated our research questions and hope to have dealt with them in the appropriate manner and extend.
Figures: - Fig. 5: Why is this a typical spectrum? Only one day measured!	Dealt with	There are many scans carried out under clear conditions that all have the same spectral distribution. This can also be found in several publications. The intensity at nm scale does wary but the general spectral features remain the same.
- Fig. 7: In the current format not relevant for paper.		We believe it does improve the overall quality of the manuscript as it does deliver a "big picture" visualisation showing how CO_2 exchange of Sitka spruce is influenced by a change in sky conditions on eight consecutive days, including overcast, cloudy and 4 consecutive clear days.
Technical corrections - 3826-7: "a" leaf area index - 3837-12: Smith (1983) also "stated"	Dealt with	Both have been corrected.

1

2

1	<u>Cover Letter</u>
2	Response of the authors to the reviewer's comments
3	<u>Manuscript:</u> Transmissivity of solar radiation within a Picea sitchensis stand under various sky conditions
4	Sigrid Dengel (corresponding author)
5	The authors would like to thank the referees for their valuable remarks, constructive comments, and
6	careful corrections which helped to increase the overall quality of the manuscript.
7	All changes are marked in bold red throughout the revised manuscript.
8	
9	Anonymous Referee #2
10	The observations were apparently well planned and executed but the manuscript lacks some key
11	methodological details.

Reviewer # 2 detailed comments	Response	Author's reasoning , comments
In the Methods section, please add the following details: - How many clear, cloudy and overcast days were observed?	Dealt with	As previously stated measurements introduced in this study were carried out on three days only. We believe by averaging over several days introduces biases as solar radiation (intensity and clearness index) would be not the same, the solar angle shifted and the exact location within the canopy not reproducible. Also measurements are influenced by wind. We have added an explanatory sentence that this study is a snapshot and days shown differ in 600 umol/m2/s, which is a fortunate coincidence.
- How long did each observation last?	Dealt with	Each measurement represent 10 (instrument internally averaged) measurement that have been repeated three times resulting in an average of 30 measurements per data point (as stated in the method section). Each measurement suite (tower, transect and TRAC measurement) took 20-30min each.
- For each sky type, how were measurements from different days processed, e.g., did you average them? If so, how?	Dealt with	Please see above.
I also find Figure 2 confusing. As the figure caption indicates, plot (c) is a visualization of plot (a) which is the solar spectrum above the canopy in a clear day. But how come the y axis of plot (c) is height above ground? The pattern in plot (c) does not appear to be	Dealt with	We agree, this figure is confusing. It has therefore been modified now. In addition we have added two extra figures showing separately the typical solar spectrum and colour coding as well as well as the main spectral features.

uniform along the y axis so it must not be an attempt to match the rest of the plots.		
Also it needs to explain, with an equation, to show how the normalization on a scale from 0 to 1 is done. Is the denominator the total energy across the full spectrum for a given height?	Dealt with	We have now included the equation showing how we have scaled the data, which is a standard way to normalise data (Normalised data = (x-min(x))/(max(x)-min(x)).
Because there are no error bars on the figures, I assume the authors display results from measurements in a single day. Then it will be necessary to explain why these particular single days are chosen.	Dealt with	Here we have shown the averaged values of the measurements mentioned above. The probability that measurements can be taken again in exact same location (time and space) under exact the same solar radiation intensity is rather small. Therefore we limited the data used in the current study to show a snapshot showing 3 distinctive sky conditions and a difference in PAR of approx. 600 umol/m2/s between clear and cloudy and cloudy and overcast. We have added an explanation in the main manuscript mentioning this reasoning. In order to carry out all these measurements we had to use six instruments (2x GER, 2 laptops, the TRAC instruments and the camera for the sky) with often at least one failing half way through the measurements.
It might be informative to point out in the plots some of the key spectral features.	Dealt with	We have modified Fig 2 (now fig 3) and have included a further figure showing the typical solar spectrum and the main spectral features. We have also included the spectra from all conditions above the canopy to show the little variation in spectral distribution according to time of year and sky condition.

1

2

<u>Cover Letter</u>

Response of the authors to the reviewer's comments

<u>Manuscript:</u> Transmissivity of solar radiation within a Picea sitchensis stand under various sky conditions

4 Sigrid Dengel (corresponding author)

5 The authors would like to thank the referees for their valuable remarks, constructive comments, and

6 careful corrections which helped to increase the overall quality of the manuscript.

7 All changes are marked in bold red throughout the revised manuscript.

8

9

10 Anonymous Referee #3

11 Dengel et al. describe a study on light extinction in a managed Picea sitchensis stand in Central Scotland,

12 addressing changes in the spectral distribution of light, which has a potential impact on photosynthesis.

13 They present a comprehensive set of measurements quantifying the horizontal and vertical variations in

14 spectral distribution, and focus on the role that sky conditions play in determining this distribution.

15 Overall, the study is concise and clearly written, and the topic is relevant for publication in Biogeosciences.

16 Relatively few data sets exist that discuss spectral changes both horizontally and vertically, and I consider

17 this paper suitable for publications once a few remarks have been addressed.

18

Reviewer # 3 detailed comments	Response	Author's reasoning , comments
Major comments: - p. 3828, l. 8: Here, three objectives of the study are listed, but for (b) and (c), it is unclear how "importance" is defined: The authors do not measure the importance for photosynthesis in the study. Rather, the study determines whether spectral differences exist (b), and how gaps affect the spectral distribution (c).	Dealt with	We have reformulated our research questions and hope to have dealt with them in the appropriate manner and extend.
- The discussions paper addresses light distributions in great detail, but does not show the impact of these changes on photosynthesis from measurements. This is not a flaw as such, but the authors seem to try and compensate for that by adding Fig. 7	Dealt with	We believe it does improve the overall quality of the manuscript as it does the deliver a "big picture" visualisation showing how CO_2 exchange of Sitka spruce is influenced by a change in sky conditions using eight consecutive days as an example, including overcast, cloudy and 4 consecutive clear days. Unfortunately the original data measured on those days in Griffin are rather gappy and do

in the last sentence of the paper, which comes a bit out of the blue. Also, the figure is referred to as "taken from Dengel and Grace, 2010" (p. 3839, l. 25), but, although the data probably originate from there, the figure as such is not given in there. If the authors want to address the impact of sky conditions on photosynthesis, I think this figure should be placed in the results section and should be described and discussed properly, and the measurements for this should be described (briefly) in the methods section (with reference to Dengel and Grace, 2010).		not really contribute to the "big picture" intended with this section. The advice given has been followed up and additional information added to the method, results and discussion section.
- p. 3833, l. 20: The extinction plot in Fig. 4, used to determine Beer-Lambert extinction coefficients, is interesting, but I have some doubts about the discussion of the clear sky curve. The light extinction as described by Beer-Lambert law should be considered a canopy-integrated description representative for a somewhat larger area, where beams of light can get absorbed in the canopy at different heights (depending on the LAI distribution). Determining the extinction coefficients from the observations in this study works reasonably well for conditions with diffuse light only, because of the absence of a direct beam. However, for the clear sky case, the beam is intercepted relatively high up in the canopy, after which there is no direct radiation left (except for the observed sun fleck at app. 11 m height). The slope in Fig. 4 observed for the remainder of the curve is hence representative for the diffuse		We do agree. Strictly, Beer-Lambert's law is only applicable to a homogenous medium such as a solution of chlorophyll, but it has been applied to canopies since the 1960s (from Monsi and Saeki onwards). Yes, it works better for diffuse light because all beam-angles are represented fairly equally, unlike direct radiation when sunlight comes from more or less one direction and it can sometimes shine through a single gap onto the sensor. Further data integrating spatially and temporally would of course reduce the uncertainty in our estimated k-value. We acknowledge this weakness, and we do discuss it.

fraction of the radiation occurring on a clear sky day. This binary behaviour for an individual measurement is not captured by Beer-Lambert's law, but when integrated over a larger area (where interception can happen at any height, and some beams can penetrate deeper), it still holds. Hence, the extinction coefficient could be determined properly only if a larger set of measurements would exist.		
Minor comments and technical corrections: - p. 3826, l. 7: replace "an" with "a"	Dealt with	This has been now corrected.
- p. 3827, l. 26: It is unclear what "this" refers to, I presume it is the occurrence of sunflecks?	Dealt with	We mean the response to sunflecks as in saturation of photosynthesis or possibly photo-inhibition. This has been now added to the sentence
- p. 3828, l. 9: Please add the unit to LAI for consistency (you do so in l. 23).	Dealt with	This has now been corrected, also in the abstract.
- p. 3828, l. 23: Replace "are" with "were"	Dealt with	This has now been corrected.
- p. 3829, l. 10/19: "All spectral measurements": How many measurements were performed, and how were these distributed over clear days, cloudy days and overcast days?	Dealt with	Please see above for number days and measurements per data point. As stated before there are one day per sky condition. Please see above explanation as the reasoning to use such a limited number of data. There are 23 measurement point along the tower and 47 along the forest floor.
- p. 3829, l. 23: Please add that the normalization was done relative to the above canopy measurement.	Dealt with	No. The normalisation has been done by applying the standard method (Normalised data = (x-min(x))/(max(x)-min(x)), which is a standard procedure. If we would have used the above canopy values we would have estimated the transmissivity, which is shown in Fig 3 (now Fig 4). We have now included this equation as well to avoid any further confusion.
- p. 3830, Eq. 1: You use E rather than E in Eq. 2, it would be more correct to do so here as well.	Dealt with	Equation 2 (now 3) has been modified accordingly.
- p. 3832, l. 1: I am unsure what "frame" refers to here. Do you mean within the same period?	Dealt with	We mean those measurements that are part of the current study. (TRAC measurements were carried out throughout the year). This sentence has been modified to appear clearer.

- Fig. 2: It is unclear to me why panel (c) is displayed. I guess the top of panel (d) should resemble (a) (and the bottom of (d) should resemble (b))? If right, panel (c) is not necessary.	Dealt with	This figure has been modified and the c panel removed. In order to clarify this we have added another figure which is now figure 2.
- p. 3832, l. 24: The term "shifts" is somewhat misleading here: There is not more infrared radiation - rather, there is less absorption in this band than in the others, which makes the infrared relatively more important. Energy is not shifting from one wavelength to another.	Dealt with	We agree. We have changed the wording of this sentence to read better now.
- Fig. 3: Are the clear/cloudy/overcast measurements shown here all one-day measurements? And do more measurements exist? In the latter case, it may be interesting to show how these curves vary between days with comparable sky conditions.	Dealt with	Unfortunately yes. The probability that measurements can be taken again in exact same location (time and space) under exact the same solar radiation intensity is rather small. Therefore we limited the data used in the current study to show a snapshot of these conditions and a difference in PAR of approx. 600 umol/m2/s between clear and cloudy and cloudy and overcast. We have added an explanation in the main manuscript mentioning this reasoning. In order to carry out all these measurements we had to use six instruments (2x GER, 2 laptops, the TRAC instruments and the camera for the sky) with often at least one failing half way through the measurements and were rather unlucky. Also the weather conditions did not allow us to carry out the measurements as the location is 160km from the home institute away and three people involved when carrying out the measurements.
- p. 3834, l. 2: If lateral illumination occurs, as the authors suggest, it should be visible in the PPFD near the surface as well. This seems to be the case for clear sky, but the scale of Fig 3b does not allow to determine this for the other conditions.	Dealt with	Unfortunately this is only seen clearly in the clear sky conditions. We have added an insert in Fig 3 (now Fig 4) to highlight this.
- p. 3835, l. 2: "...closely resembling the "background" values shown in Fig. 6a, although 50% higher.": Would it be possible		Unfortunately this is not possible without having to interpolate the data to a fixed number of measurement points in each transect sector. The TRAC instrument does measure continuously at 32 Hz so that there

to plot the background (diffuse) part from Fig. 6a also in Fig. 6b to illustrate this?		are not exact same number of data points in each sector. We believe Fig 6b and 6a are clear enough to show the different diffuse values and that (b) is much higher. Both diffuse values show the thinning pattern.
- p. 3837, l. 17: check the spelling of "branches" - p. 3838, l. 17: replace "which" with "with" - p. 3839, l. 15: Closing brackets are missing	Dealt with	All these typos have been corrected.

1

2

3

4

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

Sigrid Dengel [1,*], John Grace [1], Alasdair MacArthur [2]

[1]{ School of GeoSciences, Crew Building, University of Edinburgh, EH9 3FF, UK }

[2]{ NERC Field Spectroscopy Facility (FSF), School of GeoSciences, The Grant Institute, University of Edinburgh, EH9 3JW, UK.}

* Current address:

Department of Physics, University of Helsinki, P.O. Box 48, FI-00014, Finland;

Correspondence to: S. Dengel (sigrid.dengel@helsinki.fi)

Ph. +358 (0)50 415 4736

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 ($\pm$ 1h)) 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 a leaf area index of approximately 5.2 m^2 m^{-2}). We recorded vertical profiles of radiation penetration (from 350 nm 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 and 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 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. **Here, we introduce a study carried out at one out of only two Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forest research sites in the UK and Europe where long-term forest growth and CO_2 exchange measurements are carried out (Dengel and Grace, 2010). This species is a non-native species to the UK/Europe, but highly valued for its fast growth and timber quality. In the UK and Ireland it is the most frequently planted commercial tree species.**

The vertical profile of irradiance through a plant canopy is often approximated by the Beer-Lambert equation of light extinction first introduced by Monsi & 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 **response (saturation of photosynthesis, stomatal regulation or possibly photo-inhibition)** 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. **Smith (1982) indicated 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.** 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). **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 by altering their allometry. Low red far-red ratio may also 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. 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.**

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 dense Sitka spruce canopy under cloudy and diffuse conditions; (b) to what extent are the light climates within the canopy spectrally different under clear, cloudy and diffuse skies and (c) how much is the light climate modified by the standard management interventions.**

2. MATERIALS AND METHODS

2.1. Site description

Measurements were carried out in 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 m^2 m^{-2}. All meteorological and micrometeorological measurements were 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).

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: W m^{-2} 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**, although the post-processing methods interpolate data to 1 nm intervals (Walker and MacLellan 2009). The performance of this instrument declines in the infra-red and so we restricted our measurements to the waveband 350 - 1050 nm.**

All spectral measurements were carried out around solar noon ($\pm$ 1 h) during summer of 2008 **of which three days are shown here as a 'snapshot' (27 May, 22 July and 23 September with max solar angles of 53.5°, 53.8° and 33.1°, respectively). These days were chosen as they show three distinctive sky conditions and a difference of approximately 600 µmol m^{-2} s^{-1} in Photosynthetic**

Photon Flux Density between the measurements. Adding more days would increase the temporal distribution of the data, but at the same time it would also add a bias as measurements could not be taken in exactly the same location under the same solar radiation intensity. The solar spectrum has a pronounced diurnal variation and so we carried out measurements at midday. 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 **variation** were measured at 1 m height with 2.5 m intervals **along a transect**. Three measurements were carried out at each point of which each measurement represents an average of 10 internally averaged scans. Measurements were carried out under (i) clear sky conditions **(clearness index of around 0.75 over the measurement period)**, (ii) cloudy conditions (we selected conditions with altostratus clouds to guarantee minimal changes in cloudiness over the measurement period **(clearness index of 0.60)** and (iii) on a completely overcast day **(clearness index of 0.23)**. In all cases light conditions above the forest canopy did not change significantly over the measuring period. **The spectral distribution of the incoming solar radiation also did not show any significant differences as can be seen in Fig. 2 (a & b).** To facilitate comparison, data were normalised to the range 0 to 1 **where appropriate**. **In order to scale the data we have applied the following scaling method:**

$$ND_i = \frac{x_i - \min(x)}{\max(x) - \min(x)} \tag{1}$$

where $x = (x_1, \ldots, x_n)$ and ND_i is the ith normalised data.

2.2.2. Leaf Area Index

The vertical distribution of Leaf Area Index (LAI) was estimated from hemispherical images taken every 2 metres down the tower using a Nikon digital camera (Coolpix 4500, 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). **Images were taken along the same path as the spectral measurements (south facing, opposite side from the artificial gap/thinning line),**

halved and mirrored in order to avoid tower structural elements being recorded as part of the canopy. 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 section 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 **converting** irradiant energy (W m^{-2} nm^{-1}) to quanta (μmol m^{-2} s^{-1}) and integrating from 400 - 700 nm (Combes *et al*. 2000) (eqn. 1):

$$\mathrm{PPFD} = \int_{\lambda=400}^{\lambda=700} Eh\upsilon \left(\delta\lambda \right) \tag{2}$$

where the limits of wavelength (λ) were 400 and 700 nm. *E* is the spectral irradiance, *h* is the Planck constant and υ is frequency, given by $1/\lambda$. The wavelength increments used for the numerical integration were 1 nm. **Blue light is often indicated as being 400 – 500 nm but we chose 430 - 470 nm as it has been shown that those wavelengths evoke stomatal opening (Kuiper 1964; Mansfield and Meidner 1966; Zeiger and Field 1982; Karlsson 1986).**

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):

$$R\!:\!FR = \dfrac{\int_{655\,nm}^{665\,nm} Ed\lambda}{\int_{725\,nm}^{735\,nm} Ed\lambda} \tag{3}$$

where E 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 PPFD

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 were carried out 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 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).

2.2.5 Canopy CO_2 exchange under such conditions

As mentioned above, there are only two Sitka spruce forest sites with long-term canopy CO_2 exchange measurements: Griffin and Harwood forest (in Northern England). CO_2 exchange at canopy scale were carried out in Griffin forest as described in Clement et al. (2007) and Dengel and Grace (2010). Corrections and quality control are applied to data including exclusion of data recorded at low turbulence, reducing the data availability (also for the three represented days). Therefore data from the other Sitka spruce forest (250 km away, same age, spacing, plantation, etc.) were included in the current study in order to provide a "big picture" on how canopy CO_2 exchange of forests are affected by changes in sky conditions and hence light distribution within the forest canopy. Eight consecutive days were included here, as already introduced in Dengel and Grace (2010).

1

2

3 **3. RESULTS**

4 Fig. 1 illustrates the schematics of the forest, along with visual impressions of canopy structure and

5 fish-eye photographs of the canopy and sky **taken during the measurements**. This forest structure

6 is typical of many commercial coniferous plantations. **All above-canopy irradiance spectra display**

7 **the expected features (Fig 2c)**: they have their peak spectral irradiances in the blue region at around

8 480 nm; both oxygen absorption bands are clearly seen (687 nm and 761 nm), as are the water

9 absorption bands at around 730 nm and 940 nm.

10 **Below the canopy the absorption pattern is changing, showing high absorption in the PPFD**

11 **region while little absorption occurs from 700 nm onwards. Fig. 3a** visualises the spectral/energy

12 change that occurs once radiation penetrates the forest canopy **on the clear sky day**. An abrupt shift

13 is observed at the height where the canopy is closed, with a large sunfleck becoming visible at the

14 heights of around 11 m above ground **in this dataset**. Hereafter the majority of the energy **appears**

15 **in** the infrared region. Once radiation reaches the forest floor which is illuminated partly by sunflecks

16 and by large open parts of the canopy this shift reverses to similar distributions as seen above and

17 close to the top of the canopy. Fig. **3b** and Fig. **3c** represent the spectral flux density recorded in

18 cloudy and overcast conditions, respectively. Here, under both sky conditions, high energy levels

19 within the blue region of the spectra remain conserved much lower/deeper into the canopy, with

20 overcast conditions showing a more even distribution. Within the canopy (around 8 m above ground)

21 some important differences can be noted between the sky types. Under both cloudy and overcast

22 conditions there is relatively more blue radiation **although in absolute irradiances this isn't always**

23 **true.** Much less of the incoming radiation is in the photosynthetically -active part of the spectrum

24 (400 - 700 nm) in the case of the clear sky compared with the cloudy/overcast conditions. **Fig. 3 (d,**

25 **e & f) show the energy distribution at 2 m above the forest floor in absolute irradiances showing**

26 **very similar values for clear and overcast. Higher in the canopy, at 5 m above the ground (Fig.**

27 **4) this pattern is changing with less energy in the blue fraction under the clear sky.**

28

29 The spectra were re-expressed as quanta and numerically integrated between 400 and 700 nm to yield

30 values of PPFD (eqn. **2**). Above the canopy on top of the 22 metre tall tower PPFD was approximately

31 1600 µmol m^{-2} s^{-1} on the clear day, 1000 µmol m^{-2} s^{-1} under cloudy conditions and 400 µmol m^{-2} s^{-1}

32 when overcast, **representing three distinctive sky/clearness conditions separated by approx. 600**

33 **µmol m^{-2} s^{-1} between conditions**. The mean and cumulative LAI (Fig. **5**a) and PPFD distributions

34 (Fig. **5**b) down the vertical profile, and the transmissivity values associated with PPFD (Fig. **5**c) and

blue light (Fig. **5**d) are shown as attenuation curves in Fig. **5** respectively. The attenuation of direct radiation ('clear') is abrupt in the top-most part of the canopy (14-15 m) (Fig. **5** b, c). The canopy is inhomogenous and at around 11 m above the ground 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 **5** b, c). These data may also be presented as a classical Beer-Lambert log-plot (Fig. **6**), wherein the slope may be used to yield **an estimate of** the attenuation coefficient (*k*). The classical Beer-Lambert approach applied to diffuse conditions (Fig. **6** –solid grey and black line) yields *k* values of 0.79 and 0.81 respectively. However, under clear sky conditions this approach is unreliable **and cannot be used here,** 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).

Fig. **5d** 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. **5**e – 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 **5**e. 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. **7**) and then with the TRAC device (Fig. **8**). The spectral flux density, illustrated in Fig. **7** shows clearly the thinning lines. 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. Fig. **7a** and **7b** illustrate 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. **8**), 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. **8**a), often reaching photon flux values of several hundred μmol m^{-2} 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 μmol m^{-2} s^{-1}. Overcast conditions (Fig. **8**b) show highly regular behaviour, closely resembling the 'background' values shown in Fig. **8**a, although **much** higher.

As a "big picture" overview on how canopy CO$_2$ exchange and the light use efficiency (LUE) in Sitka spruce is behaving under such conditions we included data from eight consecutive days from Harwood forest. Canopy CO$_2$ fluxes from Harwood forest show generally the same flux variability and range throughout the year as in Griffin forest (data not shown here). These eight days 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 and are evident in Fig. 9.

4. DISCUSSION

The study introduced here carried out in 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-Gutuérrez 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). **Differences in the directional properties of direct versus diffuse radiation may also have a role in explaining this difference.** 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,

23

red light being ineffective; thus, if **Smith's** 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 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). 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 versus 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 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 **the canopy's** inhomogeneity. **Further data integrating spatially and temporally would of course reduce the uncertainty in our estimated k-value. T**here was marked variation in the attenuation coefficient k, **also in the data** 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 **stated** 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 part of 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 **branches** and stems (Norman and Jarvis 1974; Schulze et al. 1977; Ford 1982; Leverenz et al. 1982; Stenberg et al. 1998).

One obvious difference between clear sky radiation and overcast skies is the directional distribution of the radiation. From a general consideration of the angular distribution of brightness of an overcast sky (Grace 1971), it is apparent that proportionately more energy from low-angle rays of skylight will penetrate the canopy. Such low-angle light may be important in the photosynthesis of vertically aligned leaves but this effect will be under-estimated by a cosine-corrected horizontal sensor. For this reason, spherical sensors have sometimes been advocated for in-canopy use (Biggs 1986), as they more closely resemble the near-spherical distribution of leaf angles in a forest canopy.

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; Pearcy 1990; Chazdon and Pearcy 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 compared with the diffuse skies. 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 **with** 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.

4.4.   Implications for CO_2 exchange under such conditions

As shown in many studies (Gu et al. 1999, 2002; Urban et al. 2007, 2012 and 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 µmol m^{-2}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, North and Los 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 µmol m^{-2}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 **9**, **insert is modified** 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 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).

6. AUTHOR CONTRIBUTION

SD has designed, carried out the experiment, processed the data and written the manuscript. JG has contributed to the design of the experiment, the data interpretation and actively contributed to the manuscript writing. AM has taken part in the training and experiment itself and has contributed to the data processing and manuscript writing.

7. REFERENCES

Alton, P.B., North, P.N., Los, S.O. The impact of diffuse sunlight on canopy light-use efficiency, gross photosynthetic product and net ecosystem exchange in three forest biomes. Global Change Biology 13, 776-787, 2007.

Ballaré, C.L., Scopel, A.L., Sánchez, R.A. Photocontrol of stem elongation in plant neighbourhoods: effects of photon fluence rate under natural conditions of radiation. Plant, Cell and Environment 14, 57-65, 1991.

Biggs W. Radiation Measurement. Advanced Agricultural Measurement 111, 3-20, 1986.

Cape, J.N., Percy, K.E. Environmental influences on the development of spruce needle cuticles. New Phytologist 125, 787-799, 1993.

Carter, G.A., Knapp, A.K. Leaf optical properties in higher plants: linking spectral characteristics to stress and chlorophyll concentration. American Journal of Botany 88, 677-684, 2001.

Casal, J. J. Photoreceptor signaling networks in plant responses to shade. Annual Review of Plant Biology, 64, 403-427, 2013.

Chazdon, R.L., Pearcy, R.W. The Importance of Sunflecks for Forest Understory Plants. BioScience 41, 760-766, 1991.

Chen, J.M., Blanken, P.D., Black, T.A., Guilbeault M, Chen S. Radiation regime and canopy architecture in a boreal aspen forest. Agricultural and Forest Meteorology 86, 107-125, 1997.

Chen, J.M., Cihlar, J. Quantifying the effect of canopy architecture on optical measurements of leaf area index using two gap size analysis methods. Geoscience and Remote Sensing, IEEE Transactions on 33, 777-787, 1995.

Chen, J.M., Rich, P.M., Gower ST, Norman JM, Plummer S. Leaf area index of boreal forests: Theory, techniques, and measurements. Journal of Geophysical Research-Atmospheres 102, 29429-29443, 1997.

Clement, R. Mass and energy exchange of a plantation forest in Scotland using micrometeorological methods. PhD Thesis. School of Geosciences, University of Edinburgh, 2004.

Clement, R., Moncrieff, J.B., Jarvis, P.G. Net carbon productivity of Sitka Spruce forest in Scotland. Scottish Forestry 57, 5-10, 2003.

Combes, D., Sinoquet, H., Varlet-Grancher, C. Preliminary measurement and simulation of the spatial distribution of the Morphogenetically Active Radiation (MAR) within an isolated tree canopy. Annals of Forest Science 57, 497-511, 2000.

Corre, W. Growth and morphogenesis of sun and shade plants. II. The influence of light quality. Acta Botanica Neerlandica 32, 185-202, 1983.

Dengel, S., and Grace, J. Carbon dioxide exchange and canopy conductance of two coniferous forests under various sky conditions. Oecologia, 164(3), 797-808, 2010.

Dengel, S., Aeby, D., and Grace, J. A relationship between galactic cosmic radiation and tree rings. New Phytologist, 184(3), 545-551, 2009.

Endler, J.A. The Color of Light in Forests and Its Implications. Ecological Monographs 63, 1-27, 1993.

Escobar-Gutiérrez, A.J., Combes, D., Rakocevic, M., de Berranger, C., Eprinchard-Ciesla, A., Sinoquet, H., Varlet-Grancher, C. Functional relationships to estimate Morphogenetically Active Radiation (MAR) from PAR and solar broadband irradiance measurements: The case of a sorghum crop. Agricultural and Forest Meteorology, 2009.

Federer, C.A., Tanner, C.B. Spectral Distribution of Light in Forest. Ecology 47, 555-560, 1966.

Ford, E.D. High Productivity in a Polestage Sitka Spruce Stand and its Relation to Canopy Structure. Forestry 55, 1-17, 1982.

Franklin, K.A., Whitelam, G.C. Phytochromes and Shade-avoidance Responses in Plants. Annals of Botany 96, 169-175, 2005.

Gholz, H.L., Vogel, S.A., Cropper, W.P., Jr., McKelvey, K., Ewel, K.C., Teskey, R.O., Curran, P.J. Dynamics of Canopy Structure and Light Interception in *Pinus Elliottii* Stands, North Florida. Ecological Monographs 61, 33-51, 1991.

Grace, J. The Directional Distribution of Light in Natural and Controlled Environment Conditions. Journal of Applied Ecology 8, 155-160, 1971.

Grace, J., Woolhouse, H.W. A Physiological and Mathematical Study of the Growth and Productivity of a Calluna-sphagnum Community. II. Light Interception and Photosynthesis in Calluna. Journal of Applied Ecology 10, 63-76, 1973.

Grace, J., Malcolm, D.C., Bradbury, I.K. The Effect of Wind and Humidity on Leaf Diffusive Resistance in Sitka Spruce Seedlings. The Journal of Applied Ecology 12, 931-940, 1975.

Grant, R. Partitioning of biologically active radiation in plant canopies. International Journal of Biometeorology 40, 26-40, 1997.

Gu, L., Baldocchi, D., Verma, S.B., Black, T.A., Vesala, T., Falge, E.M. and Dowty, P.R. Advantages of diffuse radiation for terrestrial ecosystem productivity. Journal of Geophysical Research 107, 4050, 2002.

Gu, L., Fuentes, J.D., Shugart, H.H., Staebler, R.M., Black, T.A. Responses of net ecosystem exchanges of carbon dioxide to changes in cloudiness: Results from two North American deciduous forests. Journal of Geophysical Research 104, 1999.

Hale, S.E. The effect of thinning intensity on the below-canopy light environment in a Sitka spruce plantation. Forest Ecology and Management 179, 341-349, 2003.

Hayward, P.M. Determination of phytochrome parameters from radiation measurements. In: Smith, H., Holmes, M.G. (Eds.), Techniques in Photomorphogenesis. Academic Press London, 159–173, 1984.

Hertel, C., Leuchner, M., & Menzel, A. Vertical variability of spectral ratios in a mature mixed forest stand. Agricultural and Forest Meteorology, 151(8), 1096-1105, 2011.

Holmes, M.G., Smith H. The Function of Phytochrome in the Natural Environment IV. Light Quality and Plant Development. Photochemistry and Photobiology 25, 551-557, 1977.

Jeffree, C.E., Johnson R.P.C., Jarvis P.G. Epicuticular wax in the stomatal antechamber of sitka spruce and its effects on the diffusion of water vapour and carbon dioxide. Planta 98, 1-10, 1971.

Kanniah, K. D., Beringer, J., North, P., & Hutley, L. Control of atmospheric particles on diffuse radiation and terrestrial plant productivity A review. Progress in Physical Geography, 36(2), 209-237, 2012.

Karlsson, P.E. Blue light regulation of stomata in wheat seedlings. II. Action spectrum and search for action dichroism. Physiologia Plantarum 66, 207-210, 1986.

Kasperbauer, M.J. Spectral Distribution of Light in a Tobacco Canopy and Effects of End-of-Day Light Quality on Growth and Development. Plant Physiology 47, 775-778, 1971.

Kasperbauer, M.J. Far-Red Light Reflection from Green Leaves and Effects on Phytochrome-Mediated Assimilate Partitioning under Field Conditions. Plant Physiology 85, 350-354, 1987.

Knapp, A.K., Carter, G.A. Variability in leaf optical properties among 26 species from a broad range of habitats. Americal Journal of Botany 85, 940-946, 1998.

Krause, G.H. Photoinhibition of photosynthesis. An evaluation of damaging and protective mechanisms. Physiologia Plantarum 74, 566-574, 1988.

Kuiper, P.J.C. Dependence upon Wavelength of Stomatal Movement in Epidermal Tissue of *Senecio odoris*. Plant Physiology 39, 952-955, 1964.

Leakey, A.D.B., Press, M.C., Scholes, J.D. High-temperature inhibition of photosynthesis is greater under sunflecks than uniform irradiance in a tropical rain forest tree seedling. Plant, Cell & Environment 26, 1681-1690, 2003.

Leblanc, S.G. DHP-TRACWin Manual. Natural Resources Canada, Canada Centre for Remote Sensing. Version 1.0.1, 2008.

Leblanc, S.G., Chen, J.M., Kwong, M. Tracing Radiation and Architecture of Canopies. TRAC Manual Version 2.1 27. Natural Resources Canada, Canada Centre for Remote Sensing, 2002.

Leuchner, M., Menzel, A., Werner, H. Quantifying the relationship between light quality and light availability at different phenological stages within a mature mixed forest. Agricultural and Forest Meteorology 142, 35-44, 2007.

Leuchner, M., Fabian, P. Werner, H. Spectral Multichannel Monitoring of Radiation within a Mature Mixed Forest. Plant Biology 7, 619-627, 2005.

Leuchner, M., Hertel, C., Rötzer, T., Seifert, T., Weigt, R., Werner, H., & Menzel, A. Solar radiation as a driver for growth and competition in forest stands. In Growth and Defence in Plants (pp. 175-191). Springer Berlin Heidelberg. 2012.

Leverenz, J., Deans, J.D., Ford, E.D., Jarvis, P.G., Milne, R., Whitehead, D. Systematic Spatial Variation of Stomatal Conductance in a Sitka Spruce Plantation. Journal of Applied Ecology 19, 835-851, 1982.

Leverenz, J.W., Jarvis, P.G. Photosynthesis in Sitka Spruce. VIII. The Effects of Light Flux Density and Direction on the Rate of Net Photosynthesis and the Stomatal Conductance of Needles. Journal of Applied Ecology 16, 919-932, 1979.

Leverenz, J.W., Jarvis, P.G. Photosynthesis in Sitka Spruce (*Picea Sitchensis* (Bong.) Carr.): X. Acclimation to Quantum Flux Density Within and Between Trees. Journal of Applied Ecology 17, 697-708, 1980.

Lewandowska, M., Hart, J.W., Jarvis, P.G. Photosynthetic Electron Transport in Shoots of Sitka Spruce from Different Levels in a Forest Canopy. Physiologia Plantarum 41, 124-128, 1977.

Long, S.P., Humphries, S., Falkowski, P.G. Photoinhibition of Photosynthesis in Nature. Annual Review of Plant Physiology and Plant Molecular Biology 45, 633-662, 1994.

MacArthur, A., MacLellan, C. J., & Malthus, T. The fields of view and directional response functions of two field spectroradiometers. Geoscience and Remote Sensing, IEEE Transactions on, 50(10), 3892-3907, 2012.

Mansfield, T.A., Meidner, H. Stomatal Opening in Light of Different Wavelengths: Effects of Blue Light Independent of Carbon Dioxide Concentration. Journal of Experimental Botany 17, 510-521, 1966.

Middleton, E.M., Chan, S.S., Rusin, R.J., Mitchell, S.K. Optical properties of black spruce and jack pine needles at BOREAS sites in Saskatchewan, Canada. Canadian Journal of Remote Sensing 23, 108-119, 1997.

Middleton, E.M., Walter-Shea, E.A. Optical properties of canopy elements in the boreal forest. In Geoscience and Remote Sensing Symposium, 1995. Quantitative Remote Sensing for Science and Applications 1, 789-793, 1995.

Monsi, M., Saeki, T. (orig. 1953) On the Factor Light in Plant Communities and its Importance for Matter Production. Annals of Botany 95, 549-567, 2005.

Morgan, D.C., Warrington, I.J., Rook, D.A. 1985 Some observations on the spectral distribution characteristics of short-wave radiation within *Pinus radiata* D. Don canopies. Plant, Cell and Environment 8, 201-206.

Morison, J.I.L., Jarvis, P.G. Direct and Indirect Effects of Light on Stomata .1. in Scots Pine and Sitka Spruce. Plant Cell and Environment 6, 95-101, 1983.

Muller, R.A. Transmission components of solar radiation in pine stands in relation to climatic and stand variables. Pacific Southwest Forest & Range Experiment Station, Forest Service, U.S. Department of Agriculture; 13 pp, 1971.

Navrátil, M., Špunda, V., Marková, I., Janouš, D. Spectral composition of photosynthetically active radiation penetrating into a Norway spruce canopy: the opposite dynamics of the blue/red spectral ratio during clear and overcast days. Trees - Structure and Function 21, 311-320, 2007.

Neilson, R.E., Jarvis, P.G. Photosynthesis in Sitka Spruce (*Picea-Sitchensis* (Bong) Carr) .VI. Response of Stomata to Temperature. Journal of Applied Ecology 12, 879-891, 1975.

Norman, J.M., Jarvis, P.G. Photosynthesis in Sitka Spruce (*Picea sitchensis* (Bong.) Carr.). III. Measurements of Canopy Structure and Interception of Radiation. Journal of Applied Ecology 11, 375-398, 1974.

Norman, J.M., Jarvis, P.G. Photosynthesis in Sitka Spruce (*Picea sitchensis* (Bong.) Carr.): V. Radiation Penetration Theory and a Test Case. Journal of Applied Ecology 12, 839-878, 1975.

Pearcy, R.W. Sunflecks and Photosynthesis in Plant Canopies. Annual Review of Plant Physiology and Plant Molecular Biology 41, 421-453, 1990.

Pecot, S.D., Horsley, S.B., Battaglia, M.A., Mitchell, R.J. The influence of canopy, sky condition, and solar angle on light quality in a longleaf pine woodland. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 35, 1356-1366, 2005.

Powles, S.B. Photoinhibition of Photosynthesis Induced by Visible Light. Annual Review of Plant Physiology 35, 15-44, 1984.

Reicosky, D.A., Hanover, J.W. Physiological Effects of Surface Waxes: I. Light Reflectance for Glaucous and Nonglaucous Picea pungens. Plant Physiology 62, 101-104, 1978.

Reifsnyder, W.E. Control of solar radiation in agroforestry practice, In Reifsnyder WE, Darnhofer TO, eds., Meteorology and Agroforestry. ICRAF, Nairobi, Kenya. pp. 141-156, 1989.

Reitmayer, H., Werner, H., Fabian, P. A Novel System for Spectral Analysis of Solar Radiation within a Mixed Beech-Spruce Stand. Plant Biology 4, 228-233, 2002.

Ritchie, G.A. Evidence for red:far red signaling and photomorphogenic growth response in Douglas-fir (*Pseudotsuga menziesii*) seedlings. Tree Physiology 17, 161-168, 1997.

Schulze, E.D., Fuchs, M.I., Fuchs, M. Spacial distribution of photosynthetic capacity and performance in a mountain spruce forest of Northern Germany. Oecologia 29, 43-61, 1977.

Sellers, P.J. Canopy reflectance, photosynthesis and transpiration. International Journal of Remote Sensing 6, 1335 – 1372, 1985.

Smith, F.W., Sampson, D.A., Long, J.N. Comparison of Leaf-Area Index Estimates from Tree Allometrics and Measured Light Interception. Forest Science 37, 1682-1688, 1991.

Smith, H. Light Quality, Photoperception, and Plant Strategy. Annual Review of Plant Physiology 33, 481-518, 1982.

Smith, N.J. Estimating leaf area index and light extinction coefficients in stands of Douglas-fir (*Pseudotsuga menziesii*). Canadian Journal of Forest Research 23, 317–321, 1993.

Sonohat, G., Balandier, P., Ruchaud, F. Predicting solar radiation transmittance in the understory of even-aged coniferous stands in temperate forests. Annals of Forest Science 61, 629-641, 2004.

Stenberg, P. Penumbra in within-shoot and between-shoot shading in conifers and its significance for photosynthesis. Ecological Modelling 77, 215-231, 1995.

Stenberg, P., Smolander, H., Sprugel, D., Smolander, S. Shoot structure, light interception, and distribution of nitrogen in an Abies amabilis canopy. Tree Physiology 18, 759-767, 1998.

Urban, O., Janous, D., Acosta, M. et al. Ecophysiological controls over the net ecosystem exchange of mountain spruce stand. Comparison of the response in direct vs. diffuse solar radiation. Global Change Biology 13, 157-168, 2007.

Urban, O., Klem, K., Ač, A., Havránková, K., Holišová, P., Navratil, M., et al.. Impact of clear and cloudy sky conditions on the vertical distribution of photosynthetic CO_2 uptake within a spruce canopy. Functional Ecology, 26(1), 46-55, 2012.

van Gardingen, P.R., Jackson, G.E., Hernandez-Daumas, S., Russell, G., Sharp, L. Leaf area index estimates obtained for clumped canopies using hemispherical photography. Agricultural and Forest Meteorology 94, 243-257, 1999.

Walker, P., Maclellan, C. Guidelines for Post Processing GER 1500 Spectral Data Files using a FSF Excel Template. NERC Field Spectroscopy Facility. http://fsf.nerc.ac.uk, 2009.

Wherley, B.G., Gardner, D.S., Metzger, J.D. Tall Fescue Photomorphogenesis as Influenced by Changes in the Spectral Composition and Light Intensity. Crop Science 45, 562-568, 2005.

Woodward, F.I. Instruments for the Measurement of Photosynthetically Active Radiation and Red, Far-Red and Blue Light. Journal of Applied Ecology 20, 103-115, 1983.

Zeiger, E., Field, C. Photocontrol of the Functional Coupling between Photosynthesis and Stomatal Conductance in the Intact Leaf: Blue Light and Par-Dependent Photosystems in Guard Cells. Plant Physiology 70, 370-375, 1982.
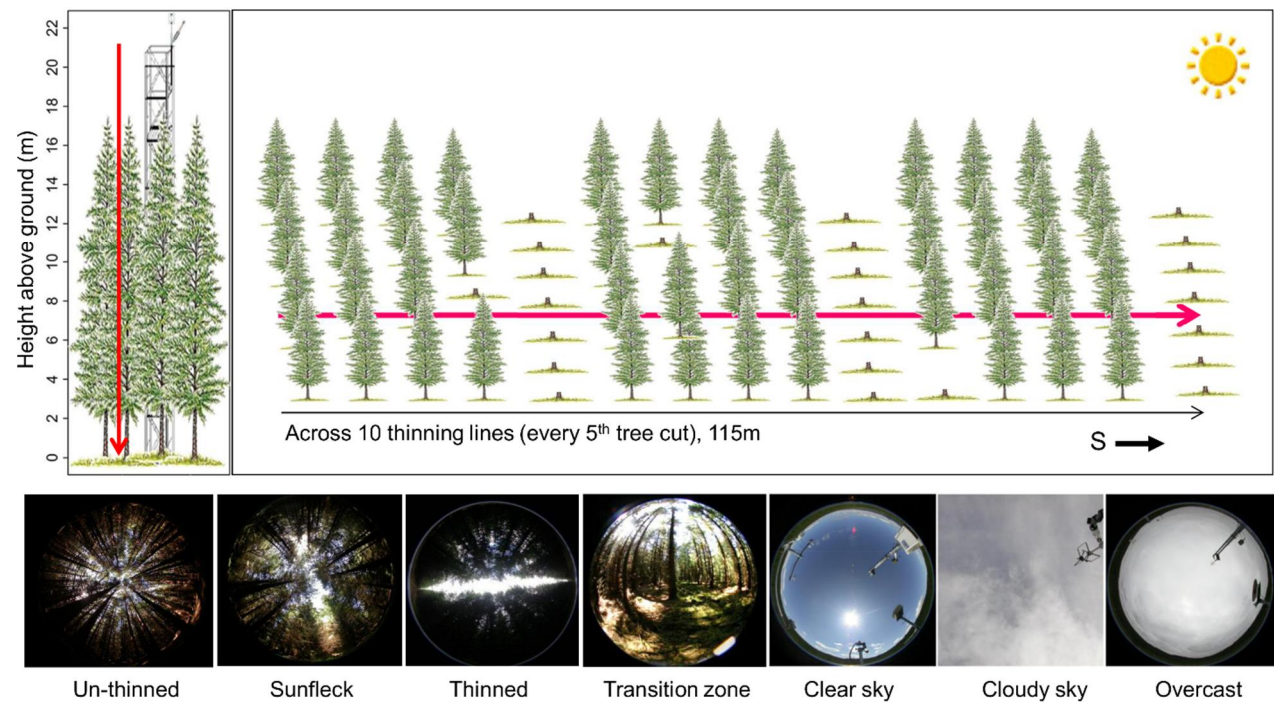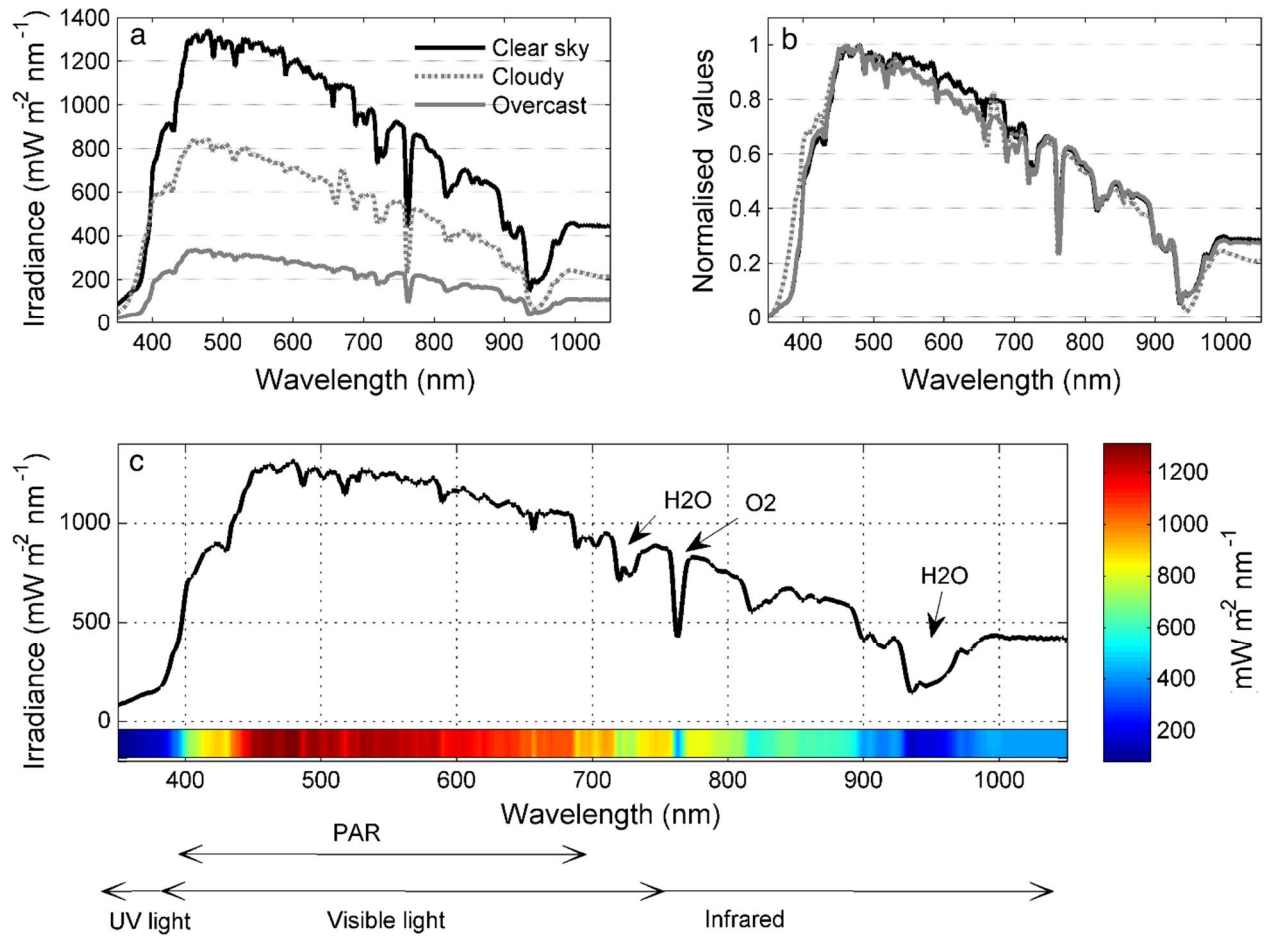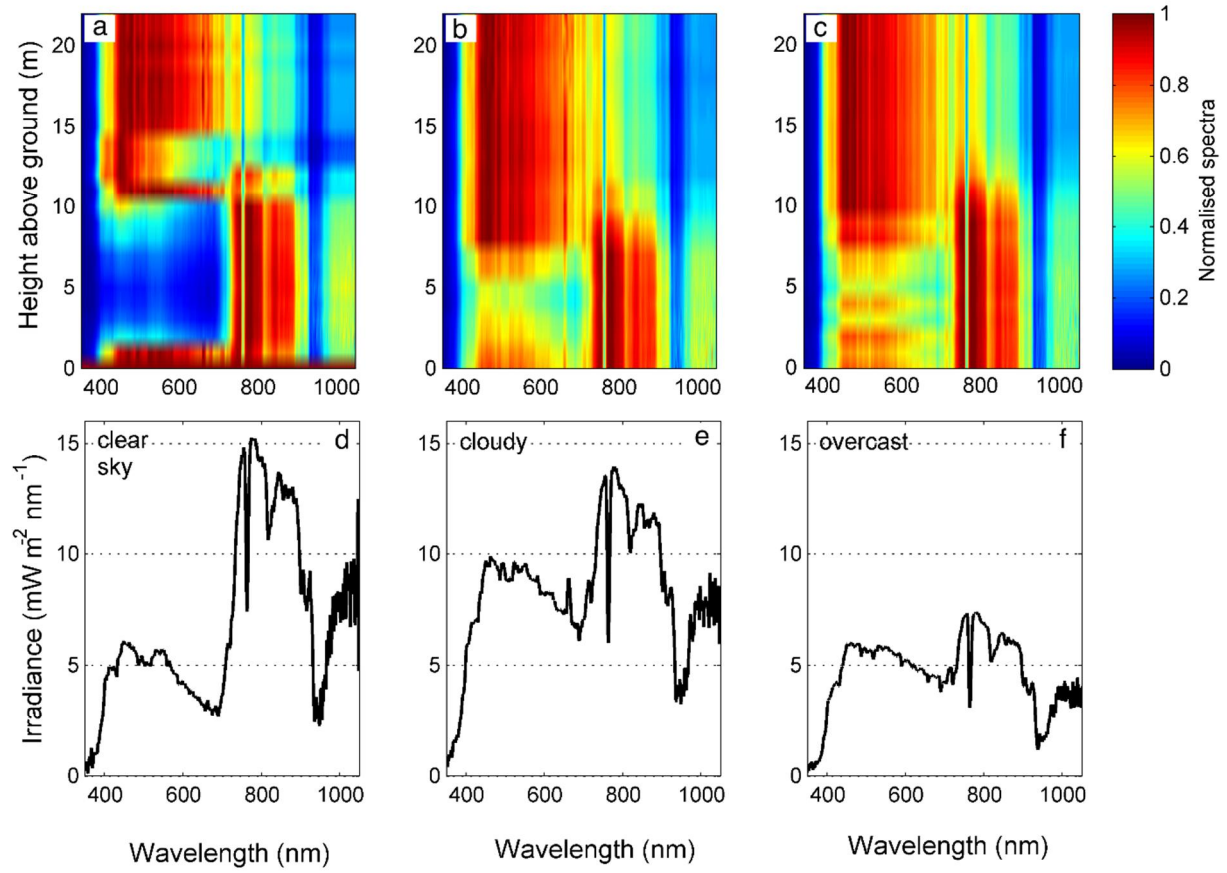
Figure 1:

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.
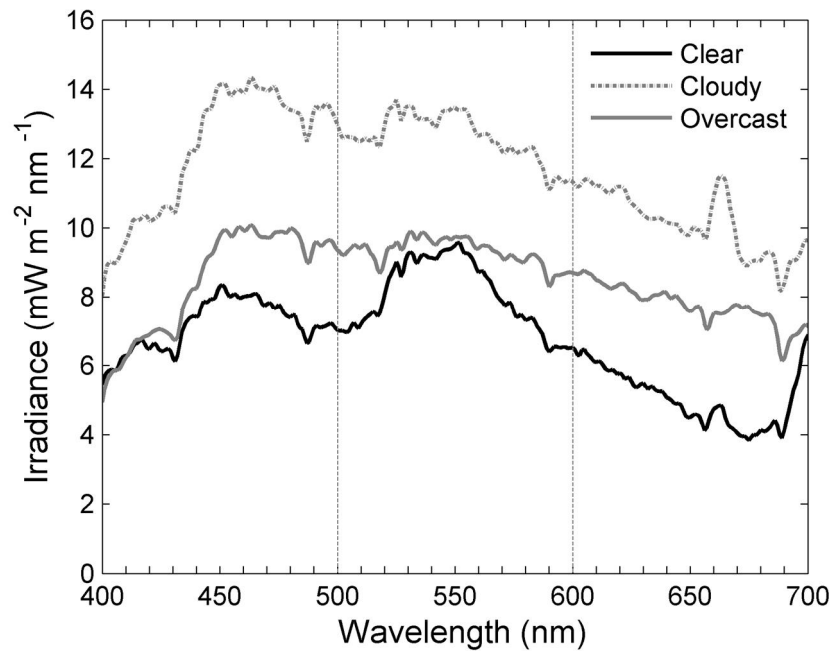
Figure 2. a, Spectral distribution of solar radiation above the canopy for the three conditions, while (b) is the normalised data of the same data, showing the little variation according to sky condition and time of year. Fig. 2c visualises the spectrum under clear sky, together with the intensity colour-coded in addition. This visualisation should help to interpret the spectral distribution in Figure 3. Furthermore, the main spectral features together with the wavelength distribution for the visible and PAR are shown.

Figure 3

Figure 3. Vertical profile of spectral distribution of solar radiation traversing the forest canopy on a clear, cloudy and overcast day. a, vertical profile on the clear day; b, vertical profile on the cloudy day; c, vertical profile on the overcast day. For the visualisations the data are normalised on a scale from 0-1. d, e and f show the spectral distribution at 2 m above ground in absolute terms, showing the exact energy distribution across all wavelength.

Figure 4:

Figure 4. Spectral distribution of solar radiation at 5 m above the ground for the wavelength range of PAR, showing the various distributions of blue and in particular the fraction of blue wavelength (430 – 470) that does evoke stomatal opening (*sensu* Kuiper 1964, Mansfield and Meidner 1966, etc.).
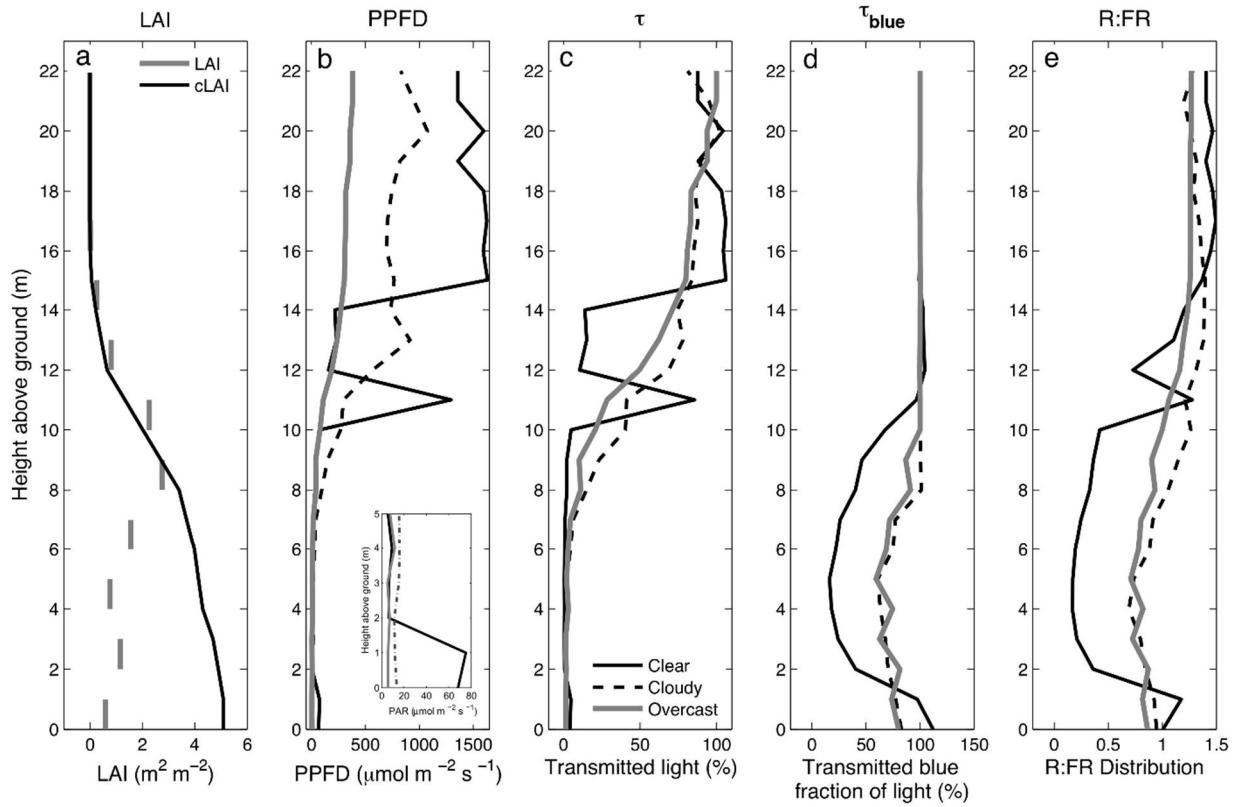
Figure 5:

Figure 5. 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). The insert is a magnification of the lowest 5 m above the forest floor, showing the forest floor illumination caused by sunflecks; 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).
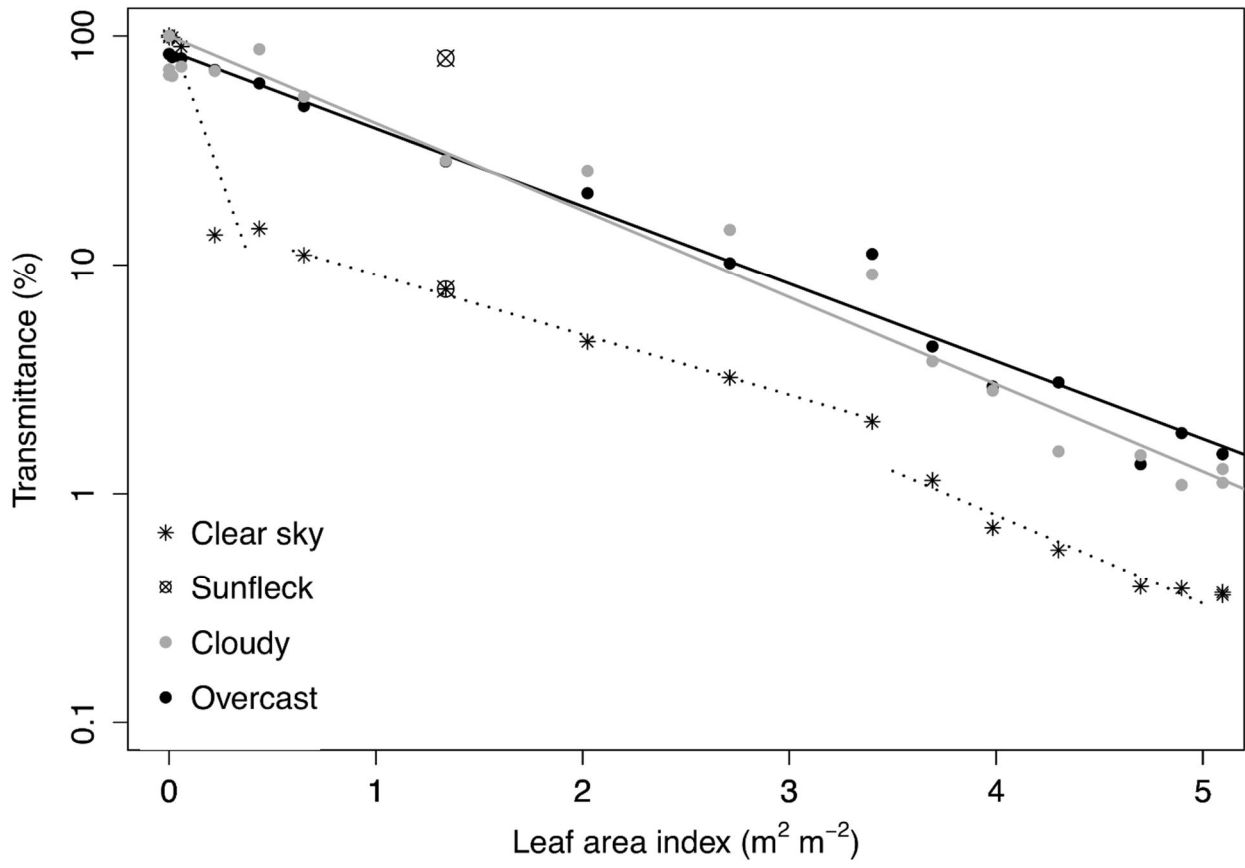
Figure **6**. Transmissivity and attenuation curves according to the Monsi & Saeki (1953) method. Transmissivity and light attenuation through the forest canopy after applying the Beer-Lambert attenuation law. Stars and dotted lines represent clear sky, grey solid circles and line represent cloudy and solid black circles and line represent the overcast conditions.
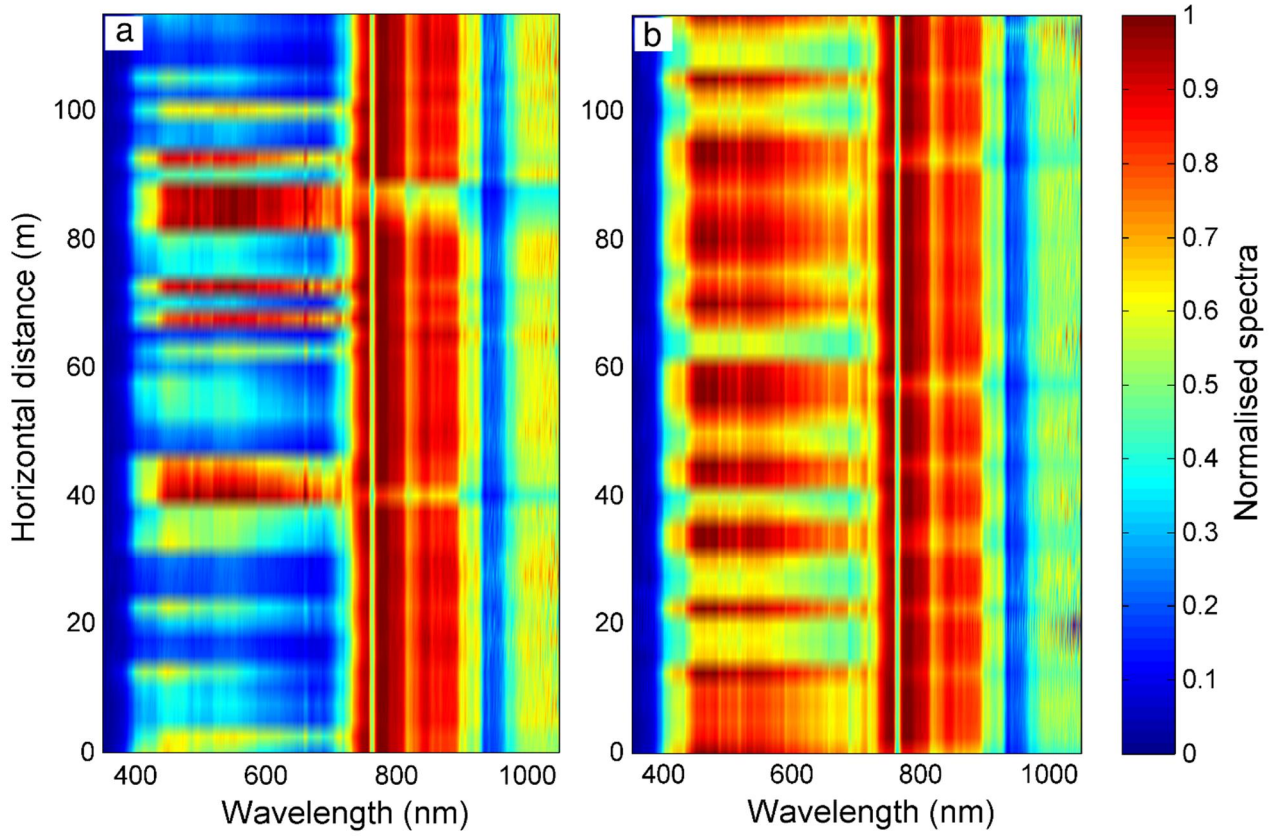
Figure 7:

Figure 7. Normalised spectra along the 115 m transect on the clear (a) and on the overcast day (b), respectively, showing clearly the distribution of sunflecks and open spaces (on the clear day) and the thinning lines on the overcast day (b).
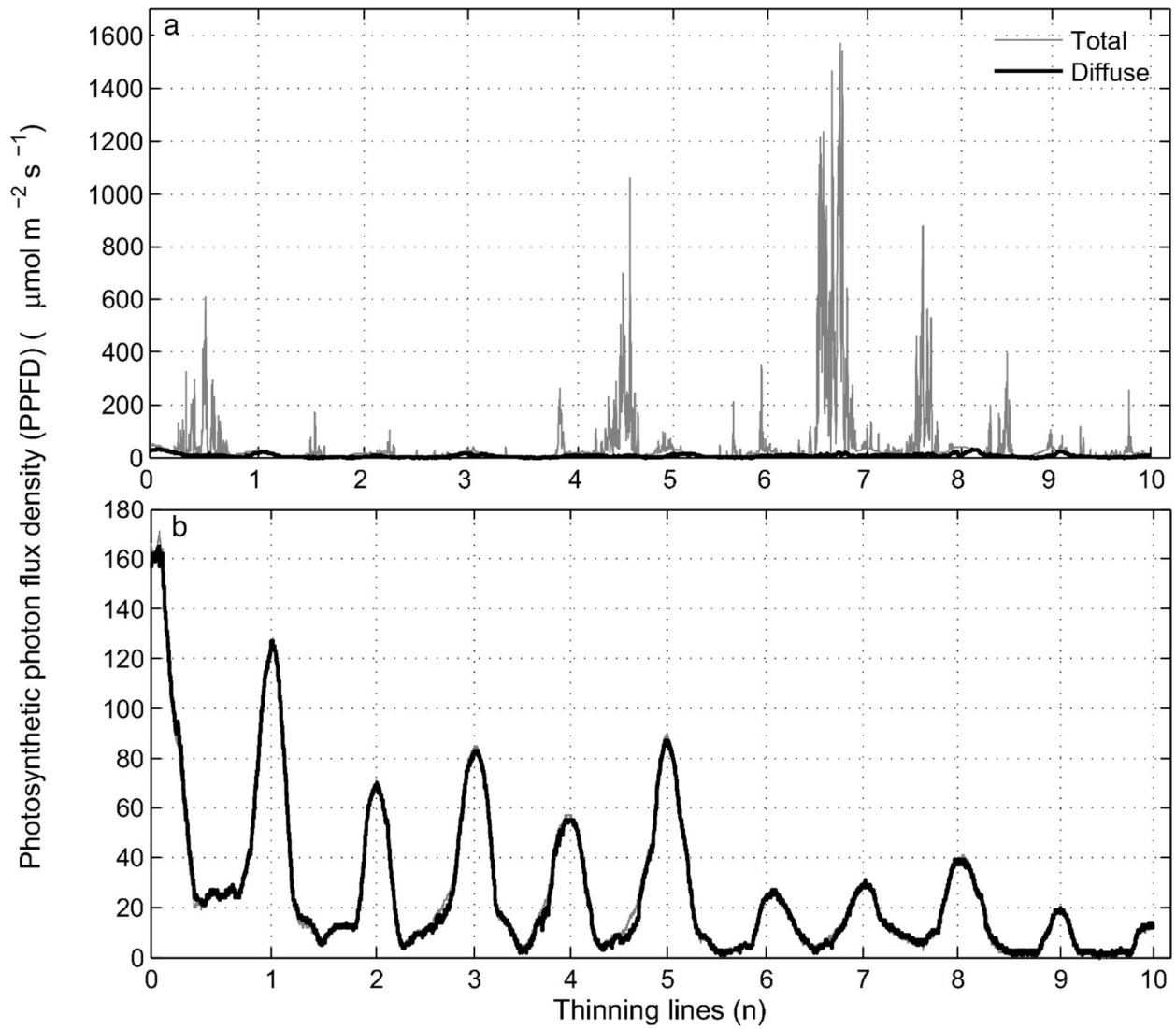
Figure **8**. Photosynthetic photon flux density (PPFD) distribution below the forest canopy under clear sky (a) and under overcast (b) conditions. Total (global) PPFD is marked as a solid grey line while diffuse PPFD measured simultaneously (using a shading strip) is marked as a solid black line. Thinning lines are every 11 m.
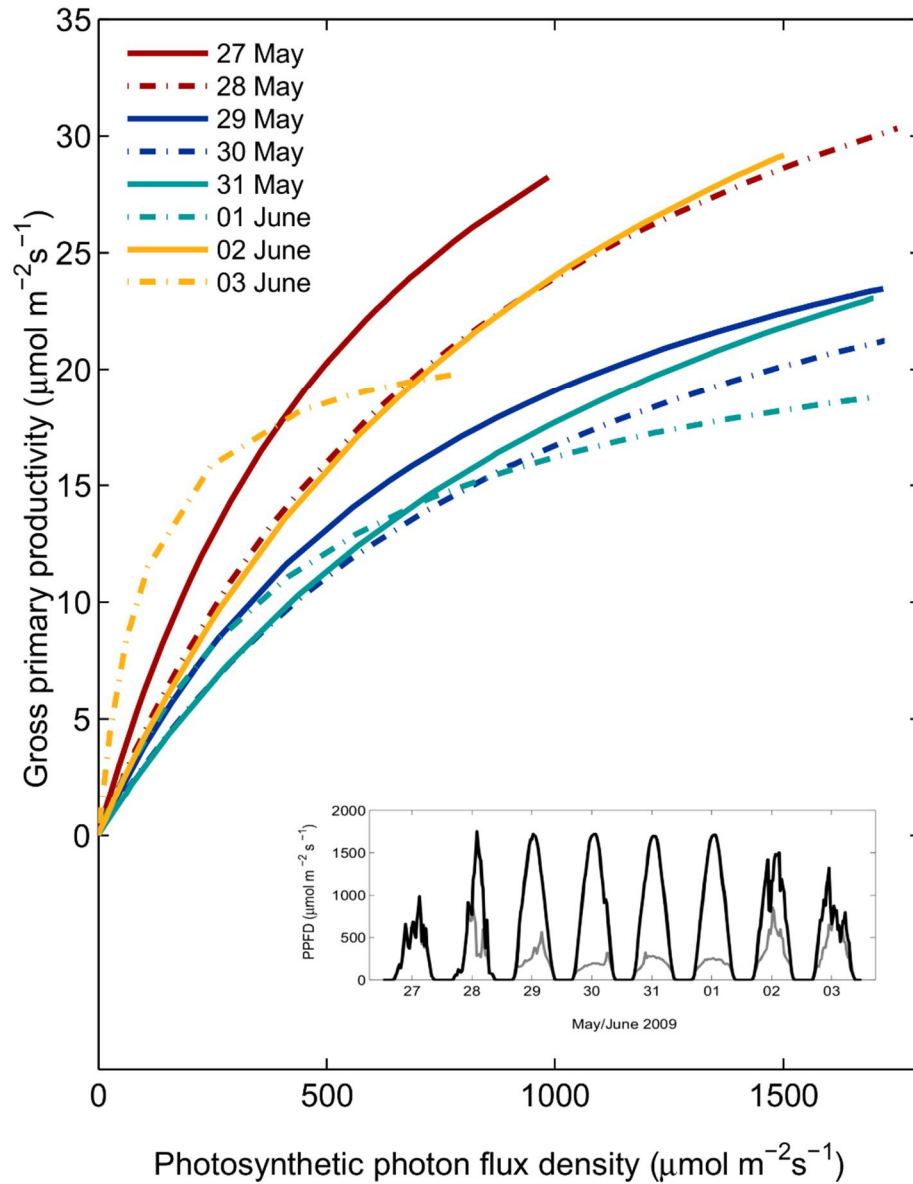
Figure **9**. Light use efficiency (LUE) curves for eight consecutive days **previously introduced in** Dengel & Grace (2010). These show the day-to-day changes in light use efficiency when sky conditions change from overcast to cloudy to clear sky conditions. After four consecutive clear days (lowest 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 & Grace (2010, **Fig. 2c**), representing global radiation in black and diffuse radiation in grey.