

Arctic canopy photosynthetic efficiency enhanced under diffuse light, linked to a reduction in the fraction of the canopy in deep shade

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Summary

- We investigated how radiation conditions within a tundra canopy were linked to canopy photosynthesis, and how this linkage explained photosynthetic sensitivity to sky conditions, that is total radiation and its diffuse fraction.
- We measured within canopy radiation at leaf scales and net CO₂ exchanges at canopy scales, under varied total irradiance and diffuse fraction, in Alaskan shrub tundra.
- Normalised mean radiation profiles within canopies showed no significant differences with varied diffuse fractions. However, radiation density distribution was non-normal, being more unimodal under diffuse conditions and distinctly bimodal under direct sunlight. There was a nearly three-fold increase in the proportion of the canopy in deep shade under direct illumination, compared to diffuse conditions. Under diffuse conditions the canopy had higher light-use efficiency (LUE), resulting in up to 17% greater photosynthesis.
- The enhancement in LUE under diffuse illumination was not related to differences in the mean light profiles, but instead was due to significant shifts in the density distribution of light at leaf scales, in particular a reduced fraction of the canopy in deep shade under diffuse illumination. These results provide unique information for testing radiative transfer schemes in canopy models, and for better understanding canopy structure and trait variation within plant canopies.

Introduction

Solar radiation provides the energy source for photosynthesis, underpinning plant productivity and driving the biological component of the global carbon cycle. The biochemistry of the photosynthetic light response at the leaf level is well understood (Chapin & Matson, 2011). An initial linear response of leaf photosynthesis to increasing light is followed by a saturation response as factors other than light become limiting. These nonlinear responses can be explained by leaf models incorporating fundamental understanding of the biochemistry of electron transport and carboxylation (Farquhar & von Caemmerer, 1982), and the biophysics of gaseous diffusion (von Caemmerer & Farquhar, 1981; Harley & Baldocchi, 1995). These leaf-scale simulations are critical components for a variety of models, from crops (Wattenbach *et al.*, 2010) to ecosystems (Williams *et al.*, 1996) and the Earth System (Sellers *et al.*, 1997; Bonan, 2008). But, at the scale of vegetation canopies the sensitivity of photosynthesis to solar radiation is more complex than for leaves (De Pury & Farquhar, 1997), and significant uncertainties remain both in understanding and in model representation (Buckley *et al.*, 2013).

Alteration in sky conditions influences photosynthesis in plant canopies (Gu *et al.*, 2003; Rocha *et al.*, 2004) by changing the

balance in irradiance between direct beam from the sun and radiation scattered by the atmosphere (diffuse irradiance). Within a canopy, interactions between the light climate and the spatial arrangement of leaves create complex gradients and patterns in irradiance. These interactions are different under direct and diffuse irradiance because of their contrasting illumination geometries. Theory suggests that a greater diffuse radiation fraction (ϕ) leads to less shadowing within a plant canopy (Roderick *et al.*, 2001). With high ϕ , illumination is incident from a larger fraction of the sky hemisphere (isotropic), and so shading is minimised (Fig. 1). Direct irradiance, by contrast, is incident from the solar disk, an area which is readily shaded by typical leaf dimensions and separation distances. Theory explains that under sunny conditions (low ϕ), canopies tend to be divided into brightly illuminated and heavily shaded components. Thus, light intensity is expected to be bimodally distributed under sunny conditions (Gu *et al.*, 2002). Under diffuse conditions, canopies are more evenly illuminated (Jenkins *et al.*, 2007), with an expectation of a unimodal probability distribution. On this basis, models, such as land surface schemes (Clark *et al.*, 2012), distribute sun and shade canopy fractions with depth in the canopy according to simple statistical rules linked to Beer's Law (Norman, 1981). Measurements in forest canopies have provided some

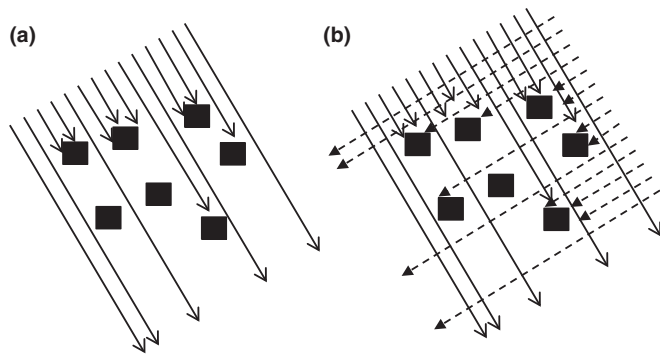


Fig. 1 The effect of direct illumination compared to diffuse illumination on the canopy radiation environment is explained in this simplified representation. Arrow lines represent streams of photons, while squares represent foliage elements. For direct sunlit conditions, foliage elements are illuminated from a single direction (a); radiation interception by leaves generates heavily shaded areas. For comparison, (b) shows the same canopy illuminated from two directions; while shading still occurs, overall there is a reduction in the shaded area, and leaves that were previously shaded are now illuminated. In real diffuse environments the picture is more complex due to incident radiation from the full sky hemisphere.

confirmation of these expectations (Urban *et al.*, 2007), but only at relatively aggregated scales, with limited sampling of the expected heterogeneity of the within-canopy light environment. Measurements and analyses of the full probability distribution of irradiance within canopies, at leaf scales, are lacking, resulting in a fundamental uncertainty about how the light climate interacts with canopy structure and leaf traits, and untested modelling of radiative transfer. So, although leaf-level studies have provided insights into within-canopy variations in photosynthesis (Ellsworth *et al.*, 2012), upscaling to canopy fluxes has been limited by the challenges of sampling within the diverse canopy environment, particularly in tall forest systems.

The nonlinear response of photosynthesis to light at the leaf scale interacts with the varied illumination of plant canopies to create complex sensitivities of canopy gross primary productivity (GPP) to light under varied sky conditions (Urban *et al.*, 2012). Sunlit leaves tend to be light saturated, with low light-use efficiencies (LUE), while leaves in deep shade are light limited, with high LUE. So, if at high ϕ the more even illumination leads to a greater proportion of the canopy operating at light saturation, canopy LUE should be greater (Gu *et al.*, 2002). For a fixed total irradiance, a canopy should have higher productivity with high ϕ , because of increased LUE. Of course, ϕ tends to correlate negatively with total irradiance, so productivity is a complex outcome of both total irradiance and ϕ (Roderick *et al.*, 2001). Disentangling these correlated changes is vital for effective response modelling (Alton *et al.*, 2007b), and requires novel approaches for measurement and observation that effectively scale from leaf to canopy (Alton, 2008).

Studies of canopy light environments and photosynthesis at the leaf and canopy scales are challenging. Eddy covariance (EC) methods, which provide continuous monitoring of net fluxes of CO_2 , have typically been used to investigate canopy responses to light climate (Fox *et al.*, 2008; Stoy *et al.*, 2013). The comparison of different EC measurement periods with differing ϕ supports

the theory that at high ϕ canopies have higher LUE (Jenkins *et al.*, 2007; Urban *et al.*, 2007). However, the analysis is complicated because changes in ϕ are often correlated with changes in other environmental factors, for instance wind direction and speed, temperature and vapour pressure deficit (Dengel & Grace, 2010). There are significant uncertainties in estimating photosynthesis from EC data linked to meteorology (Richardson *et al.*, 2008), and biases may therefore be correlated with ϕ . Furthermore, the uncertainty in the footprint of the EC sampling (Schmid & Lloyd, 1999) complicates direct linkages of fluxes to measurements of within-canopy light climate. While some measures of the light climate within the canopy have been linked to EC studies (Urban *et al.*, 2007, 2012), such data have been sparse in relation to the scale of intrinsic variation – that is, leaf scales. Thus, given that the footprint of EC flux estimates is large (ha scale), uncertain and dynamic, it is impossible to characterise the within-canopy light conditions of the flux source region. Finally, in many cases direct measurement of ϕ is rarely reported or available in EC analyses (Gu *et al.*, 2002; Alton, 2008). These problems mean that using EC data to calibrate models and improve our fundamental understanding of the photosynthetic process response to the light climate has major limitations.

Therefore, our overarching question is to determine how radiation conditions within a canopy are linked to whole-canopy photosynthesis, and how this explains photosynthetic sensitivity to sky conditions. A series of further, linked questions arise: To what degree is the canopy light environment more evenly illuminated under diffuse conditions? To what extent is the distribution of irradiance in the canopy normal and unimodal under diffuse conditions, and bimodal under direct illumination? Under high irradiance does maximum canopy photosynthesis increase with ϕ , all other factors being equal? Answers to these questions will provide novel information to test models of radiative transfer and photosynthesis under different sky conditions, which are currently poorly constrained (Alton *et al.*, 2007a; Knohl & Baldocchi, 2008). The importance of correctly modelling these responses for predicting the climate sensitivity of the global carbon cycle has been clearly demonstrated (Mercado *et al.*, 2009; Bonan *et al.*, 2012). Furthermore, these questions have relevance for understanding leaf trait variation within plant canopies (Street *et al.*, 2012; Wright *et al.*, 2013), which is known to be linked to light environments (Ellsworth & Reich, 1993; Roden & Pearcy, 1993).

Given the nonlinearity of photosynthesis–light relationships, it is important to resolve the distribution of radiation accurately within canopies simultaneously with measurements of photosynthesis. The objective of this paper is, therefore, to directly measure the within-canopy light environment at leaf scales, under a range of sky conditions (ϕ), and analyse the response of photosynthesis to variation in ϕ . In relation to the science questions, we hypothesise the following:

H1 Under higher ϕ , radiation will have a unimodal distribution within a shrub canopy, with increasingly bimodal illumination at lower ϕ . Neither distribution will be normal.

H2 Under higher ϕ , canopies will be more evenly illuminated, with relatively fewer areas of deep shade.

And so at the canopy scale:

H3 Under higher ϕ , canopies will have greater LUE, due to more even illumination.

H4 Under higher total irradiance, photosynthesis will be greater with higher ϕ .

We undertook experiments that directly manipulated total irradiance and ϕ , while holding other meteorological variables constant. Our measurements of light climate and photosynthesis were directly coincident in space and time, and were made at relevant scales, using chambers to collocate flux measurements with light measurements. This experimental design increases the signal-to-noise ratio, and reduces the likelihood of measurement bias in photosynthesis and light estimates. As far as we are aware, this is the first research to manipulate and monitor radiation climate effects on ecosystem photosynthesis at coincident scales. Our research was undertaken in arctic shrub tundra, a significant component of the Arctic biome that is currently expanding, with potential feedbacks to global processes (Myers-Smith *et al.*, 2011).

Materials and Methods

We used a well-tested method to measure the net ecosystem production (NEP) of shrub ecosystems within enclosed chambers. By making measurements across a range of light intensities, and in darkness, it is possible to determine photosynthesis–light response curves (Williams *et al.*, 2006; Street *et al.*, 2007). A diffuser screen, and natural changes in cloudiness, were used to vary ϕ . Light intensities within the chamber were recorded during each measurement, and throughout the canopy at high spatial resolution, resolving changes in radiation at mm scales. Simple empirical models were then fitted to the light curves to determine critical parameters for hypothesis testing.

Field site

We undertook field work during June–August 2012, at the Arctic Long Term Ecological Research Site near Toolik Field Station (68°38'N, 149°43'W, elevation 760 m), in northern Alaska, USA. The site has continuous permafrost, a mean annual temperature of -10°C , and a snow-free season that lasts from late May to mid-September. The vegetation is dominated by tussock tundra mixed with dwarf birch (*Betula nana* L.) and willow (*Salix pulchra* Cham.) shrubs. Research was focused on denser large stands of shrubs to the north of the field station, in areas with greater nutrient availability and higher productivity (Shaver & Chapin, 1991). These stands have been studied previously (Shaver & Chapin, 1991), and are part of the long-term LTER sites monitored at Toolik Lake. Shrub communities with closed canopies (leaf area index, LAI > 1.5) were selected for measurement, to ensure that a gradient of radiation conditions was present through the plant canopies. Typically canopy heights were 0.70–1.00 m, dominated either by *Salix pulchra* or *Betula nana*. Moss cover beneath the canopy was insignificant due to the closed canopies (Douma *et al.*, 2007).

Radiation measurements and manipulations

Top of canopy irradiance We quantified the incident total photosynthetic photon flux density (PPFD) and total diffuse PPFD every minute during study periods, using a Beam Fraction Sensor (BF3; Delta-T Devices Ltd, Burwell, Cambridge, UK). Data were also logged continuously at 5-min intervals over 7 d to track diel variations. PPFD was also measured within the flux chamber, above the canopy, using a Li-Cor 6400 photosynthesis system quantum sensor (Li-Cor Inc., Lincoln, NE, USA), logging during CO_2 concentration measurements.

Irradiance manipulations We generated different light intensities for both diffuse and sunlit light curves by starting from ambient light, and then covering the chamber with 1–5 optically neutral fine mesh net cloths (Williams *et al.*, 2006). During consistent sunny conditions during some light curves ($n = 4$), photographic diffuser panels (Fotodiox Inc., Waukegan, IL, USA), 1.5×1.0 m, were placed between sun and chamber to remove direct beam radiation. Diffuser panels were carefully positioned to intercept all direct light that would otherwise enter the chamber. In 10 cases NEP measurements were made under naturally diffuse (cloudy) conditions but with enhanced radiation, to extend diffuse light curves to high PPFD values, by using white photographic reflector panels (Fotodiox), positioned around the chamber (Fig. 2).

Field tests, using the diffuser and reflector panels, indicated that the panels effectively blocked most direct light. Measurements with the Beam Fraction Sensor (BF3) indicated that the diffuse light fraction was > 0.7 for these measurements. Therefore, BF3 data during flux measurements were used to stratify conditions into three groups: Direct (sunny measurements): $\phi < 0.40$; Diffuse (cloudy or diffused-light): $\phi > 0.70$; and Intermediate (partial sun/cloud): $0.40 < \phi < 0.70$. Analyses focused



Fig. 2 During sunny conditions, a diffuser screen (translucent panel, left) was used to manipulate the light climate, removing direct irradiance from the shrub canopy within the Perspex chamber (centre) to generate a diffuse light environment. During cloudy conditions, opaque white panels were used similarly to enhance illumination of the chamber by concentrating reflected diffuse light.

on comparing conditions and gas exchange under diffuse and direct conditions using these groupings.

Within-canopy irradiance We also measured PPFD within each studied canopy, using a Delta-T SunScan in conjunction with the BF3 sensor (Delta-T Devices). We collected PPFD measurements immediately before chamber installation and CO₂ measurements, to ensure similarity in sky conditions. The BF3 sensor recorded total irradiance and incident diffuse light simultaneously with the SunScan's 64-PPFD readings, evenly collected along the 1-m-long sensor wand. The dimensions of the individual 64 sensors were 13 × 16 mm, about the size of a *Betula* leaf, and less than the area of a typical *Salix* leaf. Readings were taken by inserting the SunScan horizontally into the base of the canopy as near to the ground as possible (typically *c.* 0.05 m from the ground as the sensor rested on top of moss). Further measurements were taken higher in the canopy, at 0.15 m vertical intervals until the top height of the canopy was exceeded, usually giving 5–6 measurement heights within each canopy, and a further set of data collected above the canopy (i.e. incident PPFD). Three replicates of these vertical profiles were collected for each chamber location, evenly spaced along one side of the chamber. Measurements were collected under both sunny conditions and diffuse conditions (i.e. with the diffuser in place or during a cloudy period). The Sunscan generated *c.* 1000 PPFD data describing canopy light environment per treatment, from which density distributions were generated. Because of the potential non-normal distribution of data, the mean absolute deviation (MAD) was selected as the most appropriate statistical measure of spread around the mean.

For each chamber and each sky condition, we normalised the raw PPFD data by the maximum radiation recorded by the SunScan during the survey. This conversion generated profiles of fraction of incident irradiance received within the canopy. These data, stratified by prevailing sky conditions ($\phi > 0.7$ or $\phi < 0.4$), were used to test H1 and H2. A total of 14 chamber sites were sampled, but because of problems with data recording in two cases, the results from 12 are presented. Of the 12 locations, seven were dominated by *B. nana*, and five by *S. pulchra*.

Chamber flux measurements

We measured CO₂ and H₂O fluxes using a Li-Cor 6400 photosynthesis system (Li-Cor) connected to a 1 × 1 m Perspex chamber. The chamber was placed on a metal frame, itself supported by legs made of PVC to accommodate canopies with heights up to 1.25 m. The frame had taped to it a semi-transparent, plastic skirt which extended to the ground and was sealed to the tundra by weighting with heavy chains. In addition, a Perspex 'sleeve' could extend the height of the rigid portion of the chamber by 0.25 m. A Li-Cor custom chamber head attachment was fitted over the holes drilled into the Perspex chamber, and sealed to the chamber with a rubber gasket. The air in the chamber was mixed using 4–8 small fans (number depending on chamber height). Further details on the methods can be found in Williams *et al.* (2006) and Street *et al.* (2007).

At each plot we made measurements of CO₂ concentration changes under varying light conditions. We created a pair of light curves, one under direct sunlight (ambient, cloud-free conditions) and one under diffuse light conditions (using a diffuser screen under sunlit conditions, and reflectors under cloudy conditions) during the middle of the day (10:00–15:00 h local time). We first made measurements under ambient light, and then made further measurements with increasing shading over the entire chamber (top and sides) using optically neutral cloth, that is reducing total incident PPFD, but not varying the diffuse/direct nature of the irradiance. After light measurements, at least three measurements were made in the dark, by covering the chamber in an opaque tarpaulin to estimate respiration, and to quantify measurement error. We assume that respiration in the dark is a measurement of ecosystem respiration (R_e), although we acknowledge the uncertainties in this assumption (Heskel *et al.*, 2013). We allowed 30–60 s for adjustment after the alteration of light climate before measurement. At each light intensity CO₂ concentrations in the chamber were recorded every 2 s over a 60 s period. Data from the first 10 s were discarded before analysis.

We calculated net ecosystem production from measurement series with a consistent linear change in CO₂ concentration ($r^2 > 0.97$). When abnormalities in CO₂ measurements were observed (likely because of leaks, very small changes in CO₂ concentration or changes in light intensities) data points were discarded from the start or end of the sequence, but at least seven continuous concentration measurements were always used for flux estimation. The net ecosystem production (NEP, $\mu\text{mol m}^{-2} \text{s}^{-1}$, positive flux indicates net uptake) was calculated by the following equation:

$$\text{NEP} = -\frac{\rho V}{A} \frac{dC}{dt} \quad \text{Eqn 1}$$

(ρ , air density (mol m^{-3}); V , chamber volume (m^3); dC/dt , the slope of chamber CO₂ concentration against time ($\mu\text{mol mol}^{-1} \text{s}^{-1}$); A , chamber surface area (m^2)). The depth of the chamber was determined with 36 measurements to ground level using a regular grid within the chamber. The surface area of the inside of the Perspex chamber was 0.884 m^2 .

A total of 14 chamber sites were sampled, and both direct and diffuse light curves were generated and analysed under a range of sky conditions. Nine of the chambers were dominated by *B. nana*, and five by *S. pulchra*. In total, 393 flux measurements were collected over the period from 23 June to 26 July 2012. The mean air temperature recorded by the Li-Cor 6400 during flux measurements over all 14 locations and sky conditions was 22.7°C (standard deviation 2.7°C). For comparison, the mean maximum temperature recorded at 3 m in the Toolik Lake Field Station weather station during the measurement days was 18.3°C . The short flux measurement period was designed to ensure minimal changes to within-chamber environments during data collection. We tested this by examining the increase in temperature that occurred in full ambient conditions (i.e. maximum irradiance) at each study site during flux measurements. There was a mean increase in temperature of 0.49°C ($n = 14$) and we

conclude that environmental changes were within required tolerances (i.e. $< 1^{\circ}\text{C}$).

Modelling photosynthesis and CO_2 exchange rates

Photosynthesis was modelled by fitting a light-response curve to the measured NEP data, corrected for ecosystem respiration, to determine the canopy scale responses. A saturating (Michaelis–Menten type) function was used for photosynthesis, with a fixed estimate of ecosystem respiration (Williams *et al.*, 2006).

The model was fitted separately for each light curve;

$$\text{NEP} = \frac{P_{\max} I}{k + I} - R_e \quad \text{Eqn 2}$$

(P_{\max} , maximum photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); I , measured irradiance ($\mu\text{mol PPFD m}^{-2} \text{ s}^{-1}$); k , half-saturation point ($\mu\text{mol PPFD m}^{-2} \text{ s}^{-1}$); R_e , measured ecosystem respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)). Best-fit parameters (P_{\max} , k) were calculated by minimising the sum of the squared errors between measured and modelled NEP values, using the Excel solver tool (Microsoft, Redmond, WA, USA). Comparison between the best-fit parameters under different sky conditions was used to address H3 and H4. The model was then fitted twice more, once using the entire flux dataset under diffuse conditions ($n = 267$), and once using all data collected under direct illumination ($n = 226$).

From the fitted parameters, several auxiliary variables were determined. The quantum yield (E_0) is the initial slope of the light curve, determined as P_{\max}/k . The light compensation point

(LCP), the PPFD at which $\text{GPP} = R_e$, is determined as

$$\text{LCP} = \frac{R_e \cdot k}{P_{\max} - R_e} \quad \text{Eqn 3}$$

Because P_{\max} represents a theoretical maximum that is rarely if ever reached, another useful statistic is the GPP attained at $600 \mu\text{mol PPFD m}^{-2} \text{ s}^{-1}$, denoted GPP_{600} , calculated as

$$\text{GPP}_{600} = \frac{P_{\max} \cdot 600}{k + 600} \quad \text{Eqn 4}$$

For seven peak season days (10, 25, 26, 29–31 July, 2 August 2012) with measurements of sky conditions (ϕ) and incident PPFD at 5-min resolution, we predicted gross photosynthesis using the first term on the right-hand side of Eqn 2. GPP predictions were generated using mean best-fit parameters for diffuse conditions, and also sunlit conditions, based on the individual light curve fittings (Table 1). We used temporal measurements of diffuse sky conditions to determine which calibration was appropriate across the diurnal cycle. In all data presented, units of m^{-2} refer to ground area.

Results

Radiation measurements

Incident radiation Radiation data recorded by the BF3 throughout the chamber flux measurements at each site recorded a mean incident PPFD of $1388 \mu\text{mol m}^{-2} \text{ s}^{-1}$, sufficient to

Table 1 Summary of measurements and model parameters under varied sky conditions

| Parameter Scale of analysis | Under high direct fraction insolation | | Under high diffuse fraction insolation: | | Two-sided pair <i>t</i> -test sig. |
|--|--|--------------|--|--------------|---------------------------------------|
| | By chamber | Full dataset | By chamber | Full dataset | |
| PPFD, maximum irradiance ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) | 1298 (50) | | 760 (60) | | **** |
| R_e , ecosystem respiration (measured) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) | 9.3 (0.5) | | 9.3 (0.5) | | NS |
| R_e , ecosystem respiration (modelled) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) | 9.5 (0.5) | 9.5 | 9.9 (0.5) | 9.7 | ** |
| P_{\max} , maximum theoretical photosynthetic rate, modelled ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) | 29.8 (2.2) | 26.7 | 28.5 (2.0) | 25.6 | NS |
| Maximum observed photosynthetic rate, measured ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) | 21.2 (0.34) | | 18.0 (0.28) | | NS |
| k , half saturation point, fitted ($\mu\text{mol PPFD m}^{-2} \text{ s}^{-1}$) | 665 (143) | 438 | 394 (59) | 292 | * |
| E_0 , quantum yield, fitted ($\text{mol CO}_2 \text{ mol}^{-1} \text{ PPFD}$) | 0.06 (0.01) | 0.06 | 0.09 (0.01) | 0.09 | * |
| LCP, light compensation point, estimated ($\mu\text{mol PPFD m}^{-2} \text{ s}^{-1}$) | 290 (42) | 243 | 199 (15) | 178 | ** |
| GPP_{600} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), estimated gross primary production at $600 \mu\text{mol PPFD m}^{-2} \text{ s}^{-1}$ | 14.9 (0.9) | 15.4 | 17.4 (1) | 17.2 | *** |
| GPP_{300} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), estimated gross primary production at $300 \mu\text{mol PPFD m}^{-2} \text{ s}^{-1}$ | 10.4 (0.8) | 10.9 | 12.8 (0.8) | 13.0 | ** |

The 'By chamber' columns show mean values (and standard errors) for observations and model parameters derived from light curves collected over 14 arctic shrub canopies, analysed under both sunlit and diffuse conditions. The 'full dataset' columns show the model parameters derived from fitting against the combined light curve datasets under consistent sky conditions. The results of a paired *t*-test on chamber data to determine parameter differences according to radiation climate are indicated in the final column.

Significance is indicated by: *, $P < 0.1$; **, $P < 0.05$; ***, $P < 0.01$; ****, $P < 0.001$; NS, no significant difference. Significance tests on measured maximum photosynthesis were not undertaken as light intensities were inconsistent between treatments.

achieve maximum or near maximum canopy GPP in our previous work (Williams *et al.*, 2006). Mean incident PPFD during cloudy diffuse measurement conditions was $519 \mu\text{mol m}^{-2} \text{s}^{-1}$. During manipulated diffuse conditions the mean PPFD was lower ($326 \mu\text{mol m}^{-2} \text{s}^{-1}$) due to clear skies. During chamber measurements of fluxes, the mean incident PPFD recorded by the Li-Cor quantum sensor within the chamber under sunlit conditions was $1298 \mu\text{mol m}^{-2} \text{s}^{-1}$. The 6% reduction compared to the BF3 data is likely a result of attenuation through the Perspex of the chamber. During measurement of within-canopy radiation, the mean above-canopy incident PPFD under sunlit conditions was $1032 \mu\text{mol m}^{-2} \text{s}^{-1}$, and the mean above-canopy value during diffuse conditions was $351 \mu\text{mol m}^{-2} \text{s}^{-1}$. Irradiance under diffuse conditions was 34% of that under direct sunlight.

Diurnal variation in PPFD followed expected patterns (Fig. 3), with solar elevation and changes in cloudiness driving low- and high-frequency shifts in irradiance. The dynamics of the diffuse fraction (Fig. 3) were clearly linked to shifts in total irradiance. Over the full set of sky measurements collected during the summer of 2012, the diffuse fraction had a bimodal frequency distribution (Fig. 4), such that the fraction tended to be > 0.8 (cloudy conditions dominated over mid-summer) but some sunny periods led to a second, minor peak in frequency for fractions from 0.15 to 0.4.

Within-canopy radiation The within-canopy data, collected over midday periods, revealed the expected decline in mean irradiance with depth in the canopy (Fig. 5). The ratio between mean irradiance under diffuse conditions to sunlit conditions for each canopy layer varied from 27% to 39%, spanning the ratio recorded for incident radiation above the canopy (34%). There was no clear trend in this ratio with depth in the canopy, with the lowest ratio at mid-canopy (0.5 m) and the highest at the bottom of the canopy (0.05 m).

Under sunlit conditions (low ϕ), the mean absolute difference (MAD) in irradiance within each canopy layer was relatively low in the highest canopy layers (at 0.8 m above the ground). The ratio MAD : mean was 11% at 0.8 m, but increased to 46% at 0.2, 0.35 and 0.5 m. Under diffuse conditions (high ϕ), the ratio MAD : mean was greater in all layers (reaching 61% at 0.5 m), except at 0.2 and 0.35 m, where its value of 34% and 41% were

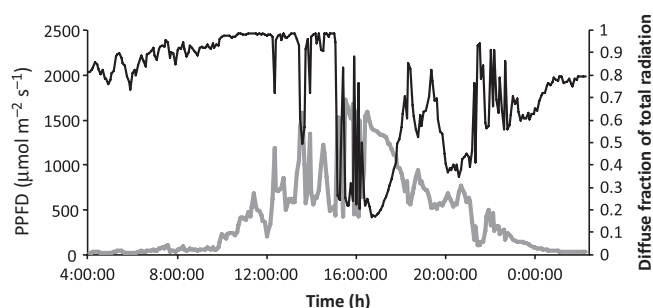


Fig. 3 Light climate on 10 July 2012 at Toolik Lake LTER, Alaska, sampled at 5-min intervals ($n = 288$). The paler line (left axis) records total photosynthetic photon flux density (PPFD), and the darker line (right axis) records the diffuse fraction of PPFD when $\text{PPFD} > 10 \mu\text{mol m}^{-2} \text{s}^{-1}$.

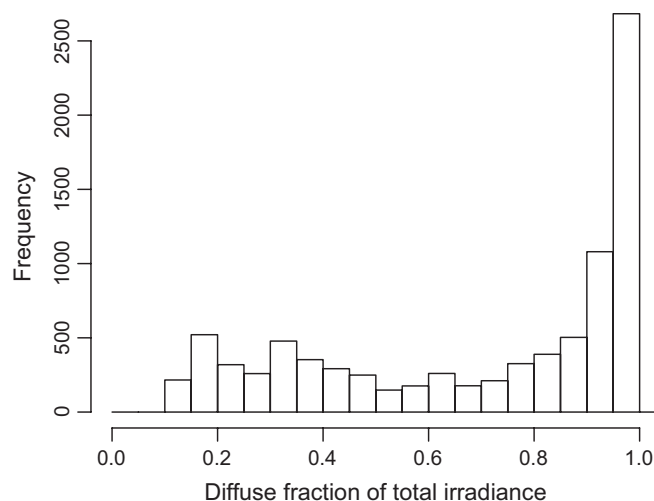


Fig. 4 Frequency distribution of diffuse fraction (ϕ) of photosynthetic photon flux density (PPFD) collected from 28 June to 8 August, 2012, at Toolik Lake LTER. Data were filtered to remove measurements when total $\text{PPFD} < 10 \mu\text{mol m}^{-2} \text{s}^{-1}$, $n = 8641$.

slightly lower than under sunlit conditions. The mean canopy ratio MAD : mean for irradiance in each canopy layer was similar under direct and diffuse illumination (36%).

The mean fraction of incident radiation at each depth in the canopy was similar under direct and diffuse sky conditions (Fig. 5); at 0.8 m, the fractions differed by only 3%. But then the fraction dropped more rapidly with depth under high ϕ , declining to 0.48 at 0.5 m, compared to 65% under sunlit conditions. In the lower canopy layers, at 0.05 and 0.2 m, the fractions were more similar under varied ϕ . As with the total radiation measurements, the variation in conditions at each depth in the canopy followed similar patterns with sky conditions. The ratio MAD : mean was highest for diffuse sky conditions in the mid-canopy (62% at 0.5 m) and lowest at canopy top (21% at 0.8 m). Under sunlit conditions the ratio MAD : mean was highest mid-canopy (47% at 0.2, 0.35 and 0.5 m) and lowest at canopy top (11% at 0.8 m).

Variation in canopy light environment Under sunlit conditions (low ϕ), the distribution of irradiance within the plant canopy normalised by maximum irradiance was distinctly bimodal. The largest peak in frequency was at a relative irradiance of 5–10% (Fig. 6) with a further similar peak (82% of the magnitude of the largest peak), at 85–90% relative illumination. 9.1% of the total readings in sunlit conditions were at the lowest level of fractional irradiance (0–5%).

The distribution of normalised irradiance within the plant canopy under diffuse conditions (high ϕ) had a peak in frequency at relative irradiance of 10–15% (Fig. 6). The overall distribution was log-normal, with a relatively consistent exponential decline in frequency of greater irradiance. At 75–80% illumination there was a relatively small extra peak in density (36% the magnitude of the main peak). Of the total readings in diffuse conditions, 3.4% were at the lowest level of fractional irradiance (0–5%). A Pearson's Chi-squared test indicated a highly significant

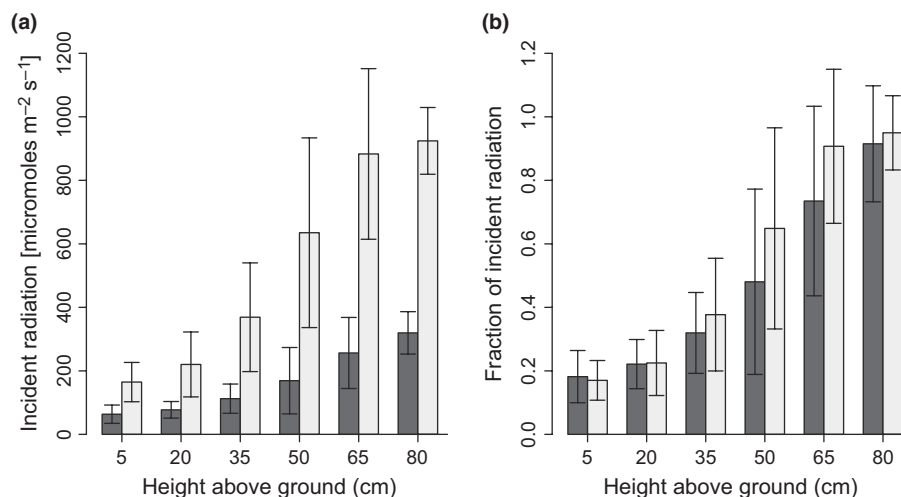


Fig. 5 Profiles of photosynthetic photon flux density (PPFD) measurements through 12 arctic shrub canopies collected between late June and early August 2012 by the SunScan sensor. (a) The mean value (columns) and median absolute deviation (error bars) of PPFD at six heights above ground level, within the canopy. (b) The fraction of radiation incident at each level relative to the maximum irradiance measured above the canopy during the sampling period. For (a) and (b) results are shown under sunlit (low ϕ , light grey) and shaded (high ϕ , dark grey) irradiance. Results are based on 12 672 measurements under diffuse illumination and 9984 measurements in direct sunlight. The similar results in the right panel should be contrasted with Fig. 6, which shows very different levels of shading under altered sky conditions.

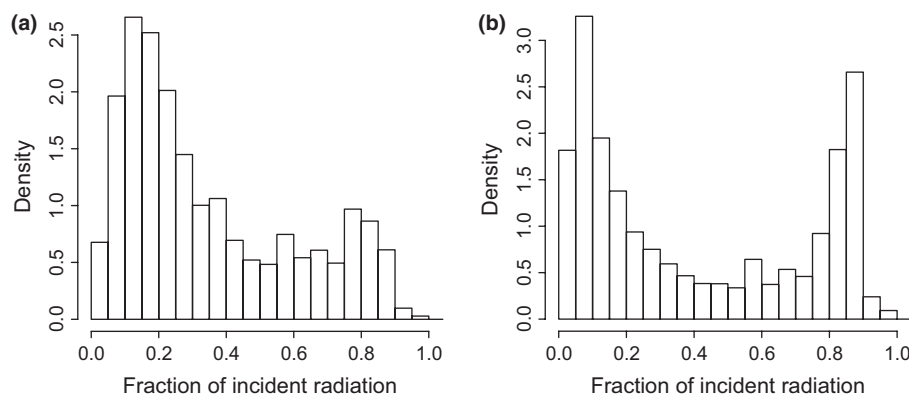


Fig. 6 The fraction of incident radiation measured within shrub canopies is presented as a probability density distribution, summing to 1. Data were recorded within 12 arctic shrub canopies, between late June and early August 2012 by the SunScan sensor. Incident radiation was normalised by the maximum value recorded during the measurement period. (a) Data collected under diffuse irradiance (high ϕ); (b) data collected under direct solar illumination (low ϕ). Results are based on 12 672 measurements under diffuse illumination and 9984 measurements in direct sunlight.

difference ($P < 0.001$) between the distributions of normalised irradiance within sunlit and shaded canopies.

Chamber flux measurements, photosynthesis and CO_2 exchange rates

We determined the standard deviation around the mean R_{eco} measurement for each sample period, using 164 sample measurements of ecosystem respiration over 34 sampling periods ($n = 3$ –7 for each period, this number depending on how many replicated measurements of NEP under zero light were collected). The mean value for the overall error estimate was $1.24 \mu\text{mol m}^{-2} \text{s}^{-1}$, reflecting the overall uncertainty on the flux estimates.

The light response curves differed between illumination conditions (Fig. 7), with NEP rising more steeply with light intensities

under diffuse conditions. The model fitting to all curves, stratified by light conditions, allowed a statistical analysis of photosynthetic and carbon cycling parameter sensitivity to light conditions (Table 1). The modelled light compensation point was significantly (46%) greater under low ϕ conditions ($P < 0.05$). Also, the chamber analysis indicated that photosynthesis at $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD was significantly greater ($2.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, or 17%) under diffuse conditions ($P < 0.001$). However, the measured ecosystem respiration and the maximum observed gross photosynthetic rate showed no significant differences between the light manipulations (Table 1). The modelled R_{eco} (i.e. the optimal fit of this parameter to the data) did indicate a statistically significant difference between manipulations, but only by 4%, which is probably not ecologically significant. There was no significant difference between the modelled maximum photosynthetic rates under varied ϕ (Table 1). The estimated

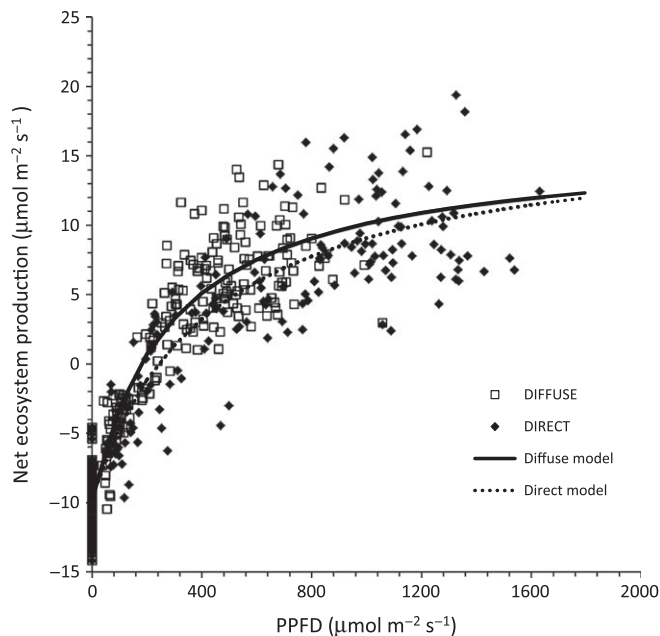


Fig. 7 Complete light response data (PPFD, photosynthetic photon flux density) for net ecosystem production (NEP) measured over 14 canopies dominated by *Betula nana* and *Salix pulchra*. Paired light curves were generated over each canopy, once with direct solar insolation (low ϕ , 'Direct') and once with a diffuser in place or cloudy conditions ensuring diffuse illumination only (high ϕ , 'Diffuse-D'). Model parameters were fitted separately to diffuse and direct data, and the optimised model curves are shown as lines.

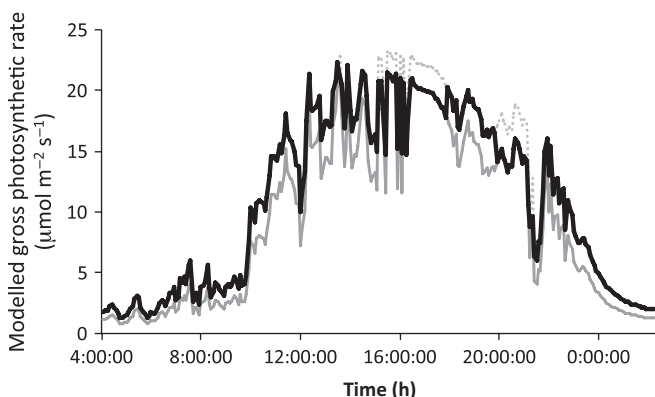


Fig. 8 Estimates of photosynthesis for a typical shrub canopy at Toolik Lake LTER on 10 July 2012, derived from the model using two different parameterisations applied at 5 min intervals ($n = 288$). One parameterisation was derived from chamber flux estimates of photosynthesis during diffuse conditions (dotted line), and the second from estimates during sunlit conditions (grey line). The measurements of the diffuse fraction (Fig. 3) were then used to generate a combined model (black line), deriving the photosynthesis estimate from the appropriate calibration depending on light conditions at that time.

half-saturation point was 69% greater under low ϕ (sunlit) conditions, and quantum yield was 30% lower. However, both these differences were only significant at $P < 0.1$.

The model fitting to data aggregated by sky conditions generated largely similar results to the fitting by individual light curves (Table 1). There were consistent patterns for GPP_{600} , GPP_{300} , light compensation point and quantum yield. There were

differences in the fitted model parameter, k and P_{max} , with lower values reported here.

Effect of sky conditions on diurnal patterns in gross primary production

The modelled GPP using shade parameters (Table 1) was consistently higher than the estimate using the sunlit parameter with a range of sky conditions. Across the seven modelled days, the mean daily integrated rate of photosynthesis was $11.6 \text{ gC m}^{-2} \text{ d}^{-1}$. Using the parameters derived from sun-lit chamber measurements alone (low ϕ parameters), the mean photosynthesis was 15% lower, $9.9 \text{ gC m}^{-2} \text{ d}^{-1}$. Using high ϕ parameters, photosynthesis was 3% greater, $12.0 \text{ gC m}^{-2} \text{ d}^{-1}$. The effects of sharp shifts in diffuse fraction and total PPFD (Fig. 3) were therefore damped in the combined model, which is clearly visible across a representative day (10th July) (Fig. 8). A reduction in total PPFD had a smaller effect on photosynthesis because of the switch to the alternate (high ϕ) parameter set, with its greater productivity at low-intermediate light intensities. The modelling assumes that full adjustment by leaves to changes in irradiance is possible on its fundamental time-scale, 5 min, which is consistent with the adjustment time noted during the shading experiments. We also assume consistent physiological activity throughout the day, whereas there is evidence of circadian rhythms in arctic shrubs (Patankar *et al.*, 2013).

Discussion

The literature on the sensitivity of GPP to sky conditions has been dominated by analyses of EC fluxes, generally inferring ϕ from total PPFD data, and by model sensitivity analyses (e.g. Gu *et al.*, 2002; Alton, 2008). We report here the first near-simultaneous measurements of ϕ , within-canopy radiation at leaf scales and GPP recorded at m^2 scales. The data provide, for the first time, a means to test hypotheses on light distribution within natural canopies and its links to sky conditions and CO_2 exchanges.

Distribution of irradiance within the shrub canopy

The first hypothesis (H1) stated that under higher ϕ , radiation will have a unimodal distribution within canopies, with increasingly bimodal illumination at lower ϕ . The density distribution of normalised within-canopy irradiance under low ϕ (sunlit conditions) supported this hypothesis (Fig. 6), with a clear indication of bimodality in the sunlit canopy. The density distribution of normalised irradiance data under diffuse illumination was more closely unimodal, but not normal, being clearly skewed towards lower values (Fig. 6). These data provide a very powerful means to evaluate radiative transfer schemes within canopies under varied sky conditions – such schemes are often employed in land surface schemes, but less often evaluated.

Evenness of canopy illumination

The second hypothesis (H2) stated that under higher ϕ canopies will be more evenly illuminated, with relatively fewer areas of

deep shade. The variability in irradiance (mean absolute difference) within a canopy layer was similar when averaged across all layers under both direct and diffuse illumination (Fig. 5). Likewise, the fraction of solar radiation incident with depth in the canopy was similar with varied ϕ , and had similar magnitudes of within-layer variation. Thus, analyses based on comparison of means, and using mean absolute deviations, failed to reveal clear differences in evenness of illumination. This was an unexpected result and indicates that simple statistical summaries of within-canopy light climate have limited information content.

However, a comparison of the density distributions of relative irradiance was revealing (Fig. 6), with more extreme values of relative illumination likely under direct irradiance. Under high ϕ the proportion of the canopy in deep relative shade was only 37% of that measured under low ϕ , and this supports H2. We conclude that under diffuse illumination there was a significant difference from sunlit conditions in the proportion of the canopy that was deeply shaded relative to above canopy irradiance. The results are expressed as relative shade, and in sunlit conditions the total irradiance tends to be larger than under diffuse conditions. So at high light, the foliage in deep relative shade in sunlit canopies may still be well enough illuminated to saturate photosynthesis. At lower total irradiance and low ϕ , our results suggest there will be a greater light limitation of photosynthesis due to deeply shaded areas.

Sensitivity of ecosystem light compensation point to irradiance and sky conditions

The third hypothesis stated that under higher ϕ , canopies will have enhanced light-use efficiency (LUE), manifested by a lower half-saturation point (k), greater quantum yield (E_0) and lower LCP. The model fitting exercise and statistical tests confirmed that there was a significant difference in E_0 and k , but only at $P < 0.1$. The weakness of this test is probably related to the correlation between P_{\max} and k in model fitting (Williams *et al.*, 2006); model fits are best constrained in P_{\max} – k space. But the significant difference in estimates of the light compensation point ($P < 0.05$) under differing sky conditions more strongly supports the hypothesis (Table 1). Given that there was only a small difference in ecosystem respiration, the lower LCP under diffuse conditions is consistent with enhanced LUE.

Sensitivity of maximum canopy photosynthesis to irradiance and sky conditions

The fourth hypothesis stated that under high irradiance maximum photosynthesis would be greater with higher ϕ . The inverse correlation between irradiance and ϕ (Knobl & Baldocchi, 2008), and the scarcity of high illumination days during the study complicates any test of this hypothesis. However, the observed similarity in maximum gross photosynthesis under the highest light intensities incident with varied sky conditions (Table 1) does not support this hypothesis (Fig. 7). The model fitting exercise also found no significant difference in P_{\max} with variation in sky conditions (Table 1), although we note the

uncertainty on this estimate linked to potential correlations with the other fitted parameter (k). This result agrees with the analysis of deep relative shading outlined above; ϕ has no impact on efficiency of light use at highest levels of insolation.

This falsification is consistent with the hypothesised determinant of higher quantum yield under diffuse conditions – the lower proportion of relative deep shade. At high incident light, even the deeply shaded fraction of sunlit canopies will receive enough illumination for saturating photosynthesis, and thereby match the GPP of diffuse conditions. Process models can be used to test this hypothesis further. We do note that periods of high illumination were rare during the study period (Fig. 4).

The interactions between sky conditions and canopy photosynthesis

The combined analysis of H3 and H4 suggests that under low-intermediate levels of incident radiation ($< 600 \mu\text{mol PPFD m}^{-2} \text{s}^{-1}$), typical for arctic environments (Fig. 4) clear differences occur between photosynthetic rates under varied ϕ . Under diffuse conditions the canopy was more efficient at using a limited light resource than it was under sunlit conditions. However, during periods of high irradiance at the study site the differences in photosynthetic rate were minimised, because the highest illumination is correlated with low ϕ .

The radiation density distributions within canopies collected under varied ϕ explain the processes behind these observations. Radiation values were not normally distributed under either diffuse or direct illumination. At similar values of incident irradiance, under diffuse conditions (high ϕ) a smaller proportion of the canopy was in deep shade than under sunlit conditions (low ϕ) (Fig. 6). Because of the nonlinear response of photosynthesis to irradiance, the highly bimodal distribution of light within sunlit canopies was responsible for reduced overall carbon fixation at the canopy scale at lower incident light intensities. Descriptive statistics of radiation change with depth in canopies (Fig. 5) failed to indicate the critical non-normal variation (Fig. 6) that explains the different photosynthetic responses of the canopies to varied ϕ . Only when viewed as a complete density distribution does the difference in shaded fractions become visible (Fig. 6). This result likely relates to complex distribution of deep shade throughout the canopy, not just in its lowest layers.

An important next step is to explain the implications of the within-canopy light environment under varied sky conditions on leaf-level photosynthesis, and upscale to the canopy. Relating the leaf-scale ($c. 100 \text{ mm}^2$) variations in irradiance to leaf distribution and leaf-level photosynthetic light response curves will allow detailed exploration and modelling of LUE within the canopy. These calculations will provide further understanding of how evenness in the canopy light environment affects photosynthesis. Variation in light conditions can also be linked to leaf-level physiology (Heskel *et al.*, 2012), and leaf trait variation within canopies, including foliar N concentration, leaf size and orientation, and leaf mass per area (Wright *et al.*, 2004). Combining this information will allow investigation of optimisation theories related to LUE (Hirose & Werger, 1987).

The data here have considerable value in evaluating models of radiative transfer and LUE for closed canopies (Huemmrich *et al.*, 2010; Bonan *et al.*, 2012). Model outputs suggest that significant increases in LUE in more diffuse radiation climates of past decades (Mercado *et al.*, 2009), resulted in greater rates of global photosynthesis during such periods, and declining rates in recent years as irradiance has increased and ϕ has fallen. However, the modelling assumed no change in canopy structure, or leaf traits, over the modelled period. It is well known that leaves adapt their structure to their local light intensities (Boardman, 1977; Brodersen *et al.*, 2008). We might also expect canopies to adapt to changing ϕ to maximise their productivity. Recent evidence suggests that this is the case. Street *et al.* (2012) showed that arctic plant communities sampled in locations with varied ϕ but similar species composition shifted the relationship between total foliar N (TFN) and leaf area index (LAI). The shifts were consistent with optimisation theory, that suggests steeper gradients in foliar N through canopies growing at low ϕ . With high ϕ , N is more evenly distributed through the canopy, to match the radiation distribution. This new evidence necessitates both a renewed focus on the interaction of radiation climate with plant canopies, and a deeper understanding of the plasticity of community aggregated traits, such as LAI and TFN (Williams & Rastetter, 1999; Van Wijk *et al.*, 2005). Based on our analysis of canopy radiation distribution, we envisage improved parameterisations of 'big-leaf' models of photosynthesis based on Beer's Law, for varied sky conditions.

A caveat of this study is its limitation to a single community, shrub tundra, at high latitudes, and, therefore, low solar elevations. However, we hypothesise comparable results for the distribution of radiation within closed canopies at lower latitudes. Sky conditions vary globally between modes of high and low ϕ , and so the underlying theory of radiation distribution according to ϕ (Fig. 1) is not dependent on sun angle. Thus, the proportion of relative deep shade in closed canopies will decline with increasing ϕ , globally. On this basis, we hypothesise that LUE should be enhanced at high ϕ across latitudinal gradients (consistent with literature cited in the introduction).

Conclusions

Uniquely detailed measurements of light conditions within shrub canopies and their net ecosystem exchange of CO₂ were made under varied sky conditions (ratios of diffuse to total irradiance, ϕ). The radiation density distributions indicated a clear difference in the within-canopy light environment dependent on ϕ , with a more unimodal distribution of relative irradiance under diffuse conditions, and a clear bimodal distribution under sunlit conditions. Profiles of mean irradiance, with their assumptions of normal distributions, failed to show these non-normal variations in the within-canopy light climate. The measurements of ecosystem gas exchange showed clear differences in the shape of the response of total photosynthesis to varied light under differing ϕ . Under diffuse conditions, the canopy had higher LUE, with a higher quantum yield, and 17% higher photosynthesis at a representative 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. Through a daily cycle, with

shifts in total irradiance and correlated changes in ϕ , the alterations in the light-response curve, for direct vs diffuse conditions, damped changes in modelled photosynthesis on fine timescales. The detailed measurements of within-canopy light explained the greater LUE under high ϕ ; this was due to the proportion of the canopy in deep shade relative to incident irradiance being 37% the value for sunlit conditions. Linked to the nonlinear response of photosynthesis to light, this alteration in the density function for illumination explains the change in light response. Further investigations must focus on how leaf traits and leaf level processes are linked to the light environment, and their plasticity under global change. Another goal must be to evaluate canopy radiative transfer models, and process models of photosynthesis, against these data, to test fundamental understanding of upscaling from leaf to canopy gas exchange.

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