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Spatial variability of photosynthetically active radiation in European beech and Norway spruce

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ABSTRACT

The vertical and horizontal variability of solar radiation within a mature European beech (*Fagus sylvatica* L.)–Norway spruce (*Picea abies* [L.] Karst) mixed stand in Southern Germany is investigated. A large dataset with more than one million spectral measurements of photon fluence rates at six vertical levels within the stand is analyzed with respect to tree species, meteorological sky conditions, and the influence of solar elevation angle on canopy penetration. Irradiance probability density functions of the photosynthetically active waveband are used to describe the three-dimensional radiation field. For a quantification of umbra, penumbra, and sunfleck frequencies, in-canopy fractions of photon fluence rates within the photosynthetically active waveband are investigated. Different phenological stages of beech and their effects on the in-canopy light climate are compared. The results show that during overcast conditions (OVC) fractions of photosynthetically active radiation (PAR) are higher at all canopy levels than during clear sky (CS) conditions due to their exclusively diffuse character. The lowest median PAR level of less than 1% of above-canopy PAR can be observed in the shade crown of beech and at ground level. More PAR can penetrate the canopy at a higher solar elevation under CS conditions. This effect is more pronounced for spruce than for beech due to the conical crown shape of the conifers that allows photons from higher angles to enter the gaps inbetween trees in contrast to the more homogeneously closed beech canopy. Solar elevation is not an important factor at uniformly overcast conditions. Differences in the vertical distribution of umbra and penumbra can be detected when comparing species or different sky conditions. The frequency of sunflecks differs more by species and by the vertical position within the canopy than by sky condition.

1. Introduction

Solar radiation plays a key role in growth and competition in plant ecosystems. It interacts with biomass by supplying the phytoelements with the necessary energetic input for photosynthesis by utilizing photons within the spectral waveband from 400 to 700 nm, termed photosynthetically active radiation (PAR). Radiation also provides cues for growth processes via the spectral composition of incoming radiation, referred to as light quality. This information is used to regulate growth by means of pigmentary absorption especially in the UV, blue, and red fraction of the solar spectrum (Ammer, 2000; Smith, 1994).

The radiation field within a forest canopy is spatially (vertically and horizontally) and temporally highly variable. This is because of wavelength-selective reflection, transmission, and absorption of photons by heterogeneously distributed phytoelements. Plant canopies operate as light filters affecting the spectral and spatial distribution of light at ground level (e.g. Grant, 1997).

The light climate at a certain location within the canopy, or at the forest floor, is therefore dependent on several parameters. Amongst these, differences in the incoming direct and diffuse radiation field, and canopy architecture, composition and density, as well as phenological development account for most of the variability (Capers and Chazdon, 2004; Wang and Jarvis, 1990a,b; Ross et al., 1986; Baldocchi et al., 1984b). Most of the absorption and spectral changes take place in the upper part of the sun crown. These processes are strongly dependent on solar elevation and sky conditions that determine incoming radiation and the incident angle of direct irradiance (Wang et al., 1992).

Factors influencing the spatial distribution of radiation result in the occurrence of different levels of shading such as umbra, penumbra, and sunflecks with varying photon quantity and spectral quality. Several studies have investigated the distribution of solar radiation in forest stands. For example, Mõttus (2004), Ross and Mõttus (2000a,b), and Ross et al. (1998) studied the statistics of PAR variability by examining measured and modeled proba-

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Nomenclature

CS	clear sky conditions
FOC	fiber optic cable
IPDF	irradiance probability density functions
k_t	clearness index
LAI	projected leaf area index
N	fractional cloud cover
OVC	overcast sky conditions
PAR	photosynthetically active radiation (400–700 nm)
PFD	photon flux density
PFR	photon fluence rate
PPFR	photosynthetic photon fluence rate
$PPFR_{rel}$	transmitted fraction of photosynthetic photon fluence rate
θ_s	solar elevation angle

bility densities of sunfleck, penumbra, and umbra as functions of duration and optical path length in willow coppice. Vierling and Wessman (2000) reported temporal and spatial PAR heterogeneity in a tropical rain forest. Penumbral effects in Scots pine canopies were reported by Oker-Blom (1985, 1984) and for shoots on a smaller scale by Palmroth et al. (1999). The linkage of sunfleck frequency and PAR variability with canopy structure and architecture has been investigated horizontally for shrub thickets (Brantley and Young, 2010, 2009), Douglas fir (Chen and Black, 1992), and soybean (Pearcy et al., 1990), and three-dimensionally for various trees including evergreen oak (Gratani, 1997). The current study investigates the vertical and horizontal PAR variability in European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* [L.] Karst) in a mixed stand using continuous, quasi-simultaneous measurements at 130 different positions within the stand over several months.

The frequency and composition of different light levels are very important factors for ecological processes such as growth and biomass allocation through providing photosynthetic energy or by triggering morphogenetic processes (Smith and Whitelam, 1997). The ecological relevance and importance of sunflecks and the variability of different light and shading levels due to its strong temporary enhancement of radiation has been emphasized in many studies (e.g. Ammer, 2003; Smith, 2000; Grant, 1997), but is beyond the scope of the current paper. A detailed overview of the importance of sunflecks to photosynthetic responses, seed germination, growth, reproduction and many other factors can be found in e.g. Chazdon (1988).

Due to high variability, snapshots in time and space can only show the instantaneous conditions of the light climate in a stand. In order to estimate the principal patterns of the light distribution and parameterize the factor 'light' for models, data have to be obtained for longer time intervals with respect to changing meteorological conditions and developmental stages with a high spatiotemporal resolution.

In ecological studies involving three-dimensional objects such as plants and phytoelements, radiation is appropriately quantified as the photon fluence rate (PFR), i.e. photons intercepted by a sphere per unit time rather than photon flux density (PFD; Björn and Vogelmann, 1996; Björn, 1995; Smith, 1982; Smith and Morgan, 1981). The omnidirectional measurement of photons thus requires detectors with spherical characteristics instead of the widely used planar sensors (Björn and Vogelmann, 1996; Björn, 1995; Smith, 1994; Hartmann, 1978; Byrne, 1966). Comparative measurements of PFR and PFD for the photosynthetically active waveband showed significant differences by a factor of 2–6 under different conditions such as changing solar elevation and cloud cover (Leuchner et al., 2005; Björn and Vogelmann, 1996). A comparison to previous studies utilizing planar sensors can only be made for conditions of uniformly overcast sky due to the greater homogeneity of incoming radiation and the fractional approach with relative radiation levels of the present work. A comparison under clear sky conditions, especially at low solar elevations (i.e. close to sunrise and sunset), is only possible with severe restrictions.

Relationships between light availability and light quality in terms of the red/far red ratio have been described e.g. by Leuchner et al. (2007), Capers and Chazdon (2004), Muraoka et al. (2001), Olesen (1992), and Lee (1987).

The key question addressed in the current paper is how to spatially and temporally characterize the PAR filter function and resulting sunfleck frequency in a mixed stand as determined by species, weather conditions and sun elevation.

2. Materials and methods

2.1. Experimental set-up and site

The system for measuring the spectral radiation distribution was previously described in detail by Leuchner et al. (2005). Thus, the following section gives only a brief overview of the methods used. Measurements were carried out at the Kranzberger Forest experimental site located approximately 35 km northeast of Munich, Germany (48°25′08′′N, 11°39′41′′E, 485 m a.s.l.). This forest is a mixed mature stand of Norway spruce and European beech and characterized by a projected leaf area index (LAI) of around 6 m^2 m^{-2} for both beech and spruce at full foliation (Reiter, 2004; Pretzsch et al., 1998). The maximum leaf area density for beech is 6.0 situated in the upper third and 2.6 for spruce in the lower half of the canopy (Häberle et al., 2003). The basal area is 46.4 m^2/ha the stand density 764 stems/ha (Wipfler et al., 2005).

A multichannel-system of 130 sensors based on fiber optic cables (FOCs) with 0.6 mm core diameter of quartz glass and sensor heads consisting of solid white polyoxymethylene spheres of 10 mm diameter was developed and deployed. An extensive calibration procedure described by Leuchner (2006) identified the directional independence of the sensitivity of the sensor heads to incoming radiation from the entire solid angle (4π sr). All FOCs were connected to a high-precision multiplexer matrix. The incoming photons were then measured by a multichannel 1024 diode-array spectrometer (MCS module UV-VIS-NIR, Carl Zeiss AG, Germany) mounted onto two high-precision stages with electrodynamical linear drives that operated as an X-Y-scanner with a positioning accuracy of <2 μm. All 130 FOC positions were sequentially encountered within a total measuring cycle of approximately 2 min.

Within the canopy the 130 sensors were mounted in a grid of 25 vertical profiles consisting of six levels within both beech (12 profiles) and spruce (13 profiles) sections. A scheme of the plot is shown in Fig. 1. Ground level (1) and canopy levels 2, 4, and 5 (3, 14, 20, and 23 m height above the ground, respectively) were equipped with 25 sensors each. A reduced number of 13 sensors was attached above the canopy at level 6 (26 m), because little spatial variability in the incoming radiation was expected. The remaining 17 sensors were mounted at canopy level 3 (17 m). The resulting data were available in a high spectral resolution of 0.8 nm within the waveband of 360–1020 nm covering a small fraction of UV-A (<380 nm), the entire visible range (380–780 nm) including PAR (400–700 nm), and parts of the near-infrared (>780 nm).

2.2. Data analysis

Data were differentiated in terms of species, cloud cover, phenological stage of beech, height, and solar elevation angle θ_s. Only data with positive θ_s were considered and grouped into classes of