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Functional relationships to estimate Morphogenetically Active Radiation (MAR) from PAR and solar broadband irradiance measurements: The case of a sorghum crop

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ABSTRACT

Light quality plays a key role in higher plants' morphogenesis. In most plant models, light is considered as a consumable resource and plants are assumed blind to light signals. However, prior to any effort for modelling photomorphogenetic mechanisms, it is necessary to characterise the spatial distribution of the Morphogenetically Active Radiation (*MAR*) over and within plant canopies. Measurements of local photosynthetic photon flux density (*PPFD*) and broadband irradiance (*Es*) are easy to carry out by using small sensors. Thus, the distribution of the *MAR* within a canopy can be estimated whenever the functional relationships between these measurements and the photon flux within any spectral band are known. The objective of this work was to determine these functional relationships from the light spectra received above and at various positions around a target plant within a growing sorghum crop. The *MAR* components considered in this work are related either to photon flux densities in various wavebands between 330 and 950 nm or to the ratio between two photon flux densities. A part of the photon flux-related variables is strictly included in the *PAR* band and might be estimated from *PPFD* measurements using linear relationships. The other variables are related to both *PPFD* and *Es* by multiple linear relationships. The phytochrome photoequilibrium and the red to far-red ratios were related to the relative transmitted *PPFD* and to the ratio *PPFD*/*Es* within the canopy using a non-linear model. Models were validated against an independent set of data. We demonstrate that the *MAR* components within a sorghum crop can be accurately estimated with the functional relationships presented in this paper.

1. Introduction

In most growth and development plant and crop models, light is viewed only as a consumable resource and plants are assumed blind to light signals. However, the perception of these signals by the plant is now well documented and light quality is considered to play a key role in the changes of plant's architecture and the dynamics of vegetation (e.g. Kasperbauer, 1992; Ballaré et al., 1997) through what is known as the Morphogenetically Active Radiation (*MAR*[2]; Varlet-Grancher et al., 1993). Phytochromes, cryptochromes and phototropins are the main systems used by higher plants to sense their light environment (Gyula et al., 2003; Wada et al., 2005).

Phytochromes absorb radiation within the wave band 300–800 nm and are capable of existing in two stable but photo-interconvertible forms: Pr and Pfr. Pr is the red absorbing form with maximum absorption at around 660 nm while Pfr is the far-red absorbing form with maximum absorption at around 730 nm. The relative concentration of these two forms of phytochromes within its tissues allows the plant to sense variations in the spectral composition of light reaching them. The most convenient method to characterise the phytochromes' action is by estimating a projected phytochrome photoequilibrium, $\varphi c = [\mathrm{Pfr}]/([\mathrm{Pfr}] + [\mathrm{Pr}])$, and the rate of phototransformation of the Pr form to the Pfr form and *vice versa*, also called the rate of cycling, *H* (Smith, 1994). φc and *H* are calculated by integrating the spectral photon irradiance with the photochemical parameters for the Pr and Pfr forms of the phytochrome A (Sager et al., 1988; Mancinelli, 1994; Smith, 1994). The ratio of red (*R*) to far-red (*FR*) photon irradiance (*R*:*FR*) is a simplified approach to estimate the phytochrome photoequili-

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[2] See Appendix A for the list of notation and symbols.

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brium (Smith and Holmes, 1977). In addition, far-red photon irradiance has also been implied in some morphological and physiological responses such as leaf movement or hypocotyl growth (e.g. Tanada, 1997; Casal et al., 1998).

Cryptochromes and phototropins are two systems acting as photon counters (Smith, 1982) in ultraviolet A (*UVA*) and blue light. Cryptochromes are active within the range 390–530 nm with a fairly flat response between 390 and 480 nm (Ahmad et al., 2002) whereas the phototropins activity show a clear peak at 450 nm (Christie et al., 1998). In practice, *UVA* and blue light signals are usually characterised by the photon irradiance integrated over various wavebands within the 350–500 nm region (Varlet-Grancher et al., 1993).

Plants react to light signals received locally by various tissues and organs that are considered the sites of perception (Lecharny and Jacques, 1974; Morgan et al., 1980; Thompson, 1995). Knowledge of the spatial distribution of the light quality over the plants is necessary to understand morphogenetic mechanisms and to model plant morphogenesis (Varlet-Grancher et al., 1993; Gautier et al., 2000; Rajcan and Swanton, 2001; Evers et al., 2007).

The need for local measurements or adapted 3D models to describe the climate perceived by individual plants and organs (phylloclimate) has been recently highlighted by Chelle (2005). Characterising the spectral light phylloclimate involves estimating the spatial and temporal distribution of photomorphogenetic signals by measurements (e.g. Pecot et al., 2005; Leuchner et al., 2007) or by modelling (Combes et al., 2000; Chelle et al., 2007). The latter approach is rather complex and not widely applied with only a few studies already published (Gautier et al., 2000; Evers et al., 2007; Dauzat et al., 2008).

The "classical" measurements and models of light transmitted under various canopies characterise the distribution of the light received on horizontal planes (light arriving from above the planes) within the vegetation as shadow and sunfleck areas. However, various studies (e.g. Kasperbauer et al., 1984; Ballaré et al., 1987; Gilbert et al., 1995) have shown the significant effect of horizontally propagated *R* and *FR* photon fluxes within a canopy on the crop structure and functioning. In order to characterise the *R*:*FR* ratio in horizontally propagated light fluxes received by a stem, Ballaré et al. (1987) used a cylindrical integrating system while Gilbert et al. (1995) built specific narrow sensors. These two devices have a narrow aperture of 10° while a vertical cylindrical organ receives radiation over the space integrated from $-\pi/2$ to $+\pi/2$ for the zenith angle and from 0 to 2π for azimuth angle of the incident light (van der Hage, 1993). Due to the non-uniformity of the geometry of the photoperceptive organs (lamina, petiole, stem, bud) of a plant, the detector's geometry of sensors used to characterise light signals cannot be standardised (Smith, 1982). However, underpinned by the assumption that any 3D geometrical form can be discretised in smaller planar elements, a cosine-corrected planar surface appears as a practical method in photomorphogenetic studies (Smith, 1982; Child and Smith, 1987; Pecot et al., 2005). The spectral photon distribution (SPD) of the horizontally propagating light flux has been measured within a canopy in only a few cases (Kaul and Kasperbauer, 1988; Smith et al., 1990). Levels of blue and other spectral bands on horizontal planes within a canopy have been expressed as a proportion of *PAR*, either as energy (Messier and Bellefleur, 1988) or as photon flux (Olesen, 1992). In a similar way, the *R*:*FR* ratio has been related to: (i) transmitted *PAR* or broader band irradiance (Frankland and Letendre, 1978); (ii) relative transmission (Holmes and McCartney, 1976; Capers and Chazdon, 2004; Leuchner et al., 2007); (iii) cumulated leaf area index (Holmes and McCartney, 1976) and (iv) gap frequency (Lasko, 1980) and overstory stocking (Pecot et al., 2005).

Measurements of local photosynthetic photon flux density (*PPFD*) and broadband irradiance (*Es*) are nowadays easy to carry out by using pyranometers and small quantum sensors (e.g. Gutschick et al., 1985; Chartier et al., 1989; Adam and Sinoquet, 1997). Thus, the local SPD within a canopy, and thus the *MAR* components, can be estimated whenever the functional relationships between these measurements and photon flux within any spectral band, as well as the φc and *R*:*FR* ratio, are known.

The objective of the work reported in this paper was to determine these functional relationships from the spectral structure of the radiation in the range 330–950 nm received above and within a canopy. We made measurements at various positions around a target plant within a population of growing sorghum crop. The places and the orientations of the sensor were chosen to be representative of the main likely perceptive organs in Poacea.

2. Materials and methods

2.1. Field conditions and plant characterization

The study was conducted in 1996 and 1997 at Lusignan research station, France (46.44°N, 0.12°E) on a clay-loam soil. Meteorological conditions, including incident global and diffuse *PPFD*, were recorded by a meteorological station near the experimental field. Fibre sorghum (*cv* H 128) was sown in N-S rows on May 15 in 1996 and, in N-S and E-W on June 15 in 1997. Rows were 0.75 m apart and plants were spaced 0.15 m within each row. There was one plot (30 m × 24 m) for each row orientation. Natural rainfall was supplemented with trickle irrigation as needed and mineral nutrition guaranteed by following local agronomic recommendations for this crop.

When the plants were at the stage of five fully expanded leaves, adjacent individuals (19 in 1996 and 15 in 1997) were tagged on three adjacent rows in the centre of each experimental plot. The structure of each plant was characterized using 3D digitising methods (Combes, 2002). For the purpose of the present work, the individual (hereafter target plant) in the centre of each set of plants was used to characterise the light environment of the plant within the canopy. These 3D and light characterisations were performed at five dates during the rapid growth phase of the crop. Leaf area index (LAI) was estimated from the mock-ups of plants reconstructed from 3D digitising data (Combes, 2002; Combes et al., 2008). On the first sampling date, plants were around 0.20 m height with LAI of 0.3 in 1996 and 0.5 in 1997. On the fifth sampling date, plants were around 2.0 m height with LAI of 3.0 in 1996 and 4.3 in 1997.

2.2. Light measurements

Light spectra were measured at 5-nm intervals from 330 to 950 nm with a LI-COR 1800 spectroradiometer (LI-COR, USA) fitted with a cosine-corrected miniature receptor at the end of a flexible quartz fibre-optic light guide. Spectral measurements were sequentially taken on 13 locations around each target plant (Fig. 1). These locations of the receptor were assumed representative of the main likely perceptive organs in Poaceae. The receptor was firstly held horizontally above the crop to measure the incident radiation and above the plant at the whorl level to measure incoming light within the whorl. Then, it was vertically oriented to measure incoming light on the north, south, east and west sides in the upper part of the plant just below the whorl, and in the same orientations at the base of the plant. For the eleventh location, the receptor was held horizontally at 0.10 m above the soil surface in the inter-row, facing downward to measure reflected light by the soil surface. Then, the receptor was turned up to measure transmitted light. The sequence finished by a second measurement of the radiation incident above the crop. In each