Simulating the red:far-red ratio of individual plant organs, a key issue for phytochrome-driven processes.

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Introduction

The red:far-red ratio (R:FR) is a key variable in many biological processes from basic ones such as the response of phytochrome to more integrated ones, such as tillering or weed competition. Accurate estimation of the red:far-red ratio of plant organs in field condition is an important issue to be able to integrate the increasing knowledge on phytochrome-driven processes from cell and organ scale to canopy scale. In this paper, we interfaced an architectural plant model (ADEL-wheat) with a 3D light model (nested radiosity) to simulate the red:far-red signal actually perceived by plant organs in crop canopies.

A coupled model

ADEL-wheat (Evers et al., 2005; Fournier et al., 2003) is an architectural model of wheat, implemented with the L-studio software. It uses the open L-system principles (Mech and Prusinkiewicz, 1996) that enable data exchange with an environmental program. From a given initial planting pattern of seeds, the model calculates growth and development, size, shape and orientation in space of each organ in relation to thermal time. Leaf blade curvature and orientation in space are stochastic elements based on distributions derived from experiments (Fig. 2).

The nested radiosity model (NR) was adapted from the radiosity method to calculate light transfer between plant organs within explicitly described canopies (Chelle et al., 1998). This model requires (i) a 3D description of a canopy pattern by a set of triangles, (ii) a set of light sources described as infinitely far collimated light sources, and (iii) the optical properties (reflectance and transmittance) of soil and phytoelements. To avoid border effects, the model infinitely repeats the canopy pattern (Chelle et al., 1998). From these parameters, the irradiance and absorbed energy of each triangle describing the canopy can be calculated. The NR model is coupled with the ADEL-wheat model using the Caribu interface (Chelle et al., 2004) to manage the data exchanges and programs synchronization.

Experiment and simulations

An experiment using two contrasting wheat canopies (low and high plant population density) was performed in Wageningen (NL) during spring 2004. Downward and sideward R:FR ratios were measured using a Skye SKR100/116 sensor at soil level near midday at six dates during the vegetative cycle. Plant measurements, described in Evers et al. (2006; 2007) were used to fit ADEL-wheat so that the time course of simulated plant architecture matched the measured one.

Light simulations were performed for six dates (Julian days 111, 118, 125, 132, 139, and 146), which corresponded to a large range (0.1-10) of leaf area index (LAI). Four types of sky condition were used: three sun courses respectively corresponding to 6-8 UT hour (Universal Time), 11-13 UT hour and the whole day, an overcast sky (SOC; CIE, 1994). To enable the comparison with measurements, virtual flat square sensors with an area of 13 cm² were randomly located at 24 positions in the canopy, at a height of approximately 8 cm above soil surface. Calculations were performed for five orientations of each sensor (horizontal facing zenith and vertical facing North, East, South and West) and three

different fields of view (FOV) (hemispherical, 40°, and 80°, the latter corresponding to the Skye SKR100/116 sensor).

A variable very sensitive to measurement conditions

Downward and sideward R:FR at soil level calculated by the ADEL-wheat x NR model at the six dates for two plant population densities agreed well with measurements. Simulations were also consistent with previously published results, showing a decrease of R:FR with LAI (Sattin et al., 1994; Sparkes et al., 2006), this decrease being sharper for sideward radiation than for downward one. Simulated R:FR also decreased at low sun elevation, as previously measured by Battla et al (2000). More specifically, the simulations showed an important effect of the measurement conditions on the relationship between LAI and R:FR. (sensor orientation and FOV, duration, sky type). Figure 1a illustrates that, under overcast condition, the decrease of sideward R:FR with LAI was highly depending on sensor FOV, due to the contribution of direct sky light in the measured signal. Figure 1b compares the sideward R:FR measured by a North looking sensor to that obtained by the average of North- East-, South-, and West- looking sensors. As expected, measurements compared well in the case of an overcast sky, but large difference occurred under clear sky conditions, whatever the time of measurement. Such results showed that extreme care should be taken when comparing experimental results obtained by following different measurement protocols.



Fig. 1 Interactions between sensor field of view and illumination conditions on the relationship between LAI and R:FR at soil level (a) North-coming sideward fluxes simulated with various FOV (180° - solid line; 80° - long-dashed line; 40° - short-dashed line), (b) North-coming (solid symbols) and North-, East-, South-, West- coming (open symbol) sideward fluxes simulated with 180° FOV. Sky conditions were overcast sky (\bullet), noon clear sky (\bullet), and morning clear sky (\blacktriangle). R:FR ratio were normalized with the R:FR ratio at top of the canopy.

Estimating the R:FR of target organs within crop canopies

This high variability of R:FR to changing environment and to the orientation of the receptor also underlines the necessity of a direct estimation of the red:far-red ratio at the organs of interest (e.g., internodes) in order to calculate the response to R:FR and to integrate such responses over the plant geometry/structure. The proposed coupled model enables the calculation of the R:FR of plant organs (or even part of organ) within crop canopies (Fig. 2). Level and variability of R:FR from organ to canopy scale may be calculated from the wheat simulations and discussed in relation to the response functions proposed in the literature to model phytochrome-driven processes.

The ability to estimate the R:FR distribution on individual plant organs makes this coupled model a powerful frame to test hypotheses on photomorphogenetic processes from organ to plant to canopy scale. Also, it would provide a way to link the vast body of results obtained at smaller scales from genomic and physiological studies to canopy behavior. Moreover, due to recent progresses in plant architecture modeling, the proposed tool would be suitable for other crop species studied, such as rice, maize, and faba bean.



Fig. 2 Simulated normalized R:FR of plant organs within a low-density wheat canopy at Julian day 132 near midday under clear sky: (a) top view of a single plant, (b) side view of the same plant, (c) grey scale of R:FR.

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