ON THE ASYMMETRY OF THE RED TO FAR-RED RATIOS OF LIGHT PROPAGATED BY THE ADAXIAL AND ABAXIAL SURFACES OF BIFACIAL LEAVES

Gladimir V. G. Baranoski

Natural Phenomena Simulation Group, School of Computer Science, University of Waterloo
200 University Avenue, Waterloo, Ontario, Canada N2L 3G1

ABSTRACT

The integration of remote sensing technologies, ground-based data and predictive modeling has been instrumental in the increase of agricultural output, particularly with respect to the large-scale cultivation of ubiquitous C_3 species such as protein-rich soybean. Further advances can be pursued in this area, however, since key aspects directly associated with crop productivity still remain relatively unexplored. It has been recognized that variations in the red to far-red ratio of light propagated by a plant leaf can influence the growth and the photosynthetic efficiency of adjacent leaves, adjacent plants and, ultimately, affect the entire crop. Soybean plants, like other C_3 species, are characterized by having bifacial leaves whose adaxial (face) and abaxial (back) surfaces depict distinct reflectance and transmittance profiles. In this work, we investigate the impact of these profiles on the red to far-red ratios of light propagated by these leaves, and discuss its implications for the optimization and monitoring of cultivation conditions. Our findings provide a comprehensive portrait of the angular and directional (downward and upward the plant canopy) variations of these ratios. Accordingly, they are expected to contribute to the elucidation of fundamental processes associated with the variation patterns of these ratios within cultivated fields. Such a knowledge is essential for the effective management of agricultural resources required for the cultivation of high-yield and healthy crops.

***Index Terms*—** reflectance, transmittance, red to far-red ratios, bifacial leaves, C_3 crops, *in silico* experiments.

1. INTRODUCTION

The bulk of agricultural output worldwide comes from a relatively small number of crop species. Within this selected group of crops, protein-rich legumes, notably soybean (*Glycine max* L. Merr.), have substantially increased in importance for food production in the last decades. These C_3 plants, characterized by the presence of bifacial leaves, can fix atmospheric nitrogen for its own growth, which minimizes the use of inorganic fertilizers in their cultivation [1].

Due to the high demand for these C_3 crops, it is becoming increasingly necessary to employ a diverse array of management procedures and cultivation strategies in order to enhance their yield. Crop management procedures are often associated with the monitoring (remote and *in situ*) of crop development [2] and the predictive *in silico* (computational) assessment of crop responses to crucial environmental stimuli [3], notably light. Cultivation strategies (*e.g.*, involving plant spacing [4], plant architecture design [5] and crop row orientation [6]) are mainly focused on the optimization of the crops' photosynthetic capacity and growth conditions. These two aspects, in turn, are intrinsically dependent on the amount and spectral quality of light interacting with their canopies.

The spectral quality of light is quantified in terms of the ratio between its red and far-red components. It is known to be one of the main drivers of a myriad of crucial photomorphogenic processes associated with many aspects of plant development such as growth regulatory mechanisms and photosynthetic efficiency [7, 8]. For example, leaves that develop under shade have lower chlorophyll contents, which decreases their photosynthetic capacity [1, 9]. Soybeans are a shade-avoiding plant species [5]. Shade-avoidance is a developmental response mediated by the red to far-red ratio of light impinging on plant organs [10]. In the case of soybeans, variations in the red to far-red ratios of light impinging on their bifacial leaves are believed to trigger shade-avoidance and, thus, lead to an improvement of these plants' photosynthetic apparatus [1, 5].

The light reaching the bifacial leaves of a C_3 plant in a cultivated field can have a direct (sunlight) and an indirect component [11]. The latter may have been propagated, for instance, by the soil underneath the plants or by other leaves (belonging to the same plant or adjacent plants). Relevant experimental studies (*e.g.*, [1, 3, 5, 7, 8]) have examined the variations in the red to far-red ratios of light propagating intra-, under- and intercanopy. These studies employed a global light transport approach in which the influence of local light-leaf interactions on these ratios are usually accounted for in an aggregated manner.

In this work, we aim to contribute to these scientific efforts by focusing on the local light-leaf interactions. More specifically, we investigate how the distinct reflectance and

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transmittance profiles of bifacial leaves affect the red to far-red ratio of light propagated by these photosynthetic organs. We also discuss the practical implications of our findings to the strengthening of the current knowledge about the photomorphogenic processes affecting plant development and, in consequence, crop yield. Finally, we comment on how the understanding about the interconnections of these process from organ, to plant, to canopy scales can be translated into more efficacious crop cultivation and monitoring (remote and *in situ*) methodologies.

2. MATERIALS AND METHODS

In our investigation, we considered a typical bifacial leaf specimen. In its characterization, we employed structural and biochemical measured datasets available in the LOPEX database [12]. These datasets were obtained from a bifacial leaf specimen collected during the period of maximum phenological activity of a soybean plant, as well as morphological observations reported in the literature. For conciseness, these observations are specified elsewhere [13, 14].

Parameter	Value
Thickness (cm)	0.01660
Mesophyll percentage (%)	50
Chlorophyll a concentration (g/cm^3)	0.00392
Chlorophyll b concentration (g/cm^3)	0.00117
Carotenoids concentration (g/cm^3)	0.00108
Protein concentration (g/cm^3)	0.11064
Cellulose concentration (g/cm^3)	0.01074
Lignin concentration (g/cm^3)	0.01014
Cuticle undulations aspect ratio	5
Epidermal cell caps aspect ratio	5
Palisade cell caps ratio	1
Spongy cell caps aspect ratio	5

Table 1. Parameters employed in the characterization of the selected bifacial leaf specimen.

We employed an *in silico* experimental framework in our investigation. More specifically, we performed controlled experiments using a first-principles hyperspectral model of light interactions with bifacial plant leaves, known as ABM-B [13, 14], and supporting measured data provided in the literature. These experiments involved the computation of directional-hemispherical reflectance and transmittance curves for the selected specimen. These curves were obtained considering variations in the angle of incidence (with respect to the specimen's normal) from 0° to 80°. To enable the full reproduction of our investigation results, we made ABM-B available for online use [15] along with the supporting biophysical data (*e.g.*, refractive indices and extinction coefficients) employed in our *in silico* experiments.

To quantify the ratios of red to far-red reflected light, researchers often use as sampling references the wavelengths that correspond to the absorption peaks of chlorophyll (with the red and far-red bands of interest) obtained under *in vitro* conditions [11], namely 660 and 730 nm respectively. Accordingly, we employed the following formula, henceforth referred to as *in vitro* red to far-red ratio, to quantify the spectral quality of the light transmitted by the selected specimen:

$$R/FR = \rho(660)/\rho(730), \tag{1}$$

where $\rho(\lambda)$ denotes the reflectance at the wavelength λ.

It has also been observed that the chlorophyll peaks are shifted under *in vivo* conditions to 645 and 735 nm, respectively [8]. Hence, for completeness, we also employed the following formula, henceforth referred to as *in vivo* red to far-red ratio, in the quantification of the spectral quality of the light reflected by the selected specimen:

$$R^*/FR^* = \rho(645)/\rho(735). \tag{2}$$

For the quantification of the spectral quality of the light transmitted by the selected specimen, the $\rho(\lambda)$ values were replaced by transmittance ($\tau(\lambda)$) values in the formulas above.

3. RESULTS AND DISCUSSION

Woolley [16] has performed reflectance and transmittance measurements on a soybean leaf considering light impinging on its adaxial (face) and abaxial (back) surfaces at two angles of incidence, namely 0° and 70°. In order to establish modeled baselines for our investigation, we initially computed reflectance and transmittance curves for the selected specimen under the same conditions (Fig. 1) and qualitatively compared them with the measured curves provided by Woolley [16] .

As shown in Fig. 1 (left), in the 400 to 730 nm range, the modeled reflectance values obtained considering light incident at 0° on the specimen's back are higher than the values obtained for light incident on its face. In the 730 to 800 nm range, however, this behaviour is reversed. Considering light incident at 70°, the reflectance values obtained for the specimen's back are higher than those obtained for its face within the entire range from 400 to 800 nm. Moreover, the absolute differences between the back and face reflectance values in the 400 to 730 nm range increase with a higher angle of incidence, and decrease in the 730 to 800 nm. We note that all of these qualitative traits are also depicted in the measured reflectance curves provided by Woolley (Fig. 16 in [16]). As depicted in Fig. 1 (right), within the entire range from 400 to 800 nm, the transmittance values obtained considering light incident on the specimen's back are higher than the values obtained for its face. Again, this qualitative trait is also depicted in the measured transmittance curves provided by Woolley (Fig. 14 in [16]).

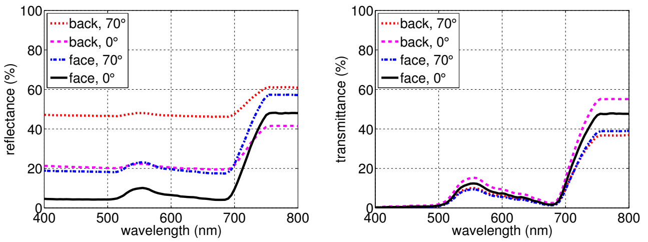

Fig. 1. Modeled reflectance (left) and transmittance (right) curves obtained considering light impinging on the selected leaf specimen's adaxial (face) and abaxial (back) surfaces at two angles of incidence (0° and 70°).

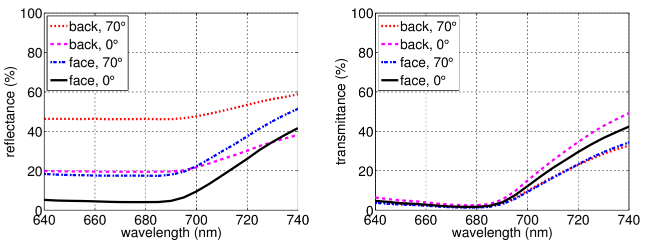

Fig. 2. Zoom-in of the modeled reflectance (left) and transmittance (right) curves obtained considering light impinging on the selected leaf specimen's adaxial (face) and abaxial (back) surfaces at two angles of incidence (0° and 70°).

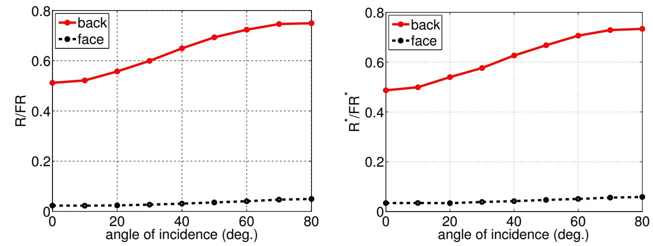

Fig. 3. *In vitro* (left) and *in vivo* (right) red to far-red ratios of light reflected by the selected leaf specimen considering light impinging on its adaxial (face) and abaxial (back) surfaces at distinct angles of incidence.

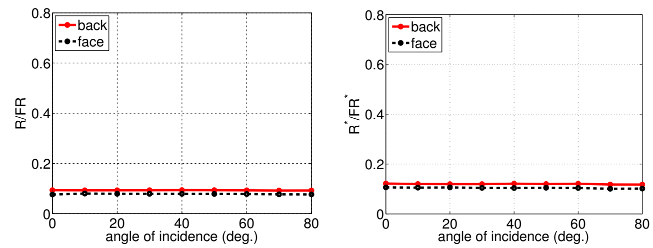

Fig. 4. *In vitro* (left) and *in vivo* (right) red to far-red ratios of light transmitted by the selected leaf specimen considering light impinging on its adaxial (face) and abaxial (back) surfaces at distinct angles of incidence.

We present in Fig. 2 a zoom-in of the modeled reflectance and transmittance curves provided in Fig. 1. More specifically, the graphs depicted in Fig. 2 were plotted considering the spectral region of interest for the computation of red to far-red ratios. As expected, one can observe in these graphs the qualitative traits highlighted earlier, which are also depicted in the corresponding sections of the measured curves provided by Woolley [16]. Thus, we proceed to compute the red to far-red ratios of light propagated by the selected leaf specimen using the reflectance and transmittance values obtained considering light impinging on its face and back surfaces at different angles of incidence.

As it can be observed in Fig. 3, the red to far-red ratios of light reflected on the selected specimen's face are significantly lower than the ratios obtained considering light reflected on its back. Moreover, they also depict distinct trends with respect to changes in angle of incidence. The ratios computed for the light reflected on the specimen's face increase linearly following a linear increase in the angle of incidence. Their increase, however, is minor. It becomes more noticeable only for large angles of incidence. On the other hand, the ratios computed for the light reflected on the specimen's back show a non-linear increase following a linear increase in the angle of incidence. This increase is more accentuated for intermediate angles of incidence.

Finally, as shown in Fig. 4, the red to far-red ratios of light transmitted by the selected specimen when its back is toward the light source is slightly higher than the ratios obtained when its face is toward the light source. Moreover, the variation of red to far-red ratios of light transmitted by the specimen with respect to changes in angle of incidence are negligible for practical purposes. We remark, however, that although these ratios are small, they are higher than those computed for light reflected on the specimen's face (Fig. 3).

Bifacial leaves differ markedly in the structure of their two sides [16], which leads to noticeable differences in their reflectance and transmittance curves (Fig. 1 and 2). Such differences, in turn, result in an asymmetry in the red to far-red ratios computed for their face and back surfaces (Fig. 3 and 4). More precisely, the red to far-red ratios of light propagated by the back surface are noticeable higher than those computed for light propagated by the face, with the former varying non-linearly with a linear increase in the angle of incidence.

As light is propagated through a plant canopy, its red to far-red ratios are reduced [5, 7]. In the case of canopies composed of bifacial leaves, the results of our *in silico* experiments indicate that this reduction is more accentuated when light is propagated downward. We remark that foliar shade can lead to a reduction of the photosynthetic capacity of adjacent leaves subject to this partial screening of incoming light [1, 9]. Also, it has been postulated that low red to far-red ratios may act as shade-avoidance signals [1, 5]. Taking these aspects into account, our findings suggest that the characteristic morphology of bifacial leaves, by reducing the red to far-red ratio of light propagated downward, may contribute to an intensification of such signals received by leaves placed at lower canopy levels. This, consequently, would mitigate a possible reduction in their photosynthetic capacity by being under the shade of other leaves placed at upper canopy levels.

It has been demonstrated [9, 17] that an increase in the plant foliage density aggravates the negative effects of shade on the future photosynthetic capacity of young leaves placed under mature ones, regardless of whether or not the former are located in relatively high positions within the canopy. Thus, even seemingly subtle variations in the red to far-red ratios of light impinging on bifacial leaves (*e.g.*, due changes in the plants' architecture) can lead to substantial fluctuations in C_3 crops' yield. This aspect underscores the importance of appropriately taking into account photomorphogenic processes mediated by red to far-red ratios in the planning and monitoring (remote and *in situ*) of C_3 crop cultivation conditions.

4. CONCLUDING REMARKS

Advances in precision farming have led to the prediction that it will be possible to monitor crops on a plant-by-plant basis in the future. The effective translation of information obtained through this high-resolution paradigm into a sustainable increase in agricultural output will require, however, a more comprehensive understanding about the interconnected biophysical mechanisms affecting crop yield, at the leaf, plant and canopy scales. This will enable the development of more effective crop management strategies needed to meet the food production demands of an increasing world population. To acquire this fundamental knowledge, in turn, we believe that it will be necessary an intensification of scientific initiatives toward the synergistic use of data-acquisition systems (involving satellite, aerial and ground-based platforms) and high-fidelity modeling frameworks.

The work described in this paper aimed to contribute to the achievement of the long-term goals outlined above. Clearly, many aspects related to the influence of light spectral quality on photomorphogenic processes affecting plant development warrant further studies, particularly with respect to concomitant changes in the availability of other essential agricultural resources like water. Accordingly, we plan to extend the scope of our subsequent investigations in this area by also taking into account the effects of water stress on the red to far-red ratios of light propagated by bifacial leaves.

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