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Atmospheric moisture controls far-red irradiation: a probable impact on the phytochrome**

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Abstract. It is commonly accepted that an important role of the phytochrome lies in signalling the proximity of competing plants. However, not all photoresponses conveyed by the phytochrome can be explained by the competition only. Because a better description of the natural variability of solar spectral irradiance is necessary to recognize the other roles of the phytochrome, long-lasting spectroradiometric measurements have been performed. Special attention has been paid to the relations between the far-red and red bands of the solar spectrum, which have an impact on the phytochrome. The effect of atmospheric moisture on far-red irradiance (attenuated in the 720 nm band of water vapour absorption) is described. The far-red irradiance, active in the 'high irradiance response' of the phytochrome, and the red/far-red ratio, important for the 'low fluence response', may vary very strongly relative to the atmospheric moisture. Together with other facts known from photophysiology, the results of the measurements enabled us to formulate a thesis that the phytochrome monitors the amount of water vapour and opens appropriate metabolic pathways to cope with the danger of drought. The recognition of this novel role of the phytochrome might broaden the knowledge in the area of plant photomorphogenesis and ecology.

Keywords: atmospheric absorption, far-red irradiation, high irradiance response, phytochrome, precipitable water

INTRODUCTION

Light plays a dual role in the life of plants. It provides energy for photosynthesis on the one hand and transfers information about recent and future environmental circumstances on the other. Over the last decades, various informative photoreceptors have been described (Briggs, 2009) that respond to duration, intensity, direction, and spectral composition of light. Among them, the best recognized and probably the most universal is the phytochrome.

The classical phytochrome (Borthwick, 1972) has two interconvertible forms (named as P_r and P_{fr}) with its absorption maxima respectively in the red (660 nm) and in the far-red (730 nm) parts of the solar spectrum. The red light converts P_r (inactive form) into active P_{fr}, whilst far-red light causes reversion of the P_{fr} to the P_r form. This primary model of uniform phytochrome has been profoundly expanded in recent decades (Smith, 2000). Five distinct kinds of phytochromes (designated phyA to phyE) encoded by separate genes have been characterized in *Arabidopsis* (Clack *et al.*, 1994). Three modes of action have been distinguished (Briggs *et al.*, 1984): very low fluence responses – VLFR, low fluence responses – LFR, and high irradiance responses – HIR. The extent of the HIR depends mainly on the fluence rate, the LFR is controlled by the ratio of red to far-red irradiation, and in the VLFR any weak light pulse is effective.

Since green plant tissues transmit and reflect much more far-red (FR) than red (R) light, the ratio of these two bands is a good sensor of neighbouring plants. Therefore, it has been commonly accepted that an important ecological role of phytochrome lies in signalling the proximity of competing plants along with applying this information to the appropriate control of metabolic pathways and development (Ballare *et al.*, 1987; Franklin and Whitelam, 2005; Holmes and Smith, 1977b; Smith and Whitelam, 1997). This pattern is known as the 'shade avoidance syndrome'.

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It seems unlikely, however, that the great variety of known phytochrome-related photomorphoses could be interpreted and understood only in relation to mutual shading and shade-avoidance functions (Górski and Górska, 1979). The message about the competing structures is not the only information that the phytochrome system acquires from the changing environment (Casal and Smith, 1989). In this context, the solar irradiation acting in the HIR mode seems to be an especially interesting.

Because a better description of the natural variability of solar spectral irradiance in open stands is necessary to recognize the other roles of phytochrome, we undertook long-lasting spectroradiometric measurements. Special attention was paid to the far-red and red bands of the solar spectrum, which have an impact on the phytochrome.

MATERIALS AND METHODS

Measurements of irradiance were performed at our meteorological station in Puławy (51.42 N, 21.95 E, 142 m a.s.l.) in all seasons over many years. The spectrum was recorded using a spectroradiometer LI-1800 (LI-COR Instruments, Lincoln, Nebraska) in the range of 350-1100 nm and at a half-band width of 4 nm. Global irradiance was determined on the horizontal plane and direct solar irradiance on a perpendicularly oriented receiver mounted in a pyrheliometric tube of the Yanishevskiy type (Robinson, 1966).

The quantity of water vapour in the atmosphere (precipitable water) was determined by aerologic soundings at Legionowo (52.4 N, 20.93 E, 73 m a.s.l.) performed by the Institute of Meteorology and Water Management, Warsaw, and made accessible by the University of Wyoming (2014). The values of precipitable water at the moment of irradiance recording were interpolated between soundings performed twice a day. The distance from Puławy to Legionowo (*ca.* 130 km) may be the source of error, however comparison between Legionowo and Wrocław datasets (320 km distance) showed that spatial gradients of the water vapour mass are small and errors related to using Legionowo data for Puławy may be treated as not significant.

The relative optical mass of water vapour at a given solar angle was calculated using the Kasten formula (Kasten, 1965). The total mass of water vapour along with the solar rays (optical mass of water vapour – W) is the product of relative optical mass (m) and precipitable water (P_w) in a vertical column:

$$W = m\,P_w\,, \tag{1}$$

Special attention was paid to the 720 nm band. Determining the absorptance here is possible by comparing the measured irradiance (I) with that outside the absorption band. We used a 'three-channel approach' (Thome *et al.*, 1992) comparing the 720 nm (I_{720}) value with those at 682 nm (I_{682}) and 752 nm (I_{752}), where practically no selective absorption by atmospheric gases appears (Gueymard, 1995). The reference value for 720 nm (R_{720}) was calculated by interpolation between two outer bands:

$$R_{720} = 0.46\,I_{682} + 0.54\,I_{752}\,, \tag{2}$$

Transmittance (T) at 720 nm (T_{720}) was determined as a ratio:

$$T_{720} = I_{720} / R_{720}\,. \tag{3}$$

RESULTS

Calculation as well as empirical determination of transmittance by water vapour is not simple, because the absorption band consists of many lines of different intensity, and the entire absorption in it does not follow Beer law (Robinson, 1966). The detailed shape of the absorptance as a function of wavelengths depends also on the width of the measured range. At a half-band width of 4 nm (used throughout our measurements), the maximal absorptance in the 700-740 nm region lies at 720 nm as shown in Fig. 1.

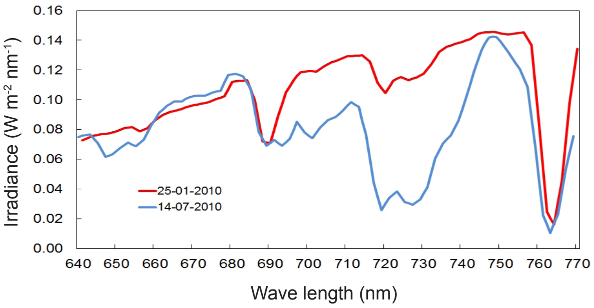

Fig. 1. Direct spectral solar irradiance at 4° solar angle over two days with diverse atmospheric water vapour content (red line: 3 mm, blue line: 32 mm). Note the 720 nm absorption peak.

The total direct solar irradiation at a solar angle of 4 degrees (Fig. 1) over two days was similar, and therefore the absorption bands may be easily compared. These two days differed strongly in the amount of precipitable water: 3 and 32 mm. Two bands of absorption by oxygen (with maxima at 688 and 763 nm) did not differ between the two days. The wide water vapour absorption band is visible between 690 and 745 nm. The strongest attenuation appears between 715 and 735 nm. In the presented cases, the transmittance at 720 nm (T_{720}) was evaluated as 0.81 in dry and as 0.20 in moist atmosphere. I_{720} irradiance was about 4 times greater in dry than in humid air, although total irradiance differed only slightly. The ratio 660/720 nm was 0.83 and 3.23 respectively.

The overall number of measurement series of direct irradiance in all seasons and at solar angles not less than 1 degree was 693. They are presented in Fig. 2 as T_{720} transmittance in the function of optical mass of water vapour (W). Considering unavoidable errors in determining W (time and geographical distance between irradiation and

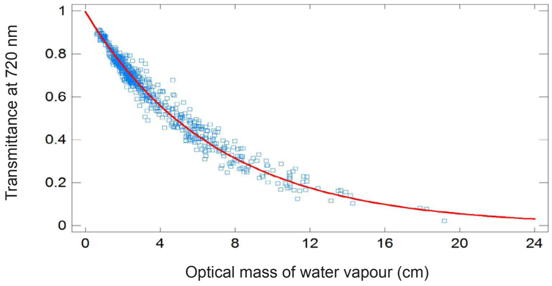

Fig. 2. The transmission of direct solar radiation at 720 nm as related to the optical mass of water vapour.

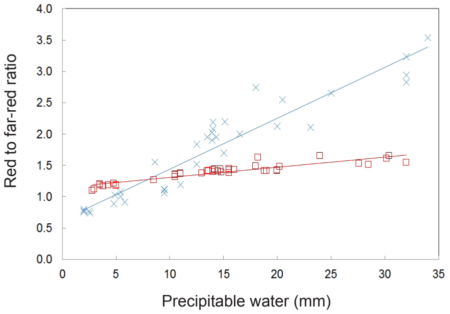

Fig. 3. The ratio of red to far-red 660/720 nm) in direct irradiation as related to the precipitable water at 30^{o} solar angle (squares) and 2^{o} (crosses). The lines show linear regression on precipitable water.

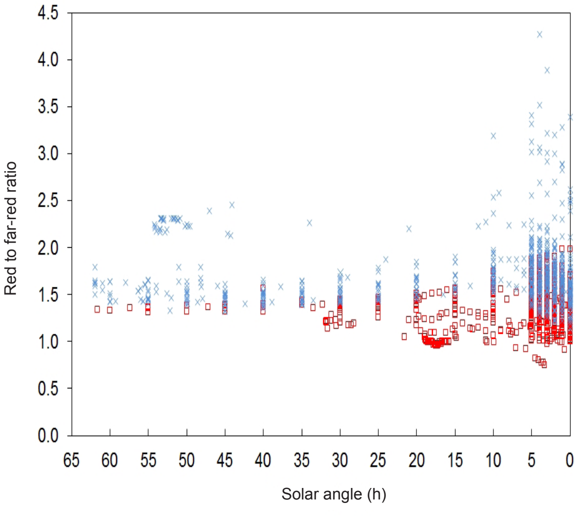

Fig. 4. The ratio of red to far-red (720/660 nm) global irradiance in dry atmospheres (water vapour content lesser than 15 mm – squares) and in moist atmospheres (higher values of water vapour – crosses) as related to the solar angle (h).

water vapour measurements, variable stratification of the atmosphere) the relation between W and T_{720} may be reckoned as fairly close. The relation may be presented as:

$$T_{720} = \exp(-0.005 - 0.144\ W^{0.6}) \qquad (4)$$

at a correlation coefficient R = 0.97.

The formula is purely empirical, the sole theoretical assumption is that the transmittance could not be negative. The exponent 0.6 gives the best fit in the sense of least squares.

Because the red (R, 660 nm) radiation is not absorbed by water vapour, the R/FR ratios (important for the phytochrome state) change along with the precipitable water. Figure 3 presents these ratios at two different solar angles: 30 and 2^{o}. The influence of the precipitable water may be observed at any position of the sun, but especially profound effects occur at low solar angles. At midday, the R/FR ratios are usually in the range of 1.1-1.7, but they decrease towards sunset in dry and increase in moist air. The highest ratios measured by us just before sunset exceeded 5 and the lowest dropped below 0.7.

The direct irradiance could be determined only with a clear sky. The global irradiance falling on a horizontal plane was measured under various weather conditions (except rain). The total number of such measurements was 1728. Because cloudiness greatly influences irradiance, the impact of water vapour on particular bands could not be clearly presented. Instead, we show the R/FR ratios (660/720 nm) at various solar angles (Fig. 4). The total sample was divided into two approximately equal parts. The first part includes cases with precipitable water less than 15 mm and the second part covers all higher values. The difference between these two subsamples is evident. In dry air, the R/FR ratio is lower throughout the day; moreover, it seems to decrease before sunset. In moist air, the ratio is higher and tends to increase with a decreasing solar angle. As a result, the variability of the R/FR ratio is much greater at a low than at a high solar angle. These patterns are obviously an effect of two simultaneous optical processes: the spectrum shifts towards longer waves along with the decreasing solar angle, but the optical mass of water vapour increases much more than that of other gases, because the main body of water vapour lies in the lower stratum of the atmosphere (Robinson, 1966). At sunset, the relative optical mass of mixed gases (Rayleigh atmosphere) is 38, but that of water vapour is 74 (Gueymard, 1995).

The lowest measured 660/720 nm ratio in the global irradiance was 0.75 at P_w = 3 mm and the greatest 4.34 at P_w = 38 mm. These values were obtained at small solar angles. During the day, they were less changeable, usually between 1.2 and 1.6, although in a very humid atmosphere (P_w = 39 mm) they increased even to 2.2 at noon (Fig. 4).

DISCUSSION

The described relations between far-red irradiation and atmospheric water vapour may be hardly observable when the weather conditions are little differentiated; therefore, they are better reckoned if monitored and analyzed in a yearly cycle (Górski, 1976), especially in a tropical zone. Lee and Downum (1991) working at Miami, Florida, found a strong correlation between the R/FR ratio at mid-day and atmospheric water content. In the tropical zones with an evident seasonality, the P_w values may be very changeable; in the equatorial zone, the average P_w may be as great as 60 mm (Jin and Luo, 2009), which means that the T_{720} before sunset may be close to zero and the R/FR ratio can reach very big values.

The decrease in the R/FR ratio before sunset mentioned by some authors (Holmes and Smith, 1977a; Kasperbauer, 1987) is not a general phenomenon; it may occur in a relatively dry atmosphere, especially when the 730 nm band (and not 720 nm) is considered. In a moist air, this ratio increases, even in northern regions as shown on figure 6.2 by Björn (2015).

Confronting the above-described features of far-red irradiation with phytochrome responses, we may hypothesize that another important role of the phytochrome (apart from competition signalling) lies in adapting the plant development to moisture conditions. There is no strict evidence for such a hypothesis, but many facts seem to provide a strong argument for it.

The strict coincidence of the wavelengths ought to be taken into consideration. The photomorphogenetically active FR spectrum (Borthwick, 1972; Mohr, 1972) corresponds to the 700-740 nm band of water vapour absorption (Robinson, 1966). Moreover, the maximum of the action spectrum in the high irradiance response (HIR) lies at 720 nm (Hartmann, 1966), which coincides with the peak of absorption (Gueymard, 1995; Sierk *et al*., 2004) in this band (Fig. 1). This implies that the phytochrome must (and not only can) monitor the water vapour content of the atmosphere. It should be noted here that the spectroradiometric measurements of atmospheric water vapour, in meteorology often called precipitable water (Thome *et al*., 1992), have been used in precipitation forecasting for a long time. A relatively weak absorption band in the FR may be more useful for quantitative determination of vapour than stronger bands in the infrared range, especially at greater air humidity (Kiedron *et al.*, 2001).

Some interesting observations were made concerning the photoresponses outside angiosperms. Phytochromes or phytochrome-related proteins have been identified in a broad spectrum of prokaryotic and eukaryotic phyla (Hughes and Lamparter, 1999; Montgomery and Lagarias, 2002; Sharrock, 2008). It is probable that the light signal in the FR range has been utilized by prokaryota before any canopy shade occurred. Davis *et al.* (1999) stated that 'bacteriophytochrome functions as a light-regulated histidine kinase, which helps protect the bacterium from visible light'. Light in the 720 nm band may be especially important, because it signals the threat of desiccation. However, we ought to stress here that - in the case of water organisms – a different causal relationship should also be considered: any irradiation above 700 nm means a position at or near the surface, because of strong attenuation of this spectral range by water (Ragni *et al*., 2004; Smith and Morgan, 1981).

The absorption or action maxima in the FR band have often been determined at or near 720 nm. Among them: cyanobacterium *Anabaena* – 720 nm (Ohmori and Okamoto, 2004), green alga *Mesotaenium caldariorum* – 722 nm (Kidd and Lagarias, 1990), green alga *Mougeotia scalaris* – 720 nm (Jorissen *at al*., 2002), liverwort *Sphaerocarpos* - 720 nm (Taylor and Bonner, 1967), moss *Ceratodon purpureus* – 722 nm (Lamparter *et al.*, 1995), and slime mould *Physarum polycephalum* – 720 nm (Hato *et al*., 1976). These values differ significantly from 730 nm that are given broadly in the literature for Angiospermae in LFR responses.

Now it may be speculated that the FR-HIR mechanism arises primarily as an effect of light absorption by water or/and water vapour. A recent report (Possart and Hiltbrunner, 2013) states that the HIR signalling is more ancient than phytochrome A. 'Even though cryptogams plants such as mosses or ferns do not have phy A, they show FR-induced responses' (Possart *et al.*, 2014). The shade-avoidance function could not arise before the shade itself; the spectrally diversified shade might occur in water after establishment of phototrophs, *ie* well after bacteriophytochrome in chemotrophic species. As concerns land plants, the origin of canopy shade may be dated between 360 and 380 million years ago (Mathews, 2006) along with vascular plants.

A great diversity of the spectral features of the photoreversible receptors has been reported in various species. The reversion may proceed between two spectral bands other than red and far-red (Ulijasz *et al*., 2009). In some cases, the postulated activity of the R/FR irradiations has been excluded, but in others, such actions have been clearly seen. For example, Hübschmann *et al.* (2005**)** stated that the R and FR light reversibly affected gene activity in a freshwater cyanobacterium *Synechocystis*. FR had a suppressive effect on the expression of genes; genes stimulated by FR are known to be inducible by stress. The activity of the system is 'in accord with the FR high-irradiance response mediated by phytochrome A in plants'.

It seems most likely that the FR signal may help to prepare for desiccation and therefore the responses to the FR signal in algae coincide with terrestrial (*ie* not marine) habitats, where desiccation is likely to occur. Both the green algae mentioned (*Mougeotia* and *Mesotaenium*) live in fresh water. A lack of any phytochrome-related responses has been stated in three species of marine macroalgae (of Rhodophyte, Chlorophyte, Phaeophyte) by Gordillo *et al.* (2004) and in a brown alga (Stramenopile) by Shi *et al.* (2005). The marine algae have developed other systems to monitor light signals that give information on changing circumstances and position; the message on water vapour carried by the 720 nm band would be useless here.

An important argument in favour of our hypothesis is also provided by the mechanism of photoperiodism. There is no doubt that plant responses to the photoperiod are mediated by the phytochrome (Vince-Prue, 1975). Fluctuations in the length of the day signalize future moisture conditions and therein lies the ecological significance of photoperiodism, as was convincingly stated long ago by Junges (1957). Long day plants (*ie* accelerating development under long days), originating from Mediterranean-type climates with winter rains, accelerate their development before summer droughts. Short day plants, descending from monsoon-type regions with summer rains and dry winters, react in an opposite manner. Under favourable conditions, plants tend to continue their vegetative growth and accumulate the biomass. Changes in the day length anticipate and forecast worsening conditions; then the plants enter the generative phase in order to produce seeds before it is too late. The role of photoperiodism in the adaptation to drought has also been discussed by Queiroz (1983).

Many reports have shown that the inductive long day illumination must contain a considerable dose of FR; if R prevails, then the flowering of long-day plants is retarded (Lin, 2000). The response to FR during the day is mediated by phytochrome A in the HIR mode (Casal *et al*., 1998; Franklin *et al*., 2007; Jackson and Thomas, 1997) *ie* it depends on irradiance (fluence rate), although not on photophysical properties of the phytochrome itself (Rausenberger *et al*., 2011). The end-of-day irradiation with FR also accelerates the development, but then the LFR mode acts, mediated by phytochrome B and probably other phytochromes (Franklin and Whitelam, 2005). It may be speculated that both modes gradually transit into each other when the irradiation changes after dawn and before dusk. The important point is that both the FR fluence rate and the R/FR ratio in direct sunlight, as well as in global (direct + diffuse) irradiation, depends strongly on atmospheric water vapour (Figs 1-4). It follows that the development of long-day plants is accelerated in dry atmosphere, and retarded in the moist, when evaporation is smaller and rain probability greater.

Some direct experimental results on the relations between far-red irradiation and adaptation to drought are also available. Although the main role in regulating the stomatal gas exchange is played by photoreceptors other than phytochrome, the far-red irradiation can modify the responses of stomata. There are reports indicating the involvement of phytochrome in stomatal distribution and movement (Roth-Bejerano *et al*., 1985) FR usually limits the number of stomata and/or stomatal aperture directly or in interaction with other photoreceptors (Talbot *et al*., 1985). Kasperbauer and Peaslee (1973) found that 5 minutes of FR irradiation before the dark period decreased the number of stomata in tobacco leaves. In our experiments, the addition of FR irradiation caused a decrease in the number of stomata in wheat (Doroszewski, 2011**)**. All described FR effects on stomatal apparatus decrease plant transpiration. Hubac *et al*. (1986) found that 30 min of FR irradiation given before the night greatly diminished transpiration of cotton plants.

The mechanisms by which phytochrome influences water economy may be more or less complicated (Boccalandro *et al*., 2009; González *et al*., 2012; Sokolskaya *et al*., 2003). Some recent reports show that the phytochrome increases tolerance to high evaporative demand (Auge *et al*., 2012) and that phytochromes phyA and phyB can modulate drought stress responses (D'Amico-Damião *et al*., 2015).

CONCLUSIONS

1. Direct solar irradiance in the far-red range depends strongly on atmospheric water vapour. It may be several times greater in a dry than in humid atmosphere. The red/far-red ratios do change in direct as well as in total irradiance, along with water vapour; the differences are the greatest at low solar angles. Assessment by the phytochrome of the far-red fluence rate and of the red/far-red ratio in open stands serves as an input to weather forecast, similarly as in meteorology. Bright far-red irradiation signals dry conditions, causing the phytochrome to open appropriate metabolic pathways to cope with the danger of drought. A high ratio of red to far-red irradiance is typical for humid atmospheres and implies sufficient moisture conditions.

2. It is probable that the phytochrome has developed evolutionarily in such a way to be able to acquire information about various (also climatic) aspects of the unstable environment to optimize the development of an organism in view of future conditions.

3. We believe that the recognition of phytochrome as a receiver of meteorological information will broaden the knowledge in the area of plant photomorphogenesis and ecology.

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