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The effect of light spectral quality on leaf senescence and oxidative stress in wheat

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Abstract

We have investigated the effects of deprivation of specific wavelengths on the induction of leaf senescence and oxidative metabolism in wheat. Excised leaves of 18–20-day-old plants were incubated in plastic boxes on distilled water and exposed to light filters with different ratios of red (R = 660 nm) to far-red (FR = 730 nm) radiation (treatments red (R), R/FR = 0.84; green (G), R/FR = 0.12; or blue (B), R/FR = 0.13). Boxes with no added filters (white light treatment) or covered with black cardboard served as controls. Incubation in darkness induced a fast protein and chlorophyll degradation and oxidative stress development as compared to the white light (W) illuminated leaves. A decrement of the R/FR ratio failed to induce senescence symptoms in leaves exposed to the B light treatment, which behaved in a similar way as the white light control. Senescence symptoms developed to a similar extent under both the R and G light treatments. Our results indicate that light spectral quality affects the oxidative metabolism of wheat leaves, and that blue light can specifically delay the onset of senescence in shaded leaves. The effects of incubation on benzylaminopurine (BAP), $LaCl_3$ (a Ca^{2+} channel blocker), or salicylhydroxamic acid (SHAM) suggest that blue light prevents senescence by maintaining high levels of catalase activity.
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Keywords: Catalase; Light spectral quality; Oxidative stress; Peroxidases; Senescence; *Triticum aestivum*

1. Introduction

Senescence is a genetically controlled process whose regulation depends on a wide number of endogenous as well as environmental factors (e.g. [1–3]). During leaf senescence, cells undergo highly coordinated changes in cell structure, metabolism and gene expression that contribute to the recycling of nutrients to developing organs, seeds or storage tissues, culminating in cell death. This process is characterized by a cessation of photosynthesis, degradation of chlorophyll, proteins and other macromolecules, conversion of peroxisomes into glyoxysomes, and a marked increase in the production of reactive oxygen species (ROS) [1,4–6].

In annual plants, reproduction is the factor most strongly associated with leaf senescence [7]. However, other factors may initiate and/or modulate senescence rate both in the vegetative as well as the flowering stages. Amongst these factors, there is strong evidence that light plays an important role (e.g. [8,9]), though the mechanisms involved are still not clear. While continuous exposure to high light levels may cause photo-oxidative damage and induce leaf senescence (e.g. [10], and references therein), darkness also induces it when applied on individual leaves but may inhibit leaf senescence when applied to the whole plant [11]. The senescence symptoms induced by changes in light availability are very similar to those occurring under natural leaf senescence, and it has been proposed that a decrease of the antioxidant metabolism and increased over-production of ROS (particularly hydrogen peroxide) might be the basis of the process [6,12].

In densely growing plant populations, adult leaves shaded by others are occasionally induced to yellow. Leaves beneath a dense canopy experience a marked reduction of the photon flux, as well as changes in the light quality due to the spectral

Abbreviations: APX, ascorbate peroxidase; BAP, benzylaminopurine; CAT, catalase; MDA, malondialdehyde; PPFD, photosynthetically photon flux density; POX, guaiacol peroxidase; PVPP, polyvinylpolipyrrolidone; ROS, reactive oxygen species; SHAM, salicylhydroxamic acid; SOD, superoxide dismutase; TBA, thiobarbituric acid; TNC, total non-structural carbohydrates

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properties of tissue pigments. It has been shown that increasing the proportion of far-red (FR) radiation induces leaf senescence in certain plant species, and that this effect may be suppressed by application of red (R) light [8,13,14]. Similarly, increased FR illumination on leaf spots in tobacco plants significantly reduced chlorophyll content, specific leaf weight and nitrate reductase activity as compared to non-illuminated leaf spots. This effect was overcome by over expression of *PHYA* cDNA, suggesting that phytochrome was involved in the perception of light signals that can induce senescence [15]. On the other hand, analyzing the effects of different continuous lights on leaf senescence in barley, Quiles Rodenas et al. [16] showed that a near ultraviolet light receptor (probably cryptochrome) may also contribute to the control of senescence.

Except for the putative involvement of the mentioned photoreceptors, little is known about the biochemistry of leaf senescence induced by changes in light spectral quality. In non-senescent leaves the accumulation of sugars can repress the transcription of photosynthetic genes and lead to a decline in chlorophyll and photosynthetic proteins levels [9], but while the concentration of soluble sugars can increase under different light environments, its regulatory role during leaf senescence is less clear and highly dependent on other factors (e.g. [17], and references therein).

The regulation of many plant developmental processes by light is mediated through the action of plant growth regulators, and it has been shown that increased tissue concentrations of gibberellins or cytokinins may inhibit leaf senescence under certain conditions [17,18]. Even though there is some evidence that this effect might be mediated by an increment of antioxidant defenses [19], the information about how changes in the light spectral quality affects the oxidative metabolism and senescence in leaves is very scanty.

In the present paper we analyse the effect of the deprivation of specific wavelengths on the induction of leaf senescence and the development of oxidative stress in young wheat plants.

2. Materials and methods

2.1. Plant growth and experimental procedure

Wheat (*Triticum aestivum* L., cv. Don Humberto) caryopses were surface sterilized (12 min in 10% H_2O_2), germinated on wet tissue paper in the dark, and after 48 h, transplanted to plastic pots containing a mixture of sand and agrolite® (2:1), in a greenhouse at natural photoperiod. Timer regulated air conditioning reduced diurnal fluctuations of temperature inside the greenhouse. Pots were periodically irrigated with tap water and, after a week, fertilized every 3–4 days with proper amounts of a nutrient solution in order to provide 8.0 mM N (supplied as NO_3NH_4), 3.0 mM P and K (supplied as KH_2PO_4), 2.0 mM S and Mg (supplied as $MgSO_4$) and 10.0 μM Fe (supplied as Fe-ethylenediaminetetraacetic acid complex).

To study the effect of light spectral quality on leaf senescence, fully expanded leaves (usually the second and third ones) of 18–20-day-old plants were excised and incubated during 48, 72 and/or 96 h in transparent plastic boxes (13 cm × 20 cm), whose lids where covered with Lee filters (red #026, green #089 or blue #075), which supplied different proportions of red ($R = 660$ nm) to far-red (FR = 730 nm) irradiation. The lateral surfaces and the base of each box were covered with reflecting foil. The transmission spectra of the red (R), blue (B), and green (G) filters are shown in Fig. 1. Note that G and R filters have very low or null percent transmission in the 350–450 nm region. When indicated, boxes with no added filters or completely covered with black cardboard were used as white light (W) or dark (D) controls, respectively. The boxes (three to four replicates per treatment and sampling date) were randomly placed on a bench and the incubations performed in the same greenhouse where the plants had been grown. Average values for maximum photosynthetically photon flux density (PPFD), red light, far-red light and the R/FR ratio of the different light treatments are shown in Table 1. Measurements of R and FR irradiation,

Table 1
Average values for maximum PPFD, red light ($R = 660$ nm), far red light (FR = 730 nm) and R/FR ratio transmitted by the different light treatments (W = white light, G = green filter, B = blue filter, and R = red filter), in the absence or presence of an aditional $CuSO_4$ (cs) filter

Treatment	PPFD (μmol m^{-2} s^{-1})	R (μmol m^{-2} s^{-1})	FR (μmol m^{-2} s^{-1})	R/FR
W	474.0	29.6	28.9	1.02
G	92.0	1.6	13.2	0.12
B	92.0	3.0	21.8	0.13
R	92.0	18.3	22.0	0.84
Wcs	357.0	12.8	4.2	3.00
Gcs	90.0	1.2	2.3	0.51
Bcs	87.0	1.8	3.3	0.53
Rcs	63.0	8.0	3.3	2.40

Values were taken at midday, in a sunny day, inside the greenhouse.

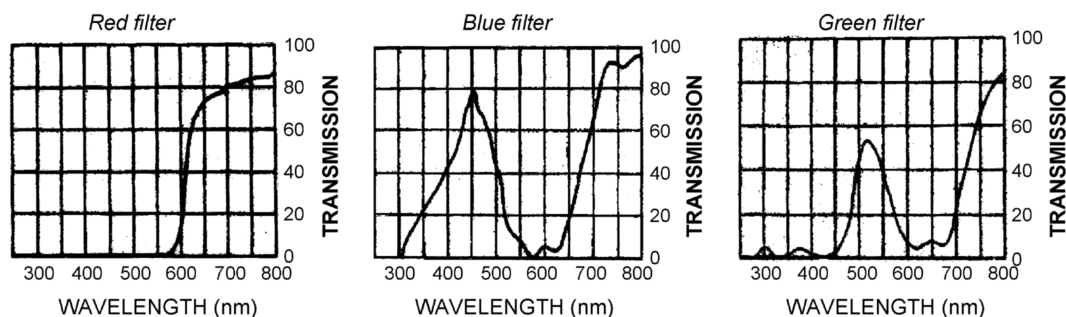

Fig. 1. Percent light transmission spectra of the Lee filters used for the blue (B), red (R) and green (G) light treatments, as supplied by the manufacturer.

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