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Basal leaf senescence in a sunflower (*Helianthus annuus*) canopy: responses to increased R/FR ratio

M. Cecilia Rousseaux*, Antonio J. Hall and Rodolfo A. Sánchez

IFEVA, Facultad de Agronomía, Universidad de Buenos Aires/CONICET, Av. San Martín 4453, 1417 Buenos Aires, Argentina
**Corresponding author, e-mail: rousseaux@vegmail.ucdavis.edu*

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Senescence of lower leaves (LS) begins before anthesis in sunflower crop canopies. Using isolated field-grown sunflower plants, it has previously been shown that pre-anthesis LS is dependent on photosynthetic photon flux density (PPFD) and is hastened by increases in far-red light. We tested the hypothesis that increasing the red/far-red ratio (R/FR) perceived by basal leaves within canopies delays LS. To do this, light impinging on the lower surface of north-oriented 8th leaves (cotyledons = 0) of crops with maximum leaf area indexes of 3.3 (Experiment 1) and 2.4 (Experiment 2) was enriched ($+8.33$ μmol m^{-2} s^{-1}) with red light using light emitting diode (LED) panels. LED panels constructed with unlit LED or with green LED (PPFD slightly greater than the red LED panels, to compensate for lower efficiency) were used as controls. Compared with controls, additional R significantly ($P < 0.05$) increased R/FR perceived by the lower surface and significantly ($P < 0.01$) delayed LS. On average, leaf duration, as time between full expansion and a 70% diminution of chlorophyll content, was 5 days greater for leaves receiving extra red light (maximum observed LD = 27 days). We conclude that an increase in the R/FR ratio can delay LS in crop canopies.

Introduction

Leaf senescence (LS) is the deteriorative process that curtails leaf activity as a photoassimilate source and ends with leaf death. The implications of leaf senescence for CO_2 assimilation and biomass production make the understanding of its control an important issue. During the pre-anthesis phase of a crop progressive LS may be triggered by several environmental factors, typically nitrogen and water stress (e.g. Wolfe et al. 1988). However, even under conditions of adequate nitrogen and water crop availability, basal leaves become senescent before anthesis, particularly in dense canopies.

A decrease in the photosynthetic photon flux density (PPFD), impinging on leaves accelerates chlorophyll loss in monocotyledonous (e.g. Ottman and Welch 1988) and dicotyledonous species (e.g. Cock et al. 1979, Rousseaux et al. 1996), suggesting that changes in this environmental variable may contribute to LS at the base of crop canopies. It is also broadly accepted that leaf nitrogen (another variable that greatly decreases during leaf senescence) within most crop canopies is controlled by the PPFD during the pre-anthesis phase (see review by Dreccer et al. 1998 and references therein). But plants can perceive a variety of light signals through different photoreceptors covering the visible spectrum (Casal 2000) apart from the PPFD. Phytochromes consist of a family of photoreceptors that can sense changes in several aspects of the light environment (spectral composition, irradiance, photoperiod) and they induce significant alterations in a number of physiological processes (Smith 1995). One of the well-known functions of the phytochromes is sensing the red/far-red ratio (R/FR) of vegetation shade-light with increasing canopy leaf area index (LAI) (e.g. Holmes and Smith 1977). Leaf duration (LD, time between achievement of full leaf size and senescence) was also shortened when the R/FR perceived by individual basal leaves of isolated plants was artificially decreased through FR enrichment (Rousseaux et al. 1996). Thus, changes in R/FR within the canopy must be regarded as another potential controlling factor of basal LS.

Much of the work on the role of R/FR in the control of leaf chlorophyll loss (an indicator of LS) has been conducted using isolated plants and/or controlled environmen-

Abbreviations – I/Io, fraction of incident PPFD; Io, PPFD above the canopy; I, PPFD received by the organ; LAI, leaf area index; LED, light emitting diodes; LD, leaf duration; LS, leaf senescence; PPFD, photosynthetic photon flux density; R/FR, red/far-red ratio.

tal conditions (e.g. De Greef et al. 1971, Casal et al. 1987, Casal and Aphalo 1989, Rousseaux et al. 1996, 1997). This makes its applicability in the context of basal LS of commercial density crops uncertain. Use of end-of-day FR irradiation as a means of altering the effects of the relatively high R/FR ratio obtained during the photoperiod (e.g. De Greef et al. 1971, Casal and Aphalo 1989) is difficult to relate to the gradual R/FR shifts, as the crop grows, in the diurnal R/FR environment of basal leaves in a canopy. In the experiments using FR irradiation of individual leaves of isolated plants (Rousseaux et al. 1996) the total radiation (both PPFD and FR) impinging on the leaves was higher than that typical of basal leaves in a crop canopy. Greenhouse or growth chamber conditions are characterized by lower PPFD conditions than those found in the field (especially summer crops) and light spectral composition is also different (e.g. very low ultraviolet radiation). Interactions between PPFD and R/FR (e.g. Rousseaux et al. 1996) and between ultraviolet radiation and phytochrome (Lingakumar and Kulandaivelu 1993) can affect some physiological processes, including LS. To the best of our knowledge, no previous experiments involving manipulations of R/FR ratios perceived by leaves have been performed in dense crop canopies. Understanding LS and its controlling factors under normal canopy conditions is important to establishing the hierarchy of possible control factors and for the improvement of senescence routines in crop simulation models, which currently ignore the effects of light quality. The methodology used in the present work involved small increases in the quantity of R light impinging on target leaves during the natural photoperiod, and had the aim of simulating changes in the leaf light environment close to those normally obtained in a canopy.

The primary hypothesis of the experiments described here is that small increases in the R/FR ratio perceived by basal leaves of the crop canopy during the natural photoperiod, will increase the duration of those leaves. To test this notion we enriched the radiation reaching individual basal leaves of a sunflower canopy using R light emitting diodes (LED). Because R supplementation altered PPFD impinging on target leaves, supplementation of PPFD with a similar level of green radiation was used as a control.

Materials and methods

Growth conditions

Sunflower crops (*Helianthus annuus* L. cv. G100, Dekalb, Argentina) were sown on 24 December 1994 (Experiment 1) and 6 October 1995 (Experiment 2), in the experimental field of the Facultad de Agronomía UBA (latitude 34°35′ S, 58°29′ W) at a density of 48 seeds m^{-2}. Final population density (4.76 plants m^{-2}; in rows 0.7 m apart and 0.3 m between plants in the row, the normal plant population density for commercial sunflower crops in Argentina) was established by thinning at 14 (Experiment 1) and 20 (Experiment 2) days after sowing (two fully expanded leaves). Rows were oriented N-S. A randomized complete block design with 4 (Experiment 1) and 6 (Experiment 2) replications was used, and all plots (9 rows × 1.5 m) received 25 kg N ha^{-1} (calcium nitrate) at sowing and 100 kg N ha^{-1} (urea) in two doses, 21 and 28 days later. Soil water content was maintained near field capacity during the experiment using trickle irrigation.

Manipulation of light environment

We enriched light impinging on the lower surface of north-oriented (midrib within 30° of north) leaves, subtending the 8th node (0 = cotyledons) with red light provided by red LED panels (RED). Green LED panels (GREEN) and unlit LED panels (UNLIT) were used as controls. The GREEN treatment was used to control the possible effect of the PPFD increase produced by the red light supply, while the UNLIT treatment was used to reproduce the solar light reflection produced by the LED and to determine whether PPFD supplied provided by red or green LED panels affected LD. We used LEDs (2 V, 20 mA; Electrónica ELKO SRL, Buenos Aires, Argentina) as light source because they provide 'cold' light and their discontinuous emission does not affect leaf photosynthetic capacity (Tennessen et al. 1994, 1995).

Each panel (20 × 10 cm) had an array of 150 uniformly distributed LEDs and was placed in a transparent acrylic box (Fig. 1) to avoid contact between the LEDs and the leaves and to protect the electrical circuit from rain. The panels were placed below the target leaves so that the long axis of the panel coincided with the maximum leaf width. Panels were turned on at sunrise and off at sunset, half an hour before darkness (times were adjusted according to the day of the year, and varied between 13 and 14 h). Light treatment started after the target leaves achieved full size.

PPFD generated by the LED panels were measured using a partly masked 1-m length linear sensor (LI 191S; Li-Cor,

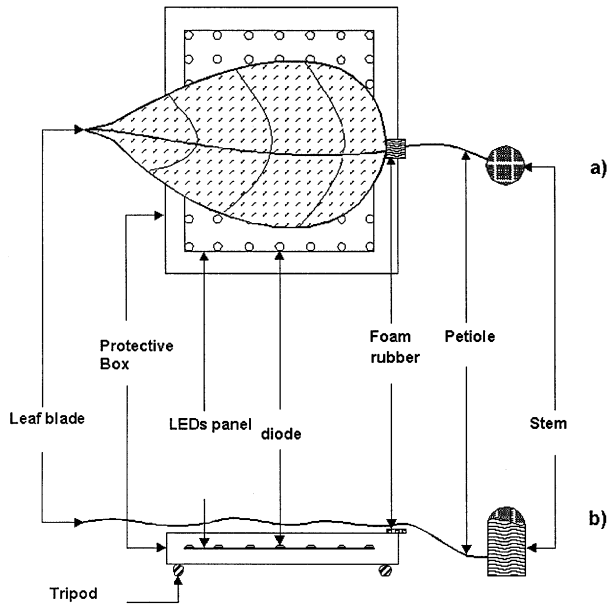

Fig. 1. Diagram of the LEDs panels used in the experiments seen from above (a) and in cross-section (b).

Lincoln, NE, USA) (unmasked section, 0.20 m, equivalent to panel length), placed 2 cm above the LEDs in 3 positions along the panel width. Irradiances were adjusted to 8.33 μmol m^{-2} s^{-1} for RED and 10.56 μmol m^{-2} s^{-1} for GREEN. The higher PPFD for GREEN compensated for the lower photosynthetic efficiency of green light (McCree 1972).

Light environment characterization

The light environment of the treated leaves and its diurnal variation were measured on 4 (Experiment 1) and 10 (Experiment 2) occasions between achievement of maximum area of the target leaf and senescence, corresponding to intervals of approximately 7 and 2 days, respectively. Photosynthetic photon flux was measured using a PPFD sensor (LI 190, Li-Cor) and R and FR irradiances using a R-FR radiometer (SKR110, SKYE, UK). Measurements were made on 3 occasions (8 h 30 min, 12 h, 15 h 30 min; Experiment 1) and 5 occasions (7 h, 9 h 30 min, 12 h, 14 h 30 min, 17 h; Experiment 2) per day. Measurements were made on the upper and the lower leaf surfaces, at 3 fixed positions per leaf (the center of each half-lamina and the apex) to reduce the variability caused by the use of point sensors. The three observations per leaf were averaged to form a single value per plant. Determination of irradiance above the canopy (sensor surface in the horizontal position) accompanied measurements at each target leaf.

PPFD, R and FR irradiances above the canopy and incident on target leaves were plotted against time for each measurement day, and curves fitted by hand to the data points. Graphical integration was used to estimate integrated daily values for each variable. Fractional PPFD (I/Io) was calculated as the ratio between total daily PPFD received by the leaf (I) and the corresponding value above the canopy (Io). Mean daily R/FR for each leaf was calculated as the ratio between daily integrals for R and FR, for the upper (R/FR_{upper}) and the lower (R/FR_{lower}) surfaces. Leaf transmittance of target leaves was determined on each measurement day in Experiment 2 and these values were used to determine transmitted R and FR fluxes (Rt and FRt) (i.e. Rt_{lower} = % leaf transmission × R_{upper}). Based on incident (Ro and FRo) and transmitted (Rt and FRt) R and FR data, we calculated the R/FR ratio (B_{upper} and B_{lower}, for the upper and lower leaf surfaces, respectively) perceived on each surface. For example, B_{upper} is the relation between $(Ro + Rt)_{upper}/(FRo + FRt)_{upper}$.

Leaf duration

During the expansion phase of the target leaves, leaf area was determined every 2 days using measurements of maximum leaf width with the aim of determining the date when full expansion was achieved (Rawson and Dunstone 1986). After full leaf expansion was achieved, leaf chlorophyll content was determined with a non-destructive chlorophyllometer (SPAD-502, Minolta, Plainfield, IL, USA) every 2 days to establish the date when the leaf became senescent; a leaf was categorized as senescent when SPAD readings fell to less than 30% of its initial value. Our response variable (leaf duration, LD) was taken as the time (in days) from end of expansion to senescence.

Leaf temperature

To check whether LED panels affected target leaf temperature, an infrared thermometer was used (14-220D, Instatherm; Barnes Engineering Co., Stanford, CA, USA). This check was performed 13 days from the achievement of maximum leaf size in Experiment 1 and showed that leaf temperature was similar between treatments (average 23.7°C) and did not differ significantly from temperature of untreated leaves of similar orientation and level of insertion. To magnify possible temperature effects due to irradiance from LED panels, measurements were performed during a cloudy and relatively cool day (air temperature during the measurement = 25°C).

Statistical analysis

A previous experiment demonstrated that LD of target leaves of isolated sunflower plants increased linearly with PPFD (Rousseaux et al. 1996). Consequently, analysis of covariance (ANCOVA) was used to determine the effects of light environment manipulation on LD and to control effects due to variations in PPFD impinging on target leaves because of microenvironmental differences in canopy structure. PPFD fraction (I/Io) was used as the covariable to explain that part of the variability in LD attributable to this variable.

Treatment effects on light environment were analyzed using a repeated measurement ANOVA (SAS Institute 1992). The ε value of Huynh-Feldt (Potvin et al. 1990) was used to determine data sphericity. Between-treatment differences for a given day were evaluated using orthogonal contrasts; comparisons performed were RED versus GREEN and UNLIT, and GREEN versus UNLIT.

Results

Treatment effects on basal leaf light environment

Leaf area index did not differ ($P > 0.05$) between treatments in either experiment, reaching maximum (close to anthesis) values of 3.32 and 2.41 for Experiments 1 and 2, respectively. Both R/FR (Fig. 2) and I/Io (Fig. 3) impinging on target leaves decreased with time from achievement of full leaf size as a consequence of LAI increase above leaf number 8.

Supplemental red light produced an increase ($P < 0.01$) in R/FR measured on the lower surface (calculated either from incident only or incident plus transmitted fluxes) with respect to the other treatments (Fig. 2). The average value ($n = 8$) during the experiment of incident R/FR_{lower} on RED treatment was 0.54, while for GREEN and UNLIT it was 0.28 (Fig. 2a). Differences in R/FR_{lower} (incident and transmitted) were smaller (RED = 0.27 and GREEN and UNLIT = 0.16, Fig. 2b). R/FR_{upper} did not differ ($P > 0.05$)

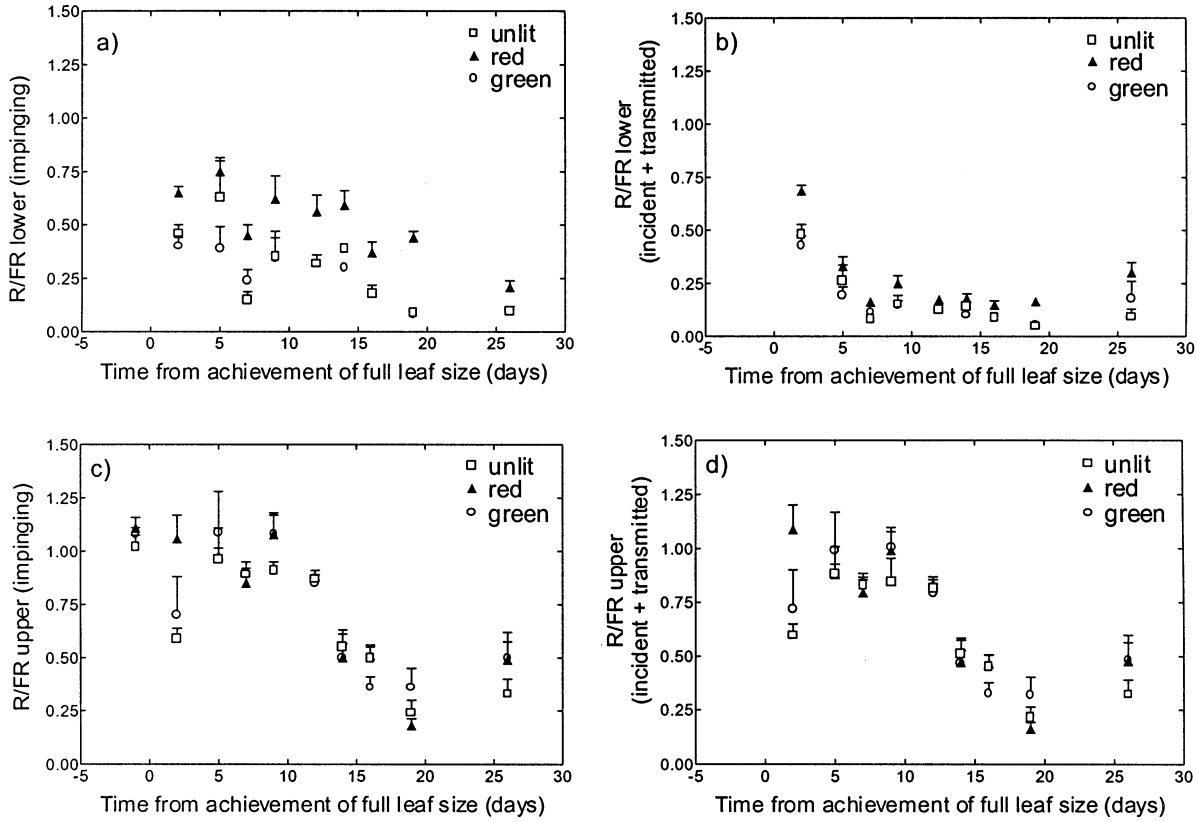

Fig. 2. R/FR ratio of light on the lower (a,b) and upper (c,d) leaf surfaces calculated from measured incident R and FR (a,c) or (incident plus transmitted) (b,d) fluxes as a function of time from achievement of full size of the target leaf for Experiment 2. Data points are means of 6 replicates and vertical bars represent standard errors.

between treatments (Fig. 2c) and R light transmitted through lamina did not modify this ratio (Fig. 2 d). The R/FR ratios for all dates for both leaf surfaces did not differ between GREEN and UNLIT treatments. Results from Experiment 1 (incident fluxes only, data not shown) were similar to those for Experiment 2. No significant differences ($P > 0.05$) between treatments were found at any measurement date for the fraction of PPFD impinging on target leaves (Fig. 3).

Leaf duration

The treatment effect on LD was evaluated using an ANCOVA to control the variability of the data due to differences in I/Io between target leaves. To establish the timing of the I/Io effect which minimized the experimental error, ANCOVA were performed using I/Io values for the various measurement dates. The date for which the ANCOVA yielded the smallest mean square for the experimental error and a significant effect for the covariable was used (i.e. the proportion of the variability explained by main effects, R supply and PPFD fraction, was highest). In both experiments, the smallest error was estimated for observations made at 197°C day (base temperature = 4°C, Villalobos and Ritchie 1992) from the end of target leaf expansion, equivalent to 7 (Experiment 1) and 12 (Experiment 2) days (Fig. 4). This approximation also allows comparisons to be made between treatments across the two experiments, which experienced different thermal environments. The effect of supplemental R was additive to the PPFD effect, LD showing a linear relationship with I/Io (Fig. 4), with both treatment and covariable (I/Io) having significant ($P < 0.05$) effects on LD. Variability between plants within a treatment for LD data was smaller in Experiment 2 (1 vs. 6 days for Experiment 1, for RED treatment) and the effect of light manipulation was significant ($P < 0.05$) even without using I/Io as a covariable. The relationship between LD and I/Io for the combined data from both experiments could be described by linear regressions for RED and (GREEN and UNLIT) treatments (Fig. 4). Fitted lines differed ($P < 0.05$) in intercept but not in slope.

LD of leaves receiving R enrichment was increased by 5 days with respect to leaves that received green or no supplementation across the range of I/Io values observed in both experiments. (Fig. 4). Although no significant differences between treatments in I/Io were found, the variability in I/Io ratios on each target leaf was quite important (e.g. 0.08–0.38 in Experiment 1 at 7 days from achievement of full leaf size).

Discussion

Enrichment with green light increased the daily PPFD integral slightly (ca 5%), but did not affect LD (Fig. 4). In

contrast, supplemental red light (ca 4% of daily PPFD integral) produced a 5-day extension of basal LD, even though red enrichment was small (8.33 μmol m^{-2} s^{-1}) and produced only a small modification of R/FR (mean RED-UNLIT difference for $R/FR_{lower} = 0.22$) (Fig. 2). This result is complementary to the previous finding that increasing FR supply reduced LD of individual leaves of isolated sunflower plants (Rousseaux et al. 1996) and provides further evidence that the phytochrome family is involved in the control of the onset of leaf senescence. Furthermore, the delay LS in a dense canopy by a small alteration of the R light strongly supports the hypothesis that the decrease in R/FR observed in dense canopies contributes to triggering LS.

Previous studies on dicotyledonous species have shown that pulses of R light delay chlorophyll loss in leaf disks (Tucker 1981, Biswal and Choudhury 1986), leaves (Behera and Biswal 1990, van Doorn and van Lieburg 1993) or in the whole plant (Casal and Aphalo 1989, Lingakumar and Kulandaivelu 1993) and that the effect is reversed with FR pulses. Most of the experiments on the effect of R or FR enrichment on chlorophyll loss have been performed in growth chambers under unnaturally low PPFD compared with field PPFD. The experiments described here constitute the first demonstration that R light supply can delay leaf senescence of individual leaves of plants growing under field conditions at a plant population density similar to the one used in commercial crops.

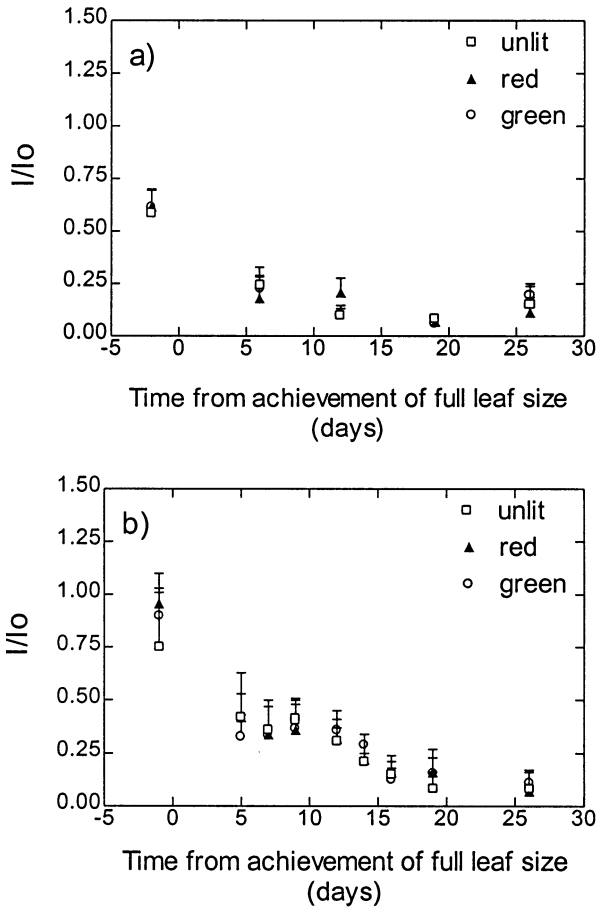

Fig. 3. Fraction of daily PPFD impinging on target leaves as function of time from full leaf size for Experiment 1 (a) and Experiment 2 (b). Fractional PPFD (I/Io) was calculated from daily PPFD impinging on the leaf (graphical integration from curve constructed with 5 daily measurements) and the corresponding value at the top of the canopy (mean daily Io integral = 30 mol m^{-2}). Data points are means of 6 replicates and vertical bars represent standard errors.

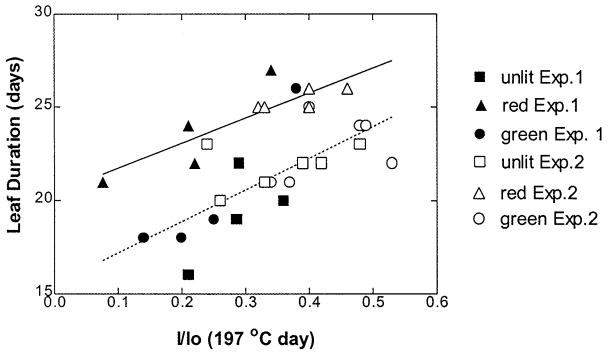

Fig. 4. Leaf duration of target leaves as a function of I/Io measured 197°C day (base temperature = 4°C) after achievement of maximum leaf size. Each symbol represents one replicate, regressions fitted to RED (—) or GREEN plus UNLIT (·····) data sets are also shown. Equations for the linear regressions are: $LD = 20.4 + 13.4 \times I/Io$ ($r^2 = 0.76$, n = 10), for RED and $LD = 15.5 + 16.9 \times I/Io$ ($r^2 = 0.50$, n = 20) GREEN plus UNLIT.

Several responses to crowding are mediated by the phytochromes (Ballaré et al. 1997, Smith and Whitelam 1997). Since LD is affected by R or FR light in opposite directions and there is a good correlation between R/FR received by a leaf and its nitrogen content (Rousseaux et al. 1999), we suggest that leaf senescence and nitrogen redistribution are likely part of the shade avoidance syndrome induced by phytochrome. Senescence and nitrogen redistribution may have a significant impact on canopy carbon gain. If the increased internode elongation after neighbor detection is accompanied by a mechanism that improves nitrogen availability in the leaves better exposed to sunlight, the chances of increased dry matter accumulation (and possibly the competitive ability) are significantly improved.

The responses to PPFD impinging on the target leaf in this experiment (Fig. 4) are consistent with those observed when PPFD was varied using neutral filters placed above leaves of isolated sunflower plants (Rousseaux et al. 1996) and generated variations in LD of about 6–11 days under conditions found in the present experiment (Fig. 4, RED treatment and controls, respectively). This may be contrasted with the 4-day reduction and 5-day increase in LD in response to FR (Rousseaux et al. 1996) and R (present experiment) enrichments, respectively. Because R/FR ratios have been shown to be a more stable signal of light environment than PPFD (i.e. less changeable with variations in degree and daily distribution of cloudiness) this variable could be a better predictor of leaf senescence than PPFD in crop simulation models, particularly as R/FR displays a robust negative exponential relationship with LAI.

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