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Laser-induced fluorescence signatures as a tool for remote monitoring of water and nitrogen stresses in plants

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Abstract. We tested the potential of leaf fluorescence as a tool for the remote sensing of water and nitrogen stresses in agricultural crops, as compared to the conventional contact techniques of leaf tissue or soil analysis. Multi-wavelength excitation fluorescence and diurnal behavior of the variable chlorophyll fluorescence were used to monitor nitrogen deficiency in corn (GEOIDE RES#54 network project, Canada) and water stress in pea plants (LURE project, France). Variable chlorophyll fluorescence was found to be a very sensitive tool, giving early indications of the drought stress and general indications of a misfunction of the photosynthetic apparatus. Some fluorescence parameters derived from ultraviolet (UV) and visible light (VIS) excitation of chlorophyll, especially the ratio FRFexUV/FRFexVIS measuring the epidermis UV transmittance, seemed to be more specifically related to the nitrogen content of leaves and precluded an ambiguous response as in the case of the more complex ratio BGF/ChlF. Despite the high variability of the biological material in the field, fluorescence could discriminate between N-deficient and N-saturated plants, and between water-stressed and non-water-stressed plants in the early stages of stress development.

Résumé. Nous avons testé le potentiel de la fluorescence foliaire comme outil pour la télédétection du stress hydrique et azoté dans les cultures agricoles, en comparaison avec les techniques conventionnelles d'analyse foliaire ou du sol. La fluorescence excitée multi-longueurs d'onde ainsi que le suivi diurne de la fluorescence chlorophyllienne variable ont été utilisés pour suivre la déficience azotée chez le mais (projet GEOIDE RES#54, Canada) et le stress hydrique chez le pois (projet LURE, France). La fluorescence chlorophyllienne variable est une méthode très sensible pour la détection précoce du stress hydrique et, de façon générale, peut apporter des renseignements sur l'état de fonctionnement de l'appareil photosynthétique. Quelques paramètres dérivés de la fluorescence chlorophyllienne émise par des feuilles suite à l'excitation UV et VIS, particulièrement le rapport FRFexUV/FRFexVIS mesurant la transmittance UV de l'épiderme foliaire, semblent reliés de façon spécifique au contenu foliaire en azote, étant plus fiable que le paramètre BGF/ChlF. Malgré la grande variabilité du matériel biologique à l'intérieur du champ, la fluorescence a permis de discriminer la déficience en azote, aussi bien que le stress hydrique, à des moments précoces de leur développement.

Introduction

Precision farming for crop management may lead to more efficient use of agronomic inputs by treating specific areas in an agricultural field. Water and nutrients are often the most yield limiting factors for the growing plant. A remote sensing system based on laser-induced fluorescence (LIF) has great potential in terrestrial vegetation mapping for detecting nitrogen (N) and water stress in crops.

Leaf fluorescence can detect nutrient stress on vegetation by blue-green (BGF) or chlorophyll fluorescence (ChlF) analysis and is a non-destructive and non-intrusive probe of plant status (for a review see Cerovic et al., 1999). Historically, however, leaf fluorescence was mainly used as a close contact technique. An important limitation of fluorescence light detection and ranging (LIDAR) in detecting vegetation is the measurement of fluorescence intensity, an extensive parameter depending on distance, canopy structure, and atmospheric transmission. Alternatives may be the use of the fluorescence ratio from different spectral bands, similar to the reflectance issued parameters, or the use of light-induced variable fluorescence, as presented in this paper.

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Long-term stress events and mineral deficiencies may eventually reduce the chlorophyll (Chl) and carotenoid content of leaves, which could be monitored by fluorescence but also by passive reflectance measurements (Daughtry et al., 2000; Gitelson et al., 1996; Lichtenthaler et al., 1996). It is noteworthy that typical fluorescence signatures occur before the loss of leaf chlorophyll (Heisel et al., 1996 for N stress), and therefore at early stages of stress development and before changes captured by reflectance. In addition, fluorescence may provide specific information about vegetation status by taking into account two characteristics: (*i*) the photo-induced variable ChlF yield, and (*ii*) the spectral characteristics (Cerovic et al., 1999).

Different stresses affect the photosynthetic capacity and are essentially monitored by decreasing the photosystem II (PSII) quantum yield (Schreiber and Bilger, 1993).

Spectral changes in the fluorescence emission spectra have also been related to stress signatures (Buschmann and Lichtenthaler, 1998; Samson et al., 2000). A number of studies measuring ultraviolet (UV) excited fluorescence spectra emitted by leaves indicated that the ratio of blue green fluorescence (BGF) to chlorophyll fluorescence (ChlF) is particularly suitable for early detection of vegetation stress, being very sensitive to changes in the environment (Stober et al., 1994; Stober and Lichtenthaler, 1993). Still, the ratio BGF/ChlF is sometimes controversial. For N stress, contradictory results have been reported by McMurtrey et al. (1994), Chappelle et al. (1984), Corp et al. (1997), and Heisel et al. (1996), as the BGF/ChlF signature is complex, depending on two independent emissions. Indeed, the red and far-red fluorescence emanates from protein-bound Chl *a* molecules in the leaf mesophyll cells. In contrast, BGF is emitted by various compounds located primarily in the epidermis and leaf veins (Cerovic et al., 1999).

Several studies indicate the ratio of red to far-red chlorophyll fluorescence (RF/FRF) as a potential parameter to judge the health state of plants, as it is affected by long-term stresses varying Chl content (Lichtenthaler et al., 1986; Lichtenthaler, 1988; D'Ambrosio et al., 1992; Buschmann et al., 1996) or short-term stresses that impair the photosynthetic quantum yield (Agati et al., 1995).

New insights into the use of LIF in monitoring vegetation status come from recent studies by Sowinska et al. (1999), Heisel et al. (1997; 1999), and Langsdorf et al. (2000) using leaf fluorescence imaging.

Limitations in the use of the BGF/ChlF and RF/FRF ratios in the remote sensing of vegetation in situ were attributed to diurnal variations due to the photo-induced changes in chlorophyll fluorescence (Agati et al., 1995; Valentini et al., 1994).

Very recently, a new ratio, FRFexUV/FRFexVIS, which measures the Chl fluorescence ratio following UV or visible light (VIS) excitation, showed great potential in the remote sensing of vegetation. It was shown to estimate epidermal UV transmittance (Bilger et al., 1997; Ounis et al., 2001). The FRFexUV/FRFexVIS ratio appeared to be specifically affected by N deficiency in greenhouse-cultivated corn plants (Samson et al., 2000). Moreover, it was shown to be independent of diurnal light variations (Ounis et al., 2001), which makes it very well suited for the remote sensing of vegetation under field conditions.

In vivo variable chlorophyll fluorescence has been known for more than half a century (Kautsky and Hirsch, 1931), and it was extensively used by physiologists in the last 10 years to characterize vegetation status (for a review see Govindjee, 1995; Schreiber and Bilger, 1993; and Apostol, 2000). Measurements of the effective PSII quantum yield ($\Delta F/Fm'$) (Genty et al., 1989) and the development of pulse amplitude modulation (PAM) fluorimeters (Schreiber et al., 1986) make variable Chl fluorescence a very popular tool in plant physiology, but it is used mainly as a close contact technique.

We present here the results of two research projects using the following two leaf fluorescence methods for the remote sensing of vegetation: (*i*) the remote detection of N stress in corn using fluorescence emission spectra following UV and VIS excitation (GEOIDE network project, Canada; Viau et al., 2000), and (*ii*) the diurnal monitoring of water stress using the frequency-induced pulse amplitude modulation (FIPAM) fluorimeter to measure remotely the variable Chl fluorescence in pea leaves (LURE project, France; Apostol, 2000).

Material and methods

Nitrogen stress experiment

Corn plants (*Zea mays* L., DeKalb 389Bt variety) were grown under field conditions during the summer of 2000 on two experimental sites in the Montréal region of Quebec (45–46°30′N, 72–75°W), Canada: l'Acadie (Agriculture and Agri-Food Canada experimental farm) and MacDonald (McGill University experimental farm). At the l'Acadie site, sixteen 20 × 20 m experimental plots were prepared, to which two nitrogen fertilizer treatments, low N and high N, were randomly applied at seeding (0 and 100 kg in low- and high-N treatments, respectively). The MacDonald site comprised thirty-two 9 × 9 m plots, to which two nitrogen levels, low N and high N (saturating), were applied at seeding (10 and 100 kg N/ha in low- and high-N treatments, respectively). Simultaneously, four weed-control levels (full weed, grass, broad leaves, or no weed control) were assigned by the use of specific herbicides (Ultim & Agral for grass and Banvel II for broadleaf weed control). The presence of weeds did not interfering with spectral measurements performed on individual corn leaves. They only influenced the corn plant growth.

Early in the season, three plants from each plot were sampled and taken to the laboratory for subsequent spectral measurements. Plants were stored in a dark, cool place and acclimated to room temperature (24°C) prior to spectral measurements. Fluorescence measurements were done on the youngest full-expanded leaves of corn plants 35 days after emergence at the l'Acadie site and 43 days after emergence at

the MacDonald site. Estimation of Chl content from the same leaves was done using a SPAD chlorophyll meter (SPAD-502, Minolta Co. Ltd., Osaka, Japan) measuring leaf transmittance.

Fluorescence emission spectra of dark-adapted leaves following laser excitation at different wavelengths (308, 360, 440, 480, and 630 nm) were recorded using a compact multi-wavelength fluorescent LIDAR system model PL (FLS-PL) prototype (Samson et al., 2000). The laser source was an excimer (XeCl) laser emitting nanosecond pulses at 308 nm that may pump a system of four alternative dyes to provide additional excitation wavelengths at 360, 440, 480, and 630 nm. Fluorescence emission was remotely (5 m) sensed by a charge-coupled device (CCD) array that enables the simultaneous measurements of emitted fluorescence between 380 and 850 nm, via a grating polychromator. Fluorescence emission spectra were normalized to the intensity of excitation wavelengths, then fluorescence ratios combining BGF, RF, and FRF emission following different excitations were computed. Results from the most relevant of these parameters are shown.

After fluorescence measurements were taken, plant shoots were dried for 48 h at 70°C. Biomass and nitrogen content were determined.

Water stress experiment

Pea plants (*Pisum sativum* L., var. Petit Provençal) were used for the water stress experiment. Plants were grown in a growth chamber under a 16 h : 8 h light–dark photoperiod at 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in pots containing vermiculite regularly watered with a nutrient solution (5× Hoagland).

Water stress was induced by withholding watering. Variable chlorophyll fluorescence measurements were performed simultaneously with gas exchange measurements, during 10 consecutive days, starting when watering was withheld. The 3rd leaf of 3 week old pea plants at the beginning of the experiment was selected for the measurements. The leaf was maintained continuously during the full length of the experiment in a LI-COR LI-6400 (LI-COR Inc., Lincoln, Nebr.) chamber for measuring gas exchange under controlled air conditions (360 $\mu mol\ CO_2\ mol^{-1}$, 20°C). Chl fluorescence was measured through a transparent LI-6400 window using a FIPAM fluorimeter as described by Apostol et al. (2001). FIPAM measures the pulse-modulated Chl fluorescence at a distance of about 1 m using a unique laser diode beam (635 nm, 2 μs pulse width, 15 mW, Philips). It determines minimal or stationary Chl fluorescence and maximal Chl fluorescence by switching the laser diode from a low-frequency regime (0.6 Hz) to a high-frequency regime (116 kHz) to obtain a saturating pulse during 3.6 s. Chl fluorescence was detected across a long-pass filter (RG665 Schott) at the entrance of the photodiode detector.

Chl fluorescence measurements were performed automatically during an artificial diurnal cycle, also triggering the LI-6400 readings. Minimal or stationary fluorescence (Fo or Fs for dark- and light-adapted leaves, respectively) was measured continuously and recorded each 30 s; maximal fluorescence (Fm or Fm′ for dark- and light-adapted leaves, respectively) was measured each 20 min. Optimum quantum yield of PSII was computed as follows:

$$\frac{Fv}{Fm} = \frac{Fm - Fo}{Fm} \tag{1}$$

The quantum yield of the linear photosynthetic electron flow was computed as follows (Genty et al., 1989):

$$\frac{\Delta F}{Fm'} = \frac{Fm' - Fs}{Fm'} \tag{2}$$

The electron transport rate (ETR) was estimated from the relationship

$$ETR = \frac{\Delta F}{Fm'} PAR f_a \frac{1}{2} \tag{3}$$

where PAR is photosynthetically active radiation; $f_a = 0.84$ is the fraction of PAR that is absorbed by the pea leaf; and multiplying by one half takes into account light absorption by the two photosystems, PSI and PSII.

Leaf water deficit (LWD) was estimated on reference plants from the same pot. Leaf discs were cut and weighed immediately and then reweighed after 24 h of rehydrating in distilled water at 4°C. Water deficit was calculated from the difference between the fresh and turgid weights, as a percent of the turgid weight (Flexas et al., 2000).

Results and discussion

Nitrogen deficiency

The nitrogen treatments in field plots produced significant differences in N content of corn plants and in leaf Chl content and biomass production (see **Figure 1**). Global differences in dry mass and chlorophyll content between the l'Acadie and MacDonald sites were due to plant phenological stage. The four weed levels in the field at the MacDonald site did not induce significant differences in the corn growth at this stage or in the fluorescence signatures. Consequently, we analyzed nitrogen stress at the MacDonald site independently of weed levels.

The LIF spectral analysis showed that Chl fluorescence yields are very low under UV excitation but increased markedly with VIS excitation, showing two distinct maximums in the red and far-red spectral region (spectra not shown). The low ChlF emission under UV excitation compared with that under VIS excitation is attributable to an UV-screening effect of the epidermis on field-cultivated plants, preventing UV radiation from reaching mesophyll cells to excite Chl. It is well known that UV radiation induces the synthesis and epidermal accumulation of UV-absorbing compounds, such as flavonoids, which are involved in protective photochemical mechanisms (Schweiger et al., 1996; Stober and Lichtenthaler, 1993).

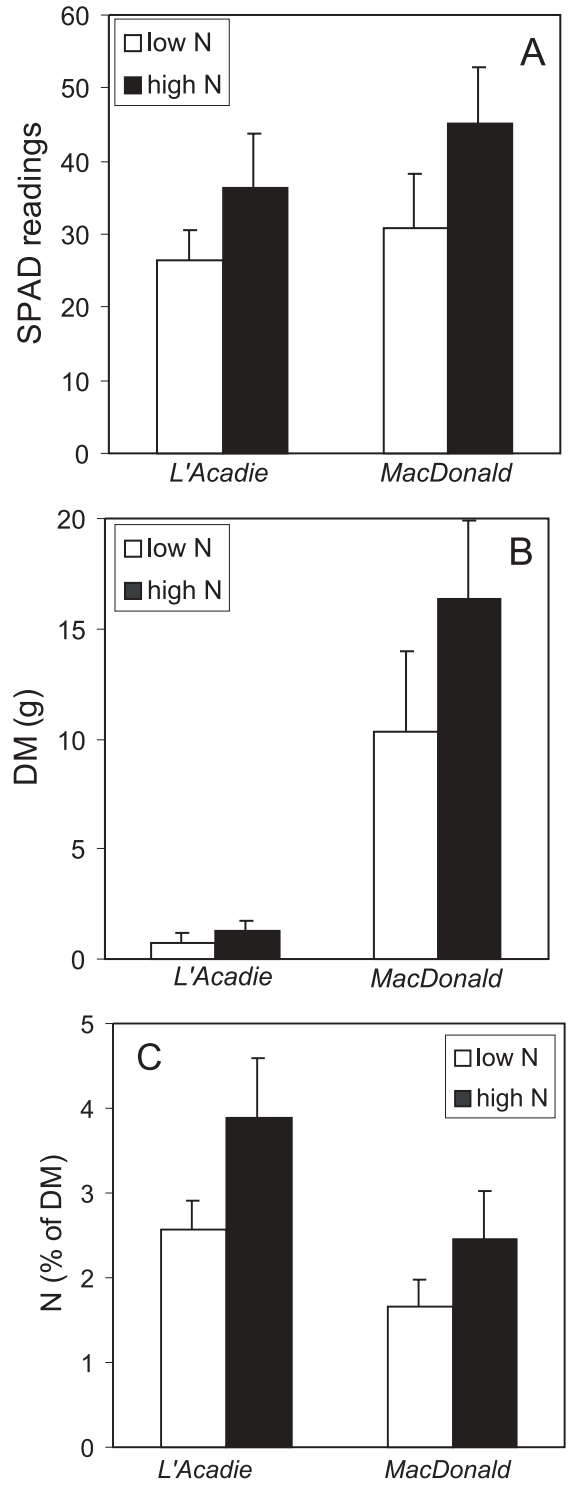

Figure 1. Chlorophyll content (A), biomass production (B), and nitrogen content (C) as a function of the N treatment at 35 and 43 days plant age in the l'Acadie and MacDonald experimental fields, respectively. Means and standard deviations (vertical bars) for 36 low-N and 12 high-N samples at l'Acadie and 48 samples at MacDonald. DM, dry matter.

We also observed that Chl fluorescence emission excited by UV radiation increased in N-saturated plants compared with that in N-deficient plants, where ChlF emission always remained very low. On the other hand, the relative emission of red and far-red fluorescence (RF/FRF ratio) differed between N-saturated and N-deficient plants, depending also on the excitation wavelength (data not shown). With increasing N availability, coupled with increased chlorophyll content in the leaf, the relative red fluorescence at 690 nm becomes smaller. This is attributable to the reabsorption of the emitted shorter wavelength red fluorescence by in vivo chlorophyll, since Chl absorption and fluorescence emission bands overlap in this spectral region. The FRF emission of Chl fluorescence in the region of 735 nm is affected very little or not at all by reabsorption (Gitelson et al., 1998) and developed with the increasing Chl content.

As a result, the ratio of red to far-red fluorescence under 630 nm excitation (RF/FRF630) (**Figure 2**) exhibited lower values for fully green plants from high-N plots compared with low-Chl content plants from low-N plots, as reported by many authors under different environmental conditions (Hák et al., 1990; Lichtenthaler, 1987; Lichtenthaler et al., 1986; 1990; 1998; Subhash et al., 1999). Decreasing mean values of the RF/FRF630 ratio following the global increase in Chl content observed for the fields at the MacDonald site compared with those at the l'Acadie site were associated with the plant development. The RF/FRF630 ratio was very sensitive at low Chl contents. Still, it reached saturation quickly at a medium Chl content, which makes it unsuitable for discriminating N stress during the early stages of stress development. The ratio between far-red ChlF excited under 360 and 440 nm (FRF360/FRF440) showed an important N-discriminating potential (**Figure 3**). A significant decrease in the FRF360/FRF440 ratio was observed in N-deficient plants, correlated with decreases in nitrogen and the chlorophyll content of leaves.

The FRFexUV/FRFexVIS ratio was shown to measure the epidermal UV transmittance (Bilger et al., 1997). Ounis et al. (2001) confirmed that this ratio was proportional to the epidermal UV transmittance; for quantitative measurements, a distortion factor depending on Chl concentration and excitation wavelength must be taken into account. The decrease of the FRF360/FRF440 ratio we observed in N-deficient plants was accompanied by a decrease of the Chl content, but was mainly due to increased epidermal UV screening. The increase of the FRF360/FRF440 ratio was correlated with the leaf N content. Samson et al. (2000) found that the FRFexUV/FRFexVIS ratio decreased as a possible specific signature of N stress, since a similar decrease in Chl content in sulfur-deficient leaves did not affect the UV epidermal transmittance.

The ratio of BGF to ChlF following UV excitation gives more ambiguous results for both 308 and 360 nm excitation wavelengths (**Figure 4**). At l'Acadie the BGF/FRF ratio increased significantly in N-deficient plants, whereas mean values from 48 samples at the MacDonald site were lower in N-deficient plants than in N-saturated plants for BGF/FRF308 and

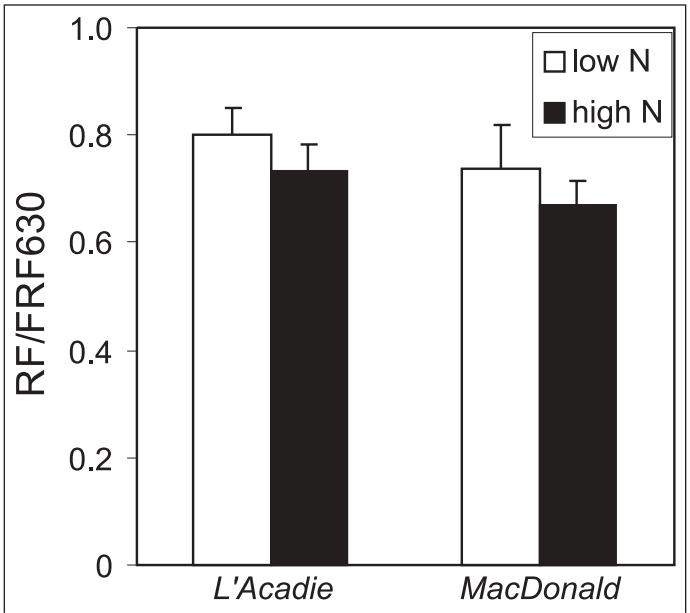

Figure 2. Red to far-red fluorescence ratio under 630 nm excitation (RF/FRF630) for the two N treatments.

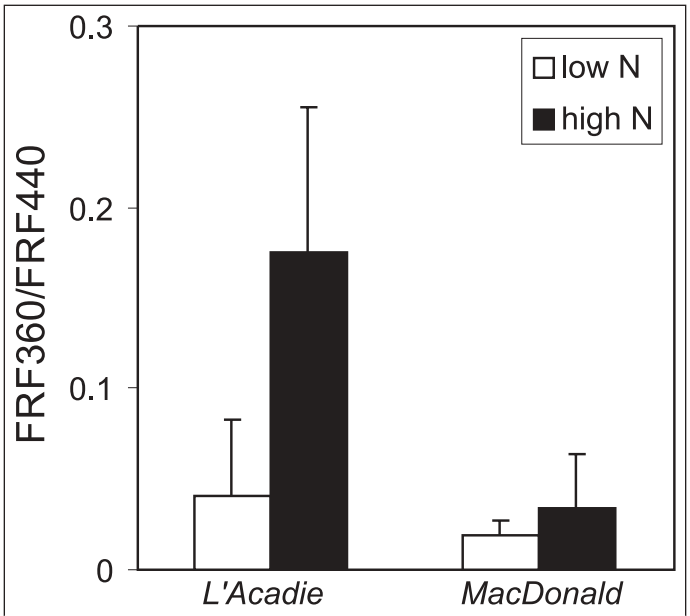

Figure 3. Far-red emission fluorescence ratio under UV 360 nm excitation (FRF360) and VIS 440 nm excitation (FRF440) for different N treatments.

non-significantly different for BGF/FRF360. However, mineral analysis indicated a significant enrichment of leaf N content and Chl content or biomass in high-N treated plots in both fields. A large increase in the BGF/ChlF ratio in the N-deficient plants compared with the unstressed plants is generally reported by other workers (Chappelle et al., 1984; Corp et al., 1997; Heisel et al., 1996; Langsdorf et al., 2000; Samson et al., 2000), but opposite trends were also observed (McMurtrey et al., 1994).

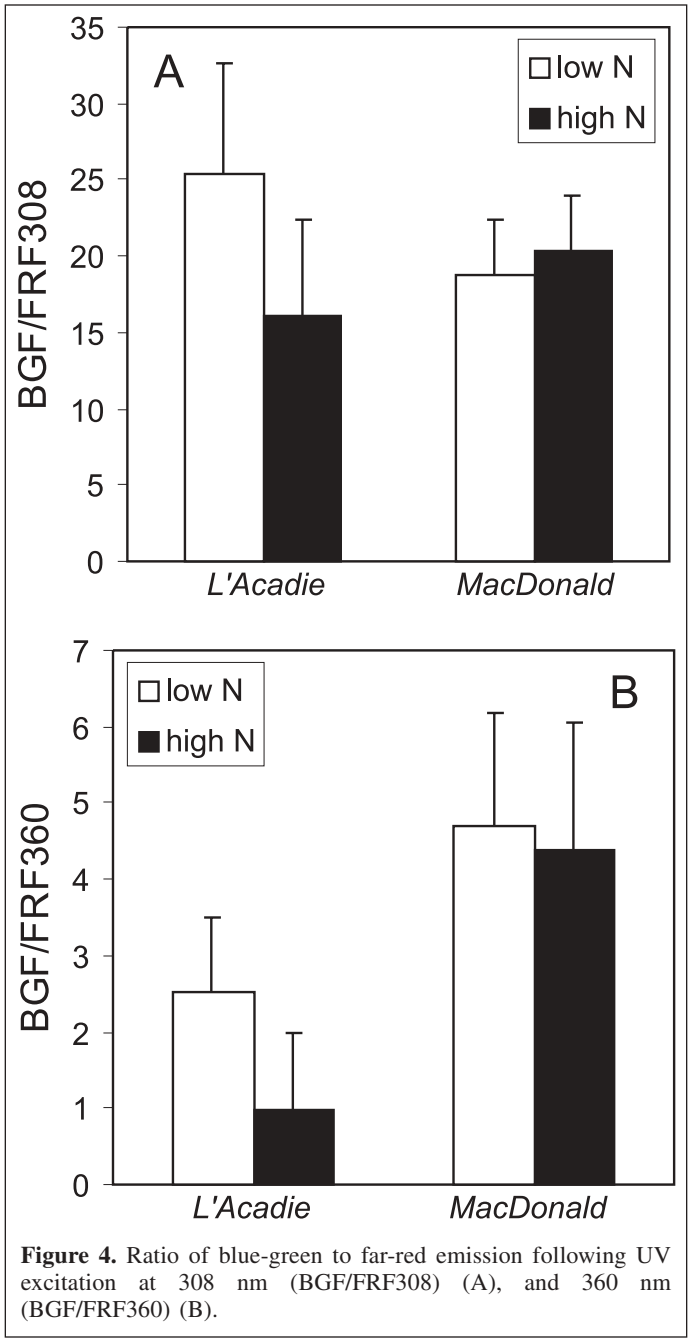

Figure 4. Ratio of blue-green to far-red emission following UV excitation at 308 nm (BGF/FRF308) (A), and 360 nm (BGF/FRF360) (B).

In our experiment, an additional stress, the water stress, possibly acted in the field at the MacDonald site during a dry period in July 2000, in contrast to the exceptionally humid period of May and June. The BGF/FRF ratio is the contribution of two independent fluorescence emissions, BGF and ChlF, with distinct origins, that can change independently in response to different physiological and environmental stresses. An overall increase of BGF paralleled an increase in FRF in N-saturated plants, compatible with the presence of water stress in that plot (Cerovic et al., 1999). Weather conditions were favorable to a limitation in the field water availability. The water deficit could be more pronounced in more developed plants from the N-saturated plots, requiring more water than the

smaller plants in N-deficient areas. Available data on plant moisture are not sensitive enough to assess the water stress, as the treatment already induces differences in crop growth. We are checking if fluorescence spectra may give some additional indications about the possible water stress. Blue versus green fluorescence was reported to be sensitive to water stress (Cerovic et al., 1999). The mean values of the ratio of blue (450 nm) to green (520 nm) fluorescence emission following 360 nm excitation (BF450/GF520) from N-saturated plots are higher (1.95 ± 0.13) than those from the N-deficient plots (1.82 ± 0.14). This was not consistent with an increase in relative GF as reported for water stress in soybean (Chappelle et al., 1984) and olive leaves (Broglia, 1993). Additional studies in which water stress is properly monitored are necessary to discriminate between nitrogen and water stress signatures in corn.

Water stress

The Chl fluorescence behavior following a 24 h diurnal cycle was monitored in pea leaf for 1 week of progressive water stress development. **Figure 5** presents results on Chl fluorescence for a well-watered plant (**Figure 5A**) compared to the same plant under mild or severe water stress after 6 (**Figure 5B**) and 7 (**Figure 5C**) days of drought.

Maximum Chl fluorescence remained constant during the night in all experiments and progressively decreased with an increase in irradiance during the diurnal cycle, as affected by nonphotochemical quenching, much enhanced even at low PAR under severe water stress conditions (**Figure 5C**). Fs was controlled by both photochemical and non-photochemical quenching and presented a complex diurnal evolution. The maximum value of Fs was assessed at lower PAR values as water stress developed. This typical stationary Chl fluorescence behavior is shown in **Figure 6**, where stomatal conductance measured simultaneously was also plotted during an ascending diurnal cycle. A close correlation is observed between the stationary Chl fluorescence and leaf conductance during diurnal evolution of PAR. For mild water stress, **Figure 6B** shows the biphasic evolution of stationary Chl fluorescence as irradiance increases. For readings taken early in the morning, before the stomatal closure, there is a positive correlation between Fs and PAR. There was a negative correlation starting when stomata openings became restricted, as indicated by a poor conductance showing a decreasing trend with increasing PAR. Under such conditions, non-photochemical quenching mechanisms were enhanced (as shown in **Figure 5B** where Fm′ decreases) to protect PSII from overexcitation.

As shown in **Figure 5C**, part of the non-photochemical quenching appeared irreversible after diurnal exposure of highly water stressed leaves to high irradiance. The limited protection against PSII overexcitation conferred by the non-photochemical quenching is no longer effective and photoinhibition is apparent.

Figure 7 presents the optimum and effective PSII quantum yield values measured from variable Chl fluorescence before

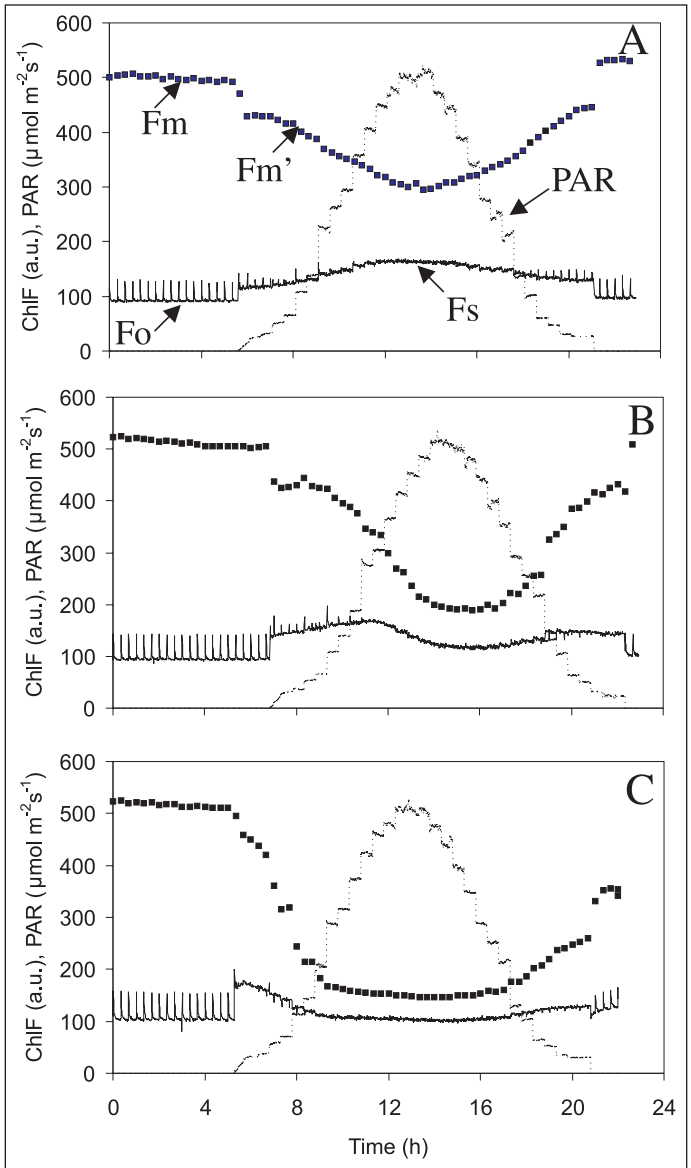

Figure 5. Diurnal evolution of variable Chl fluorescence (ChlF) with changes in photosynthetically active radiation (PAR) for a control leaf (A), for a 25% leaf water deficit (B), or for a 50% leaf water deficit (C) in a pea plant. a.u., arbitrary unit; solid line, stationary Fs or Fo; ■, maximal Fm′ or Fm; dotted line, PAR.

noon (corresponding to the ascending part of the PAR curves). The ΔF/Fm′ ratio monotonically decreases with an increase in PAR, as water stress developed from the first day until the end of experiment. A similar decrease of the photosynthetic quantum conversion under water stress was already reported in beans and grapevine leaves (Lichtenthaler and Babani, 2000; Flexas et al., 2000).

When ETR estimated from Chl fluorescence is compared with the measured CO_2 assimilation rate (**Figure 8**), a deviation from linearity characteristic of the control plants appeared in water-stressed plants. The CO_2 assimilation rate decreased at a higher rate than ETR. The photorespiration rate must be

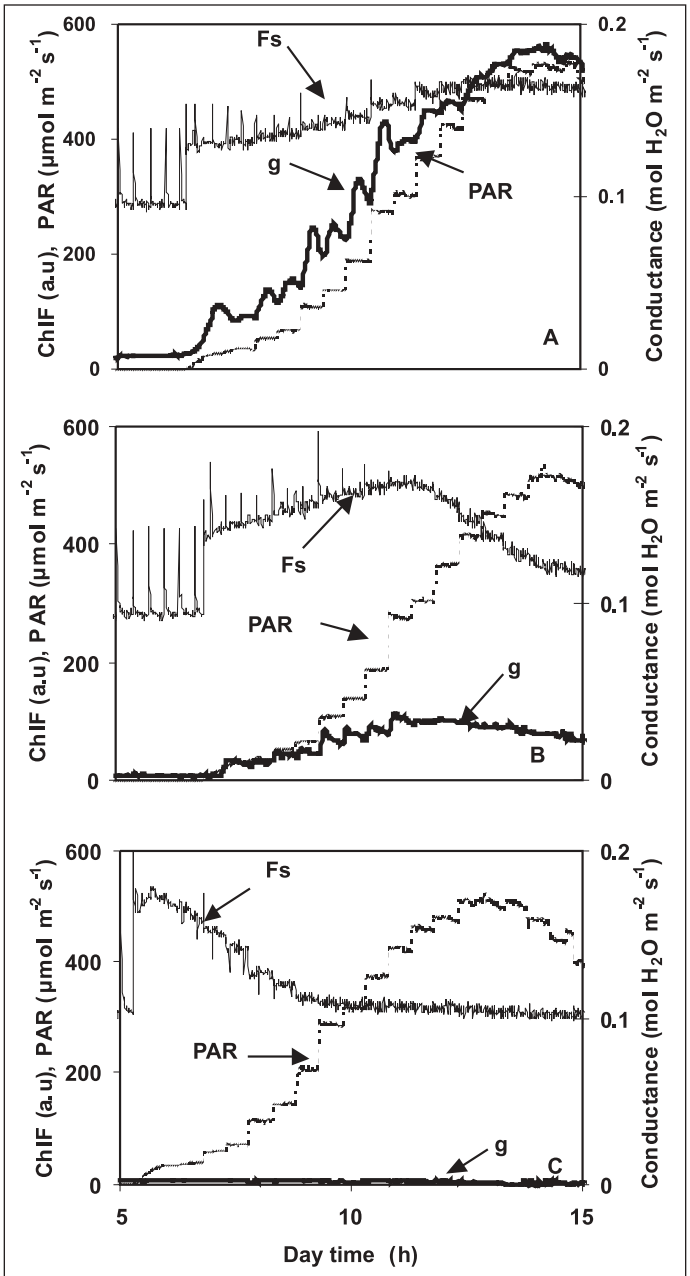

Figure 6. Diurnal evolution of chlorophyll fluorescence (Fs) and leaf conductance to H_2O (g) measured simultaneously on the same leaf at different stages during the development of water stress: (A) before water stress, (B) mild water stress, (C) severe water stress. Diurnal irradiance (PAR) is plotted as a function of time.

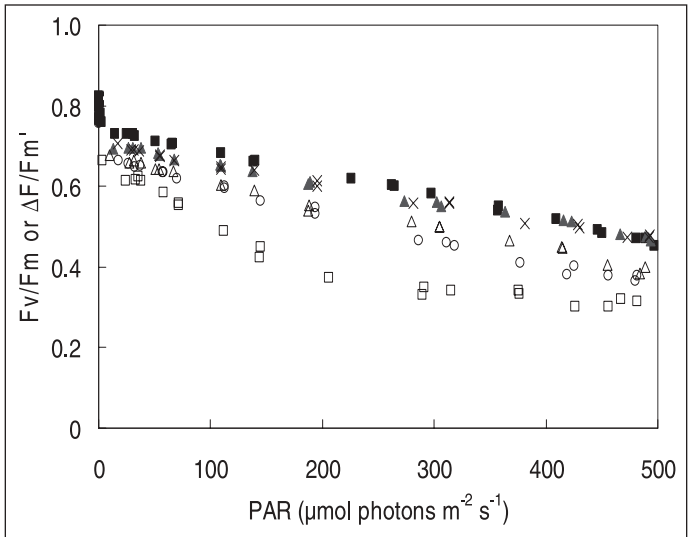

Figure 7. PSII quantum yield evolution during the development of water stress. ■, control leaf; ▲, ×, △, and □, second, third, fifth, and sixth day of withholding watering; ○, recovering 2 days after water was added.

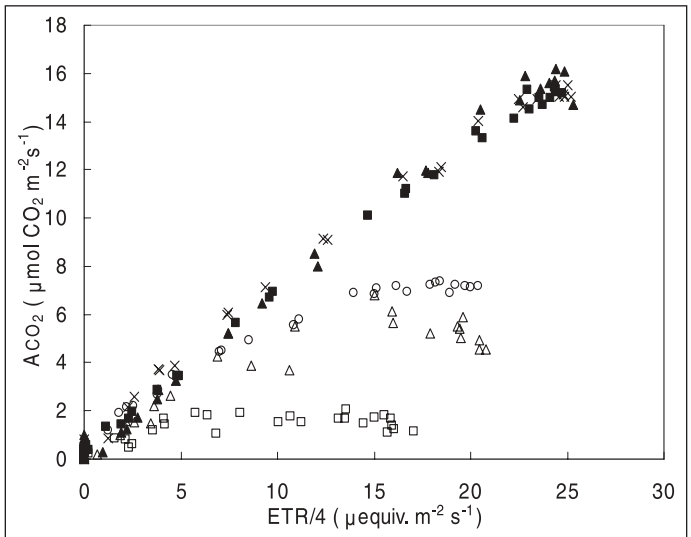

Figure 8. CO_2 assimilation rate A_{CO_2}, taking into account net photosynthesis and respiration rates ($A_{net} + R$) as measured by gas exchange versus the fluorescence estimated electron transfer rate (ETR) during the development of water stress. Symbols as in **Figure 7**.

increased in such conditions, as observed in grapevine leaves under water stress (Flexas et al., 2000).

Conclusions and perspectives

In this study, remote sensing of plant fluorescence produced accurate signatures of nitrogen and water stress. The technique is rapid, non-invasive, and non-destructive compared to conventional contact measurements and offers great potential for further use in precision agriculture. The LIF spectral analysis provides specific information on nitrogen status through the FRFexUV/FRFexVIS ratio in addition to the more widely used RF/FRF and BGF/ChlF ratios. Quenching analysis of chlorophyll fluorescence as a function of irradiance may provide additional information about the physiological status of vegetation, as shown in the study on water stress in pea plants. The study of nitrogen stress at the MacDonald site raises some questions about discrimination of concomitant stresses. The behavior of stationary Chl fluorescence with changes in irradiance indicated a possible remote signature of water stress,

with the advantages of rapidity and sensitivity compared to the plant water content measurements.

Advanced studies are necessary before fluorescence analysis can be used in precision agriculture and to monitor complex environmental situations at the field level. We propose combining the two fluorescence methods analyzed here, namely variable Chl fluorescence and multi-wavelength excited fluorescence, in a further experiment to investigate the concomitant nitrogen and water stress. Diurnal variations in LIF must be quantified to overcome present limitations in performing in situ remote sensing measurements.

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List of acronyms and symbols

A_{CO_2}	CO_2 assimilation rate
A_{net}	net photosynthesis
BGF	blue green fluorescence
CCD	charge-coupled device
Chl	chlorophyll
ChlF	chlorophyll fluorescence
DM	dry matter
ETR	electron transport rate
FIPAM	frequency induced pulse amplitude modulation
Fm, Fm′	maximal fluorescence in dark- and light-adapted leaves, respectively
Fo, Fs	fluorescence emission for dark- and light-adapted leaves, respectively
Fv/Fm	optimum PSII quantum yield
ΔF/Fm′	effective PSII quantum yield
FRF	far-red fluorescence
LIDAR	light detection and ranging
LIF	laser-induced fluorescence
LWD	leaf water deficit
PAM	pulse amplitude modulation
PAR	photosynthetically active radiation
PSII, PSI	photosystems 2 and 1, respectively
R	respiration rate
RF	red fluorescence
UV	ultraviolet
VIS	visible light