

Assessment of Vegetation Photosynthesis through Observation of Solar Induced Fluorescence from Space

Executive Summary

1. Introduction

The increase in atmospheric CO₂ due to anthropogenic emissions, and the corresponding global warming and associated Climate Change, are known to be partly countered by the active C sequestration by natural vegetation and (to a lesser extent) agricultural crops. As an example, temperate and boreal forests in the Northern Hemisphere alone cover an area of about 2×10^7 km² and act as a substantial C sink (0.6-0.7 Pg C yr⁻¹). At the European level, terrestrial vegetation is thought to absorb 7-12 % of total anthropogenic C emissions. Far from being in equilibrium with the atmosphere, natural ecosystems absorb annually as a result of photosynthetic processes more C than is then re-emitted by plant respiration and the decomposition of plant residues. It is therefore clear that the quantitative assessment of the contribution of photosynthetic processes to the global C balance is an important pre-requisite for the understanding of the impact of anthropogenic activities. The prediction of the response of vegetation to future atmospheric CO₂ and climate is also crucial for the reliable prediction of Climate Change over the next century.

Mathematical models are the only tool available for the prediction of such a large-scale and long-term response. Models incorporating the best available knowledge about physiological and ecological short-term processes are currently used with good success for the representation of ecosystem gas exchange. The amount of detail needed for their parameterisation, however, makes their large-scale application difficult.

Novel advances in quantitative remote sensing, however, pave the way for the estimation of a broad new set of DVM parameters from space. In particular, an improved parameterisation of photosynthetic processes could be derived from the measurement from space of chlorophyll fluorescence.

The absorption of solar energy by chlorophyll in green leaves is known to be the primary process leading to vegetation photosynthesis and primary production, to carbon sequestration and, ultimately, to life on Earth. Whilst most of the absorbed energy is used in photosynthetic processes or dissipated as heat, a variable fraction is re-emitted by chlorophyll molecules at longer wavelengths, in a process known as chlorophyll fluorescence, which can be detected by advanced remote sensing techniques. Of particular relevance is the fluorescence emitted by Photosystem II (PSII), which is known to compete dynamically with photosynthetic electron transport.

Although the potential of Photosystem II (PSII) chlorophyll fluorescence as a probe of photosynthetic processes has been widely demonstrated over the last decades, the attention has generally focused on

active manipulative ('pulse-saturated' or 'fluorescence induction') techniques which are not amenable to satellite remote sensing. Recent studies, however, have demonstrated the potential of passive remote sensing techniques for the detection of solar-induced chlorophyll fluorescence (SIF) from the signal in and around the two main oxygen absorption bands (O2-A and O2-B), paving the way for the application of the technique to airborne and satellite remote sensing. A model of fluorescence emission and its relationship with photosynthetic processes at the leaf and canopy level (FLUORMOD) had also been developed as part of a previous project by the European Space Agency, although its applicability was limited to ideal conditions, making it unsuitable for the analysis of vegetation processes under ambient conditions.

2. Aims of the project and proposed approach

The key objective of this study was to analyse the applicability of vegetation fluorescence observations in addition to other biophysical variables derived from optical and thermal infrared remote sensing for regional dynamic vegetation modelling.

The study was also expected to result in a range of quantitative predictions of the link between solar-induced fluorescence, reflectance and photosynthesis at the leaf and canopy level, which could guide ongoing and future campaigns aimed at the airborne and satellite observation of fluorescence and primary production.

The methodology originally outlined in the proposal was based on the application of two distinct models: (i) a very detailed model of leaf and canopy photosynthesis and fluorescence (based on the FLUORMOD model, already developed as part of past ESA projects, for the representation of the functional link between photosynthesis and fluorescence), to be included in a multi-layer canopy model and used for the simulation of expected canopy fluorescence fields and gross primary production under a range of conditions; (ii) a coarser DVM (Dynamic Vegetation Model), to be modified for the assimilation of the information coming from fluorescence remote sensing at a global scale but without a detailed representation of canopy reflectance and fluorescence. The link between the two models was to be based on the expected semi-empirical correlation between fluorescence fields and gas exchange, as derived from the application of the detailed model (e.g. between canopy fluorescence radiance and GPP or absorbed radiation, or between light-use efficiency and fluorescence efficiency). The use of predictions from the detailed model was justified by the lack at the time of any long-term experimental dataset at the canopy scale, combining parallel measurements of canopy fluorescence and GPP.

Following a detailed discussion with the Agency, the proposed methodology was later modified, since such a semi-empirical approach was not deemed to guarantee the generality of the results obtained. It was decided, on the contrary, to attempt the direct inversion of a suitable DVM (modified to include a simple representation of canopy fluorescence) on the fluorescence fields generated by the detailed model, used as a proxy for the lacking measured datasets.

An initial analysis of experimental results, derived from the literature and from ongoing, parallel experimental studies funded by the Agency (e.g. SEN2FLEX, SIFLEX, CEFLEX), however, demonstrated that the functional representation of the link between photosynthesis and fluorescence in the FLUORMOD model was not appropriate and did not provide the required level of realism under normal environmental conditions. A more detailed and realistic analysis of leaf-level processes than originally foreseen was therefore deemed desirable before the canopy-level model could be applied for the fulfilment of the original objectives.

The development and testing of an enhanced, realistic leaf-level model required an additional effort, and resulted in time and schedule constraints that led to the replacement of the assimilation activities originally foreseen by a thorough sensitivity analysis (Fig. 1). This new strategy has been successfully applied, the leaf level and canopy level models have been significantly improved and at the end of the project we are in a position to start assimilation studies, based on leaf- and canopy-level models which are fully consistent with available experimental evidence.

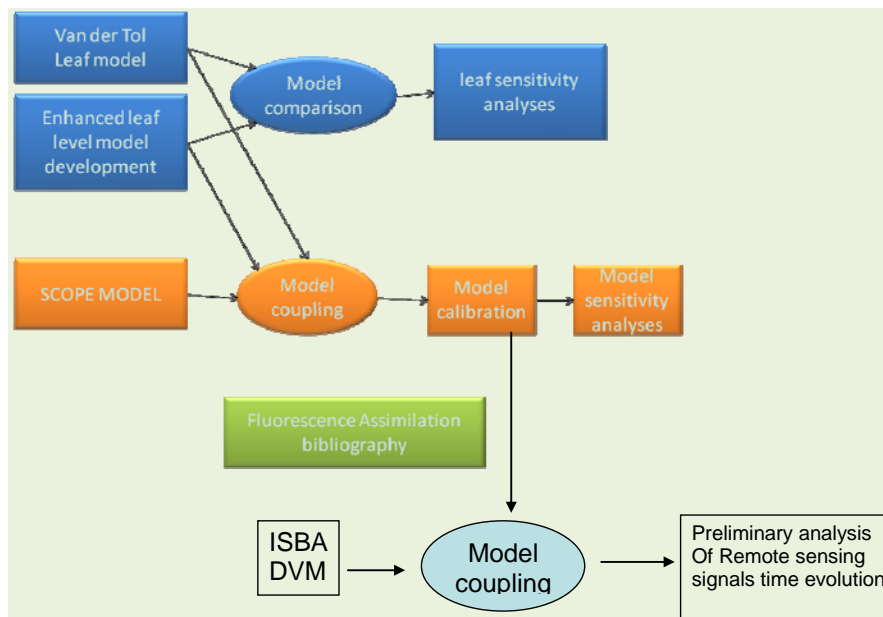


Figure 1. Final study logic, representing leaf-level model development and application (in blue), the application of the newly developed SCOPE model at canopy scale and the preliminary coupling with the ISBA-DVM prognostic model.

The project therefore resulted in (i) the further development of models available for the interpretation of vegetation SIF and (ii) their application over a range of vegetation types and conditions in order to demonstrate the potential of fluorescence remote sensing as a constraint for existing models of vegetation primary production.

3. Summary of key results of the project

3.1 The techniques and problems associated with the remote sensing of chlorophyll fluorescence have been first reviewed in the project, including the confounding effects of changes in chlorophyll content. Because of fluorescence re-absorption in the red region, chlorophyll content is arguably the single greatest factor affecting steady-state chlorophyll fluorescence ratios derived from red and far-red fluorescence (R/FR); chlorophyll content exerts its control over R/FR fluorescence mainly through re-absorption of fluorescence. Methodologies for the concurrent remote sensing of chlorophyll content from visible reflectance and for the correction of the fluorescence signal for the chlorophyll effect have therefore also been analyzed.

3.2 Another underlying problem in the analysis of the fluorescence signal is the contribution from Photosystem I (PSII), which carries little information content. Novel methods for the disentanglement of PSII fluorescence from the fluorescence signal from PSI have therefore been developed, based on the analysis of SIF in the two main oxygen absorption bands (O2-A and O2-B). The present analysis applied to the two fluorescence bands can be applied at present at the leaf level, once the relative PSI/PSII fluorescence contribution for the species investigated is known. A methodology has also been developed for the application of the method under conditions of non-saturating chlorophyll contents.

Considerable advances have been made in the project in the interpretation of the fluorescence signal.

3.3 Two novel algorithms have been developed for the interpretation of the solar-induced fluorescence signal that can be measured from airborne and satellite platforms, greatly refining the previous formulation implemented in the FLUORMOD model. The proposed algorithms differ in their degree of empiricism, and manage to provide a representation that is coherent with state-of-the-art models of pulse-saturated fluorescence and leaf gas exchange. The two algorithms (van der Tol-Verhoef-Rosema and the Magnani model) have been preliminarily tested against detailed measurements at the leaf level under controlled conditions, demonstrating a strong and non trivial relationship between fluorescence and photochemical yield. The test appears to confirm the more recent and process-based representation of the Magnani model.

The relationship between fluorescence yield (i.e. fluorescence radiance per unit absorbed light) and photochemical yield (i.e. electron transport leading to photosynthetic processes, per unit absorbed light) was found to be non monotonic, differing under light- (negative association) or CO₂-limited conditions (positive association), thus providing an elegant explanation for the contrasting results reported in the literature.

Under saturating light conditions, lower fluorescence yields are predicted and observed under conditions of low CO₂, as could be expected in response to drought and stomatal closure (Fig. 2).

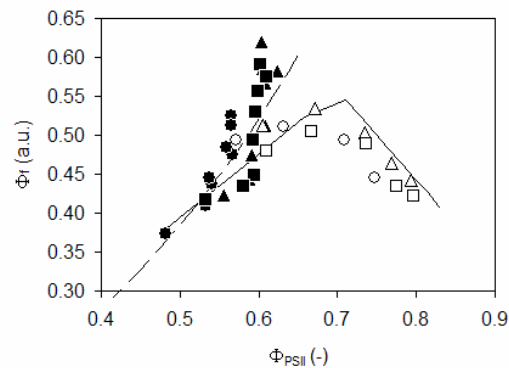


Figure 2. Quantitative test of the Magnani model against the leaf-level data of fluorescence yield (Φ_f) and PSII photochemical yield (Φ_{PSII}) described in Figure 3-12. The continuous line corresponds to simulated changes in irradiance under constant CO₂; the dashed line corresponds to changes in atmospheric CO₂ under constant irradiance. All photosynthetic and fluorescence parameters were derived from the literature, except for maximum photosynthetic potential and a fluorescence scaling factor accounting for PAM-2000 measurement light intensity.

Because of the parallel effects of light absorption on both processes, however, a general positive association between leaf photosynthesis and fluorescence radiance is predicted; according to the most refined Magnani model, moreover, leaf biochemistry is predicted to affect the relationship only marginally, suggesting SIF also as a general semi-empirical tool for the assessment of photosynthetic rates.

3.4 A more complex model of energy fate and electron transport, chlorophyll fluorescence and xanthophyll de-epoxidation state has been also developed as part of the project, in order to be able to assimilate in the proposed modelling scheme all the information that could be obtained from the proposed satellite sensor. Apart from solar-induced fluorescence, other indices have been proposed over the last few years for the remote sensing of photosynthetic processes. The Photochemical Reflectance Index (PRI), in particular, has been proposed as an effective tool for the measurement of xanthophyll de-epoxidation state and photosynthetic light-use efficiency, both at leaf and at canopy level, as demonstrated by the review included carried out as part of the project. Although not yet implemented at the canopy scale, the model could provide in the future an interesting tool for the remote sensing of vegetation photosynthesis and productivity, integrating the information content of chlorophyll fluorescence as well as PRI.

3.5 A novel model has also been developed for the interpretation of observed changes in the ratio between fluorescence contributions from PSI and PSII, and therefore on fluorescence ratio (F685/F730) once corrected for re-absorption effects. Changes in fluorescence ratio in response to temperature are interpreted in terms of exciton spillover from PSII to PSI in response to reaction centre closure. If confirmed under a wider range of conditions, the model could make it possible to exploit the information content of fluorescence ratio, and could be implemented in future versions of the canopy-scale model SCOPE.

3.6 In order to scale-up to a larger scale the new understanding of the relationship between fluorescence and photosynthetic processes achieved through the two leaf-level algorithms mentioned above, a novel canopy-level model of vegetation energy transfer, chlorophyll fluorescence and photosynthesis has been developed, extending the work carried out under past projects and making it possible to explore the relationship between canopy fluorescence radiance and gross primary production (GPP).

Apart from the inclusion of a state-of-the-art representation of physiological and ecological processes, the newly developed SCOPE (Soil-Canopy Observation, Photosynthesis and Energy balance) state-of-the-art model also includes a detailed representation of thermal energy transfer and canopy TIR radiance. Leaf-level

reflectance is simulated based on the PROSPECT model and scaled up to the canopy level using the SAIL model; leaf-level fluorescence is a function on local light absorption and photosynthetic rates, and the signal is then scaled up across a number of canopy layers using the FLUORSAIL model. Leaf-level photosynthesis response to environmental variables is captured by the Farquhar model, whilst stomatal conductance is represented according either to the Cowan model or to the Leuning model. Temperature effects on photosynthesis are also represented, as well as photosynthetic acclimation to growth temperature. Vertical profiles in photosynthetic potentials are also duly taken into account.

3.7 A sensitivity analysis of the model has been carried out for three different vegetation types (agricultural crops, deciduous forests, evergreen coniferous forests) under different environmental conditions corresponding to four sites in Italy and France, making it possible to explore the generality of model predictions.

Simulations based on the two alternative leaf-level algorithms both predict a strong sensitivity of canopy fluorescence radiance to incoming radiation and the fraction of absorbed radiation, as determined by leaf area index and chlorophyll content; the fluorescence signal is also reduced under mild stress conditions, demonstrating its potential as an early indicator of stress. More interestingly, a strong relationship is predicted between canopy fluorescence radiance and gross primary production, consistent with canopy-level observations from parallel field campaigns. Simulations based on the most advanced leaf-level algorithm predict a quasi-linear relationship between canopy SIF and GPP, which is largely insensitive to vegetation type and photosynthetic potentials (Fig. 3). The SIF signal appears to be highly sensitive to changes in GPP (in response to chlorophyll content, LAI and light absorption, environmental conditions and photosynthetic potentials), demonstrating its suitability as a tool for the quantitative measurement of GPP from space. Modelling results appear to be consistent with experimental results from parallel field campaign, both in qualitative and in quantitative terms.

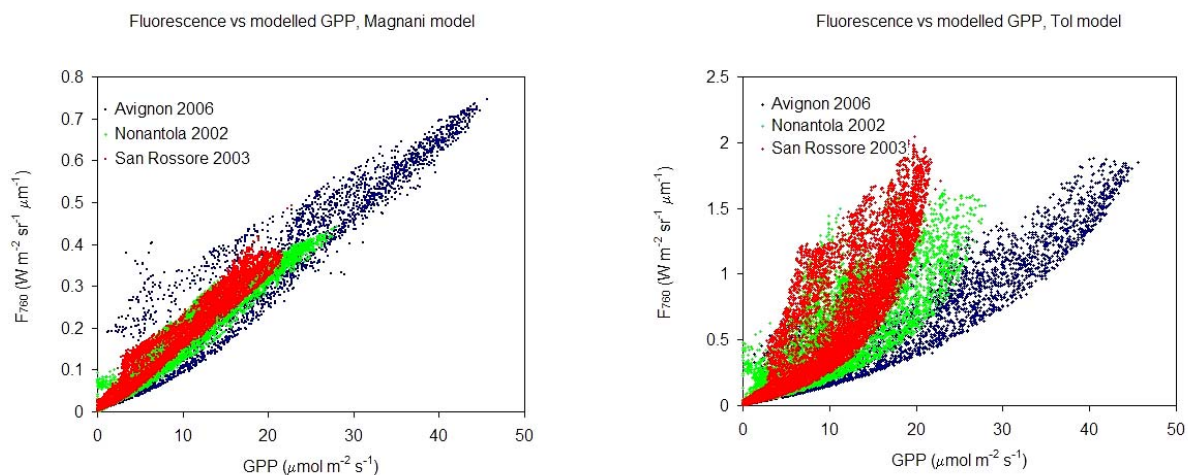


Figure 3. Simulated values of canopy gross primary production (GPP) and TOC fluorescence radiance at 760 nm (F_{760}) over the course of the year at the three test sites (winter wheat, Avignon; mixed deciduous forest, Nonantola; coniferous forest, San Rossore) according to the SCOPE model. Results are presented based both on the SCOPE-I (left) and on the SCOPE-D+ version of the model (right).

4. Conclusions and recommendations

In summary, the project has resulted in a substantial advancement of our understanding of the leaf and top-of-canopy fluorescence radiance signal, as could be observed (after propagation through the atmosphere) from an airborne or satellite platform. Model predictions are broadly consistent with experimental results at both scales, providing a sound basis for future modelling and experimental studies.

Based on the results of the project it is possible to draw a set of recommendations for the design and operation of future satellite missions aimed at the remote sensing of chlorophyll fluorescence and the estimation of vegetation photosynthetic processes and primary production. In particular:

- ▶ Measurements should be made in both O2 bands, for either (i) the retrieval of fluorescence contribution from PSII alone or (ii) the use of the full information on photosynthetic processes provided by the full fluorescence spectrum (see below).
- ▶ The parallel measurement of both fluorescence and VIS-NIR reflectance should be recommended, for the assessment of canopy chlorophyll content (from measurements in the red-edge region) and of PRI (Photochemical Reflectance Index) from measurements in the 530-570 nm region. The latter, in particular, could provide additional information on photosynthetic processes for the joint assessment of instantaneous processes and steady-state potentials.
- ▶ Measurements should be taken preferentially around midday or in the early afternoon, since according to available model simulations the sensitivity of canopy fluorescence to photosynthetic parameters appears to be highest around this time.

It is also possible to suggest further model developments that would be needed in order to improve our ability to measure photosynthesis from space:

- ▶ Further develop the detailed model of electron transport and photosynthesis proposed as part of the project into an operational canopy-scale model, for the joint simulation of fluorescence and the Photochemical Reflectance Index. Such a development has been strongly recommended by MAG members, as it would make it possible to simulate the full range of interactions between photosynthetic processes and TOC radiance.
- ▶ Develop a procedure for full model inversion and the estimation of canopy parameters from observed fluorescence. Because of the non-uniqueness of the relationship between fluorescence and photosynthesis, however, this will presumably require the inclusion of both SIF and PRI into a joint modelling scheme, based on the aforementioned detailed model of electron transport and photosynthesis.
- ▶ Include in the model a variable fluorescence matrix. In the present version of the SCOPE model, the excitation-fluorescence (E-F) matrix is fixed so that fluorescence spectra could consistently deviate from field measurements. A variable E-F matrix is available in the Fluspect model (Verhoef, pers. comm.), already applied in other studies related to the FLEX candidate mission, and could be introduced in future versions of the SCOPE model;
- ▶ In order to be able to parameterize the model for the representation of E-F matrices and fluorescence spectra, the model of energy partitioning between PSI and PSII proposed as part of the project should be further developed and tested against measurements under controlled conditions. As an alternative to the representation of fluorescence spectra, the method developed as part of the project for the isolation of PSII contribution to leaf fluorescence could be expanded into a procedure applicable at canopy scale.

Specific recommendations can also be made for additional experimental studies needed for a thorough validation of the model at both leaf and canopy scale:

- ▶ New laboratory studies are needed, to be carried out under controlled conditions, in order to test the two alternative leaf-level models developed as part of the project. The two models make it possible to predict the link between chlorophyll fluorescence and photosynthesis in response to a range of environmental and internal conditions, and their predictive ability can be therefore carefully tested at the leaf level.
- ▶ A network of long-term measurement sites should be developed, where canopy fluorescence is measured continuously over the course of the year in parallel with eddy-covariance measurements of canopy gas exchange. This would provide a robust set of measurements for the test of the SCOPE model at the canopy level.
- ▶ A limited number of carefully designed field campaigns should be carried out over selected vegetation types, where the measurement of all the parameters required by the models could be combined with fluorescence and photosynthesis measurements over a range of scales (from leaf to airborne).