The Use of Remote Sensing in Light Use Efficiency Based Models of Gross Primary Production: A Review of Current Status and Future Requirements

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Abstract

Global estimation and monitoring of plant photosynthesis (known as Gross Primary Production - GPP) is a critical component of climate change research. Modeling of carbon cycling requires parameterization of the land surface, which, in a spatially continuous mode, is only possible using remote sensing. The increasing availability of high spectral resolution satellite observations with global coverage and high temporal frequency has allowed the scientific community to revisit a number of existing approaches for modeling GPP, and reassess the potential for using remotely sensed inputs. In this paper we examine the current status and future requirements of modeling global GPP thereby focussing on the light use efficiency approach which expresses GPP as product of the photosynthetically active radiation (PAR), the fraction of PAR being absorbed by the plant canopy (f_{PAR}) and the efficiency $\underline{\varepsilon}$ with which this absorbed PAR can be converted into biomass. The capacity of remote sensing to provide the critical input variables for this approach is investigated and key issues are identified and discussed for future research.

Keywords: remote sensing, GPP, photosynthesis, light use efficiency, fPAR, carbon fluxes

1. Introduction

Terrestrial ecosystems absorb approximately 60 Gt of carbon annually through the physiological process of photosynthesis (Janzen, 2004), also referred to as Gross Primary Production (GPP) (Hamilton et al., 2002). Simultaneously, autotrophic and heterotrophic organisms release about the same amount of carbon back into the atmosphere thereby closing the terrestrial carbon cycle. As the estimated annual turnover between the atmosphere and terrestrial ecosystems is approximately 120 Gt, considerably greater than the amount of fossil fuel emissions (5 Gt), small alterations in the terrestrial carbon balance are likely to have a significant impact on atmospheric CO_2 concentrations. As a result, there is a need for a better understanding of the dynamics of carbon fluxes between biosphere and atmosphere to help quantifying potential changes due to increased atmospheric CO_2 rates (Comins and McMurtrie 1993; Luo and Reynolds 1999). Global monitoring and prediction of GPP over forested and agricultural environments is therefore an ultimate goal of Earth climate change research seeking universal, generic modelling approaches applicable across multiple biomes and a wide variety of vegetation types.

Modeling of carbon cycling requires parameterization of the land surface (Hall et al., 1995), which, in a spatially continuous mode and on a regularly basis, is only possible using remote sensing. Modeling GPP from remote sensing is largely based on the awareness that plant physiological properties are related to the biochemical composition of plant foliage, and that this composition is reflected in the spectral radiation properties of leaves. Since the launch of the first satellite based sensors in the 1970s the remote sensing community has been limited in the number and width of the spectral wavebands available, and observation frequencies of existing sensors were incapable of detecting the spatial and temporal variability of primary production of vegetation. Recently, the advent of high spectral resolution optical sensors, capable of detecting changes in leaf spectral properties with a high temporal frequency (Prince and Goward, 1995) has allowed the scientific community to revisit a number of existing approaches for modeling GPP, and reassess the potential for using remotely sensed inputs, with the ultimate aim of driving GPP models entirely from satellite based observations (Running et al., 2004; Rahman et al., 2005). This paper reviews the current status of determining GPP from remotely sensed inputs and addresses future requirements for developing remote sensing based models of the terrestrial carbon cycle, specifically on approaches based on the light use efficiency concept.

2. Light use efficiency based modeling of primary production

One of the most widely applied concepts for modeling GPP is the light use efficiency approach of Monteith (1972; 1977) (e.g. Prince, 1991; Goetz and Prince, 1999; Heinsch et al., 2002; Turner et al., 2003a,b), which expresses GPP as the product of the absorbed photosynthetically active radiation (PAR) (μmol m^{-2} s^{-1}), defined as absorbed solar radiation between 400-700 nm wavelength, and the efficiency, with which the absorbed PAR can be converted into biomass:

$$GPP = PAR \times f_{PAR} \times \varepsilon \qquad (1)$$

where f_{PAR} represents the fraction of PAR absorbed by the canopy and ε (g MJ^{-1}) is the photosynthetic efficiency term. The light use efficiency concept is based on the functional convergence theory (Field, 1991) hypothesizing that plants are scaling canopy leaf area and light harvesting by the availability of resources as a result of evolutionary processes in order to optimize their carbon fixation (Goetz et al., 1999). Detailed development and discussion of the underlying concepts behind the light use efficiency model are described in extensive studies and reviews by Field (1991), Reich et al. (1997) and Goetz and Prince (1999).

The amount of photosynthetically active radiation absorbed by a plant canopy ρ_a is defined as the difference between the PAR incident upon the canopy (Q), the amount of PAR being reflected from the canopy (ρ_r), and PAR being transmitted through the canopy (τ_t) (Beer-Lambert law):

$$\rho_a = Q - \rho_r - \tau_t \qquad (2)$$

For a given time, ρ_r and τ_t are a function of the leaf surface area (Sellers, 1985) parameterized by the leaf area index (LAI) defined as half the total foliage area per unit ground surface area (Chen and Black, 1992). Because of temporal variations in solar irradiance, chlorophyll content (Dawson et al., 2003) and leaf-sun geometry (Chen and Black, 1992) the amount of solar radiation being absorbed by a plant canopy varies diurnally as well as seasonally (Chen, 1996).

$\underline{\varepsilon}$ is determined by the most limiting of a large number of environmental stresses restraining the photochemical reaction process, such as nutrition supply, water and temperature, depends on individual vegetation types, and, as a result, varies greatly within space and time (Field and Mooney 1986; Prince and Goward 1996; Turner et al. 2003b). The biochemical process driving $\underline{\varepsilon}$ is known as photoprotection (Figure 1). In situations where plants receive more sunlight than they can actually use, light harvesting is being regulated to balance absorption and utilization of quanta as excessive light energy can cause photo-oxidative damage to the leaf (Demmig-Adams, 1990). The mechanism regulating the use of absorbed light is uniformly controlled by a group of leaf pigments named xanthophylls which occur over a broad range of species (Bilger et al., 1989; Bilger and Björkman 1990; Demmig-Adams and Adams, 2000; Demmig-Adams et al., 1998). Under excessive light conditions, the xanthophyll cycle pigment violaxanthin is de-epoxidized rapidly via intermediate antheraxanthin to zeaxanthin and this reaction is reversed when light is limiting. Antheraxanthin, as well as zeaxanthin, have photo-protective structures accepting excessive light energy from the antenna pigments of Photosystem II and safely dissipating it as heat (Demmig-Adams and Adams, 1996). Recently, a second xanthophyll cycle, the lutein cycle, has been discovered (Bungard, 1999), which is believed, within some species, to work in parallel. Photo-protection is also closely related to active emittance of light quanta in leaves, known as chlorophyll fluorescence (Demmig-Adams and Adams, 1996).

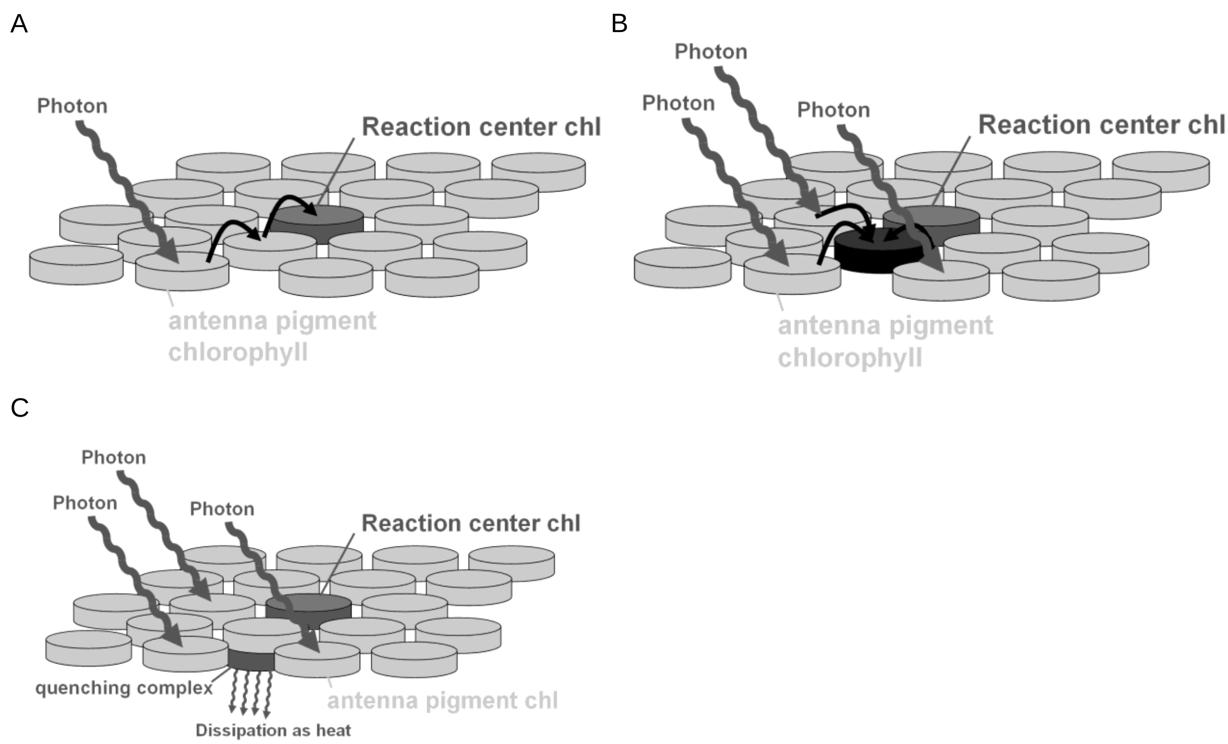

Figure 1: Schematic drawing of the photoprotective mechanism inside the light harvesting complex (LHC) of a leaf. A: Light is harvested by antenna pigments and the energy is transferred to the reaction center. B: In case plants receive more light energy than they can actually use, this excessive energy accumulates inside the LHC (illustrated by the black disk). Excessive radiation energy can potentially cause photo-oxidative damage to the photosynthetic apparatus of the leaf. C: The excessive radiation energy is safely dissipated as heat by means of a quenching complex. At the same time chlorophyll fluorescence is increased thereby re-emitting photons into space.

3. Current status of determining GPP from remote sensing

3.1 Photosynthetically active radiation

While the extraterrestrial radiation budget and its wavelength distribution are well known and relatively constant, the terrestrial reception of PAR is altered by a dynamically changing atmosphere (Van Laake and Sanchez-Azofeifa, 2004). Atmospheric radiative transfer is driven by absorption, molecular (Raleigh) and particle (Mie) scattering effects attenuating the amount of solar radiation received by the earth surface (Szeicz, 1974;

Rao, 1984; Baker and Frouin, 1987). Early estimates of broad scaled PAR were obtained from networks of surface pyranometers (Bland and Clayton, 1994; Bland, 1996), allowing long-term time series from well maintained and calibrated instruments. This method, however, is insufficient for global modeling since estimates of PAR are restricted to a few discrete observations (Frouin and Pinker, 1995). Since the launch of the first multispectral satellite sensors, numerous approaches have been developed to infer large scaled PAR from top of the atmosphere solar radiance using optical modeling (Sellers et al., 1995) to allow spatially exhaustive estimates of broadband and shortwave irradiance (Eck and Dye, 1991; Frouin and Gautier, 1992; Pinker and Laszlo, 1992). PAR is thereby often defined as a fraction of the reflected shortwave radiation (e.g., Tarpley, 1979; Gautier et al., 1980; Pinker and Ewing, 1985; Running et al., 1999), which is sufficient for most biological applications (Blackburn and Proctor, 1983; Weiss and Norman, 1985).

Recently, research focuses on incorporating the temporal and spatial variability of solar irradiance with respect to changing atmospheric conditions into global estimates of PAR to obtain highly accurate inputs for climate change modeling. Atmospheric conditions are currently assessed on a global scale by the Moderate Resolution Imaging Spectroradiometer (MODIS), on board of NASA’s EOS (earth observation system) satellites Terra and Aqua. The MODIS Atmospheric Profile products (MOD04–MOD07) consist of total-ozone burden, atmospheric stability, temperature and moisture profiles, and atmospheric water vapour, measured on a daily basis. Even though the atmospheric interactions of solar irradiance are well understood, a standardized product providing regular observations of global PAR is currently not available (Liang et al., 2006), however, techniques to derive accurate estimates of global PAR using MODIS have been developed (Van Laake and Sanchez-Azofeifa, 2004; Liang et al. 2006).

3.2 Absorbed photosynthetically active radiation

Approaches to infer the fraction of PAR which is absorbed by the vegetation canopy using remote sensing techniques can be divided into empirical techniques, primarily relying on curve fitting of reflectance measurements and physical approaches, which attempt to model the relationship between leaf, canopy and stand-level biophysical characteristics and reflected and emitted radiation (Myneni and Williams, 1994; Hall et al., 1995) (Figure 2).

3.2.1 Empirical determination of absorbed PAR

Empirical approaches are largely based on spectral vegetation indices (SVI) which are linear and non-linear combinations of discrete spectral bands, seeking to maximize the sensitivity of the index to the canopy characteristic requested while minimizing the sensitivity to the unknown and unwanted canopy characteristics (Hall et al., 1995). Starting in the early 1980s, numerous studies have shown substantial evidence of a close relationship between f_{PAR} and the top of the canopy reflectance measurements in the visible and near infrared region (Tucker 1979; Daughtry et al. 1983; Asrar et al. 1984), and theoretical work (Sellers, 1985; 1987) has given this relationship a solid basis as a measure of the solar photosynthetically active radiation absorbed by the canopy. Various linear and non-linear relationships between satellite-derived SVIs and

f_{PAR} have been found for different vegetation types and climatic conditions (e.g., Asrar et al., 1984; Badhwar et al., 1986; Fassnacht and Gower, 1997) with the most popular SVI being the Normalized Difference Vegetation Index (NDVI), defined as

$$NDVI = \frac{\rho_{NIR} - \rho_{Red}}{\rho_{NIR} + \rho_{Red}} \qquad (3)$$

where ρ_{NIR} and ρ_{Red} is the reflectance in the near infrared and red, respectively (Tucker 1979). SVIs have also been used to follow seasonal dynamics of vegetation using temporal profile analysis (Badhwar and Henderson, 1981; Henderson and Badhwar, 1984), and, when seasonally integrated, have been shown to be correlated with above-ground net primary production (NPP, defined as the difference between GPP and plant respiration) on an annual basis (Goward and Dye, 1987; Waring et al., 2006).

While the body of evidence proving these relationships is impressive (Myneni and Williams, 1994), a direct conversion of satellite spectral reflectance to surface f_{PAR} over larger areas is difficult, since empirical relationships are site and sampling condition dependant, sensor-specific, change in space and time and generally are unsuitable for application to large areas or in different phenological seasons (Goward and Huemmrich, 1992; Huemmrich and Goward, 1997; Gobron et al., 1997). Major factors influencing empirical estimates of f_{PAR} using SVIs are vegetation spectral properties, pixel heterogeneity, background reflectance, solar zenith and view zenith angle, vegetation shadow fractions, atmospheric scattering and bidirectional reflectance effects (Li and Strahler, 1985; Myneni and Williams, 1994). Some of these factors can be mitigated using more advanced indexing techniques such as the enhanced vegetation index (EVI)

(Huete et al., 2002; 2006), which seek to enhance the vegetation signal with improved sensitivity in high biomass regions thereby de-coupling canopy background signals and reducing atmospheric influences, however, broad scaled direct application of vegetation indices remains challenging (e.g. Running and Nemani, 1988).

An empirical solution to the directional reflectance problem, resulting in the first globally available LAI and f_{PAR} product as a monthly 1x1° dataset, was the FASIR (Fourier Adjusted, Solar zenith angle corrected, Interpolated and Reconstructed) approach of Sellers et al. (1994) and Los et al. (1994), based on data from the spaceborne Advanced Very High Resolution Radiometer (AVHRR) sensor (Tucker et al., 1986). FASIR accounts for the effects caused by varying illumination conditions using heuristic corrective methods to obtain spatially continuous multiyear datasets of surface variables, primarily for use in global climate models (Hall et al. 1995). Further (semi-physical) algorithms for the modeling of global LAI have also been reported by Price (1993).

3.2.2 Physical models for determination of absorbed PAR

Since the mid-1980's there has been an increase in the development of physical approaches to determining f_{PAR}, due partly to global diagnostic studies using satellite data (Tucker and Sellers, 1986), plot scale field studies (Asrar et al., 1984; Tucker et al., 1981), large field experiments (Sellers et all., 1992; Hall et al, 1992; Sellers et al., 1997; Running et al., 1999) and theoretical work (Myneni et al, 1992; Hall et al, 1990; Sellers 1985; 1987; Sellers et al,. 1992; Sellers et al., 1996a,b). This research formed the basis for physical models of canopy reflectance, transferring reflectance and biophysical property relationships from the leaf level, where they can be easily measured and related to leaf composition and structure, to the pixel level, where leaf optics interact with canopy structure, understorey characteristics, background reflectance, view and illumination geometry to produce a complicated relationship among pixel-level reflectance, stand structural, biophysical and leaf optical properties (Hall et al., 1995). The understanding gained from these models is then used to develop algorithms to relate biophysical characteristics to reflectance measurements on the landscape and global levels (Hall et al., 1995). Modeling efforts that have addressed this problem are numerous, and can be placed into four general classes (Goel, 1988): 1) turbid medium models, describing the interaction of photons in the atmosphere-vegetation-soil medium (e.g. Myneni et al., 1997), 2) geometric optical models (e.g. Li and Strahler, 1985), 3) hybrid combinations of 1) and 2) (e.g. Li et al, 1995), and 4) complex computer simulation models (e.g. Goel et al., 1991). The model parameters either depend on physical properties directly (i.e. canopy structure and vegetation type) or can be obtained from mathematical inversion of reflectance measurements (e.g. Wanner et al., 1995), allowing the estimation of both leaf and canopy parameters in a predictive mode, thereby overcoming the need of parameterisation required for the use of regressive semi-empirical models (Privette et al., 1996, Bicheron and Leroy 1999). Over the last decade, models allowing for parameter acquisition from mathematical inversion have arisen as the most promising technique for retrieving f_{PAR} (Meroni et al., 2004) and several studies have been successfully conducted for crop and forestred environments (e.g. Gao, 1994; Goel and Grier, 1988; Myneni et al., 1997). The accuracy of such estimations is dependent on the model employed, the type and quality of remote sensing data and the inversion procedure used (Jacquemoud et al., 2000).

One of the most prominent examples of a radiative transfer based global f_{PAR} model is the LAI/f_{PAR} product used in MODIS, providing 8-day averaged global LAI and f_{PAR} data at a 1x1 km spatial resolution. The algorithm uses photon transport theory to estimate both the radiation regime within the vegetation canopy and the radiant exitance, based on the architecture of individual plants and the entire canopy, optical properties of vegetation elements and soil atmospheric conditions (Knyazikhin, 1999; Myneni et al. 1989). The MODIS algorithm requires a land cover classification (also derived from MODIS data) to model the radiative transfer over larger areas. Canopy transmittance, reflectance, and absorptance are elements of a look-up table (LUT), distinguishing between biome types, each of which represents a pattern of the architecture of an individual tree (leaf normal orientation, stem-trunk-branch area fractions, leaf and crown size) and the entire canopy (trunk distribution, topography), as well as patterns of spectral reflectance and transmittance of other vegetation elements. Soil type and understorey are also biome specific, and can vary continuously within given biome-dependent ranges. Information on the leaf canopy spectral properties from MODIS and structural attributes from the LUT are then used to retrieve LAI and f_{PAR} (Knyazikhin et al. 2003). A full description of the MODIS f_{PAR} LAI product can be obtained from Knyazikhin et al. (1998; 2003), reviewed by Myneni et al., (2002).

3.3 Photosynthetic light use efficiency

Whilst determination of f_{PAR} has matured over a number of years, the estimation of ε using remote sensing techniques increased only in the past decade, encouraged by the advent of fine resolution spectral measurement devices allowing tracking of subtle changes in canopy reflectance using narrow wavebands in the visible and near infrared region. In general, approaches inferring ε from remote sensing can be classified into either indirect techniques, seeking to determine ε from environmental stresses, or direct approaches, trying to predict $\underline{\varepsilon}$ by measuring changes in leaf spectral reflectance resulting from photoprotection and chlorophyll fluorescence (Figure 2).

3.3.1 Determination of photosynthetic efficiency from environmental stresses

Stress factors driving photosynthetic efficiency are numerous and their detection over larger areas is relatively difficult due to the high temporal and spatial variability inherent to site and meteorological conditions. Remote sensing of stresses has mostly focussed on water, nitrogen and temperature related conditions. While more severe stresses, manifesting in symptoms such as chlorosis, defoliation or degradation of canopies, can be sensed using time series of broad band SVIs based on reflectance in the visible and near infrared region (Liu and Kogan, 1996), these stresses are exceptional and such techniques cannot be applied to sense more moderate stress situations where the plants' response is much less apparent (Baret et al., 2007).

Remote sensing of soil moisture related stress factors includes passive microwave systems (e.g. Prevot et al, 2003; Wigneron et al., 2003) and combinations of simultaneous measurements in the visible, near infrared, and thermal infrared radiation.

While microwave systems have shown good correspondence to soil moisture content, existing instruments lack adequate spatial and temporal resolution for sufficiently detailed estimates of water related vegetation stresses (Deshayes et al., 2006). Spectral measurements, combining SVI based estimates of the vegetation status with thermal radiation (so called temperature vegetation index – TVX (Prihodko and Goward, 1997)) predict soil moisture content from the difference between soil temperature and vegetation canopy temperature. This technique has been successfully used to determining plant water deficit (Lopez et al., 1991), water balance (Duchemin et al., 1999), and latent heat fluxes (Vidal et al., 1994) on local scales, however, application over larger areas remains complex (Prince and Goward, 1996), as 1) the difference between soil temperature and vegetation canopy temperature is not only a function of soil moisture but is also dependent on the incident solar radiation load and 2) the moisture content of sub-surface layers cannot be determined using this technique (Prince and Goward, 1995).

Like soil water related stresses, the understanding of nitrogen cycling and nitrification in forest ecosystems has greatly improved over recent decades, however the ability to characterize spatial patterns using remote sensing is limited (Ollinger et al., 2002) as derivation of stress maps is complex (Guerif and Duke, 2000). Early studies on the use of remote sensing for nitrogen stress quantification were based on empirical relationships using SVIs sensitive to the leaf chlorophyll content (Peñuelas et al., 1994; Bausch and Duke, 1996). More recent approaches suggest the use of hyperspectral imagery for direct prediction of foliage nitrogen content from narrow waveband reflectance (Wessman et al. 1988, Martin and Aber 1997). Ollinger et al. (2002)

presented a method to derive foliage nitrogen using data from NASA's Airborne Visible and Infra-Red Imaging Spectrometer (AVIRIS). A first study successfully applying spaceborne instrumentation was reported by Smith et al. (2003) using EO1-Hyperion satellite data. While the results from these hyperspectral approaches are encouraging, application over larger areas presents challenges to data analysis (Liu et al., 2006), as narrow waveband reflectance measurements are highly sensitive to atmospheric scattering and directional reflectance effects.

Arguably, the first stress based model for prediction of global ε was the Global Production Efficiency Model (GLO-PEM) of Prince and Goward (1995) based on the AVHRR Land Pathfinder dataset providing 10 day averages of daily global observations. GLO-PEM uses a TVX based approach to estimate water related stresses for a normalized solar zenith angle (Goward and Prince 1995; Nemani and Running, 1989). Estimates of atmospheric saturation deficit (D) are modeled from combinations of air temperature and atmospheric water vapour, derived from thermal infrared observations in two different wavebands. A similar approach of a global model predicting primary production was presented by Field et al., 1995 which uses estimates of ε based on the CASA model (Carnegie Ames Stanford Approach) introduced by Potter et al., 1993; calibrated using AVHRR data.

More recently, global estimation of ε from environmental stresses is undertaken using the MODIS GPP product (MOD17), which estimates GPP from 8-day averages of f_{PAR}, PAR and ε (Heinsch et al., 2002). The MOD17 algorithm models ε using a look-up table containing biome specific information about the maximum light use efficiency ε_{max}, daily minimum temperature (T_{Min}) and D for maximum and minimum ε of each biome type

(Running et al. 2000; Turner et al. 2003a). The biome specific constant ε_{max} is adjusted using 1°x1.25° estimates of T_{Min} and D, derived from GCMs (e.g. Potter et al., 1993; Sellers et al., 1996a, 1996b) to account for the limiting effects of climatic variables on ε (Heinsch et al., 2002; Turner et al., 2003a),

$$\varepsilon = \varepsilon_{\max} \times T_{Min} \times D \qquad (4)$$

For a full description of the MODIS GPP algorithm see Heinsch et al. (2002).

3.3.2 Direct estimation of photosynthetic efficiency

Thus far estimation of ε has been via environmental stresses. In the past decade research has focussed on the direct estimation of ε, as this technique not only offers the potential to determining the combined effect of vegetation stresses, but also includes information about the degree to which these stresses are limiting photosynthesis (Adams and Demmig-Adams, 1996).

Remote estimation of chlorophyll fluorescence includes both passive (Carter et al., 1990) and laser-induced active methods (Rosema et al., 1998; Corp et al., 2006). Active fluorescence measurements use laser pulses to manipulate the level of photosynthetic activity and to measure the corresponding changes in the chlorophyll fluorescence yield (e.g. Kolber et al., 2005). These pulse-modulated measuring systems, probe the yield of chlorophyll fluorescence under steady-state illumination (F_s) and during a short saturating flash delivered at close range (1–100 mm), and have been successfully used for measuring photosynthesis (Adams et al., 1999; Rascher et al., 2000). However, their application is mostly restricted to individual leaves in accessible canopies (Ananyev et al., 2005), with a few notable exceptions (e.g. Cecchi et al., 1994).

Evidence of a solar induced fluorescence signal superimposed on leaf reflectance signatures has been reported by various studies (Buschmann and Lichtenthaler, 1977; 1999; Peñuelas et al., 1995; Gitelson et al. 1999) and the effects of solar induced chlorophyll flurorescence emissions on the apparent spectral reflectance have been investigated using radiative transfer modeling (Zarco-Tejada et al., 2000). Chlorophyll fluorescence from passive remote sensing systems provides a potential for broad scaled assessment of $\underline{\varepsilon}$ (Corp et al., 2006), however, its application is technically challenging as under natural sunlight illumination chlorophyll fluorescence emitted by the vegetation represents less than 3% of the reflected light in the near infrared part of the electromagnetic spectrum (Moya et al., 2004). Consequently, passive sensing of chlorophyll fluorescence is possible only using sub-nanometer reflectance bands in the red and near infrared regions (often 690 and 760 nm) where solar radiation is not abundant as a result atmospheric absorption (so called Fraunhofer lines) (Meroni and Colombo, 2006). The intended launch of a spaceborne fluorescence sensor by the European Space Agency (ESA) as part the FLEX (fluorescence experiment) mission may provide new opportunities to exploit this method for estimation of global ε from space.

Determing ε using the photoprotective mechanism in leaves is based on observation of changes in leaf spectral reflectance resulting from the epoxidation state of the xanthophyll cycle. These changes manifest in two narrow waveband absorption features at 505 and at 531 nm and can be quantified using SVIs, such as the Photochemical Reflectance Index (PRI), defined as (Gamon et al., 1990),

$$PRI = \frac{\rho_{531} - \rho_{570}}{\rho_{531} + \rho_{570}} \qquad (5)$$

comparing the reflectance at 531 nm (ρ_{531}) to a xanthophyll-insensitive reference band at 570nm (ρ_{570}). Originally established for sunflower leaves, the empirical relationship between PRI and ε has been confirmed over a wide range of species (Peñuelas et al., 1994; 1995; Filella et al., 1996; Gamon and Surfus, 1999) thereby demonstrating the potential use of this method for global estimation of ε. Upscaling of these findings from leaf to canopy, regional and global levels, however remains challenging. First, the temporal dynamics existing in plant photosynthesis, require the observation of vegetation status under multiple illumination and viewing conditions and these observations are then, even more than in the case of f_{PAR}, subject to bidirectional reflectance and scattering effects (Los et al., 2005) overlapping with the desired reflectance signal (Huemmrich et al., 2005). Second, airborne or spaceborne sensors can only provide snapshots in time determined by a given aircraft or satellite overpass (Sims et al., 2005), however, the temporal and spatial requirements for these observations to be representative of the physiological status of plant canopies are not well understood (Hall et al., 1995). Third, the relationship between PRI and ε is species dependent and also changes with age, canopy structure, disturbances and LAI (Rahman et al., 2001), making a spatial extrapolation of empirical findings difficult.

Recent efforts to further the understanding of the temporal and spatial dynamics involved, include near surface observations using transect measurements (Sims et al., 2006), permanently established tower based observations of forest canopies (Leuning et al., 2006; Hilker et al., 2007), and airborne measurements (Nichol et al., 2000; 2002; Chen and Vierling, 2006; Rahman et al., 2001). A first spaceborne assessment of ε was introduced by Drolet et al. (2005), successfully using backscatter reflectance data from MODIS Aqua over the Canadian boreal forest with a spatial resolution of 1 km^2.

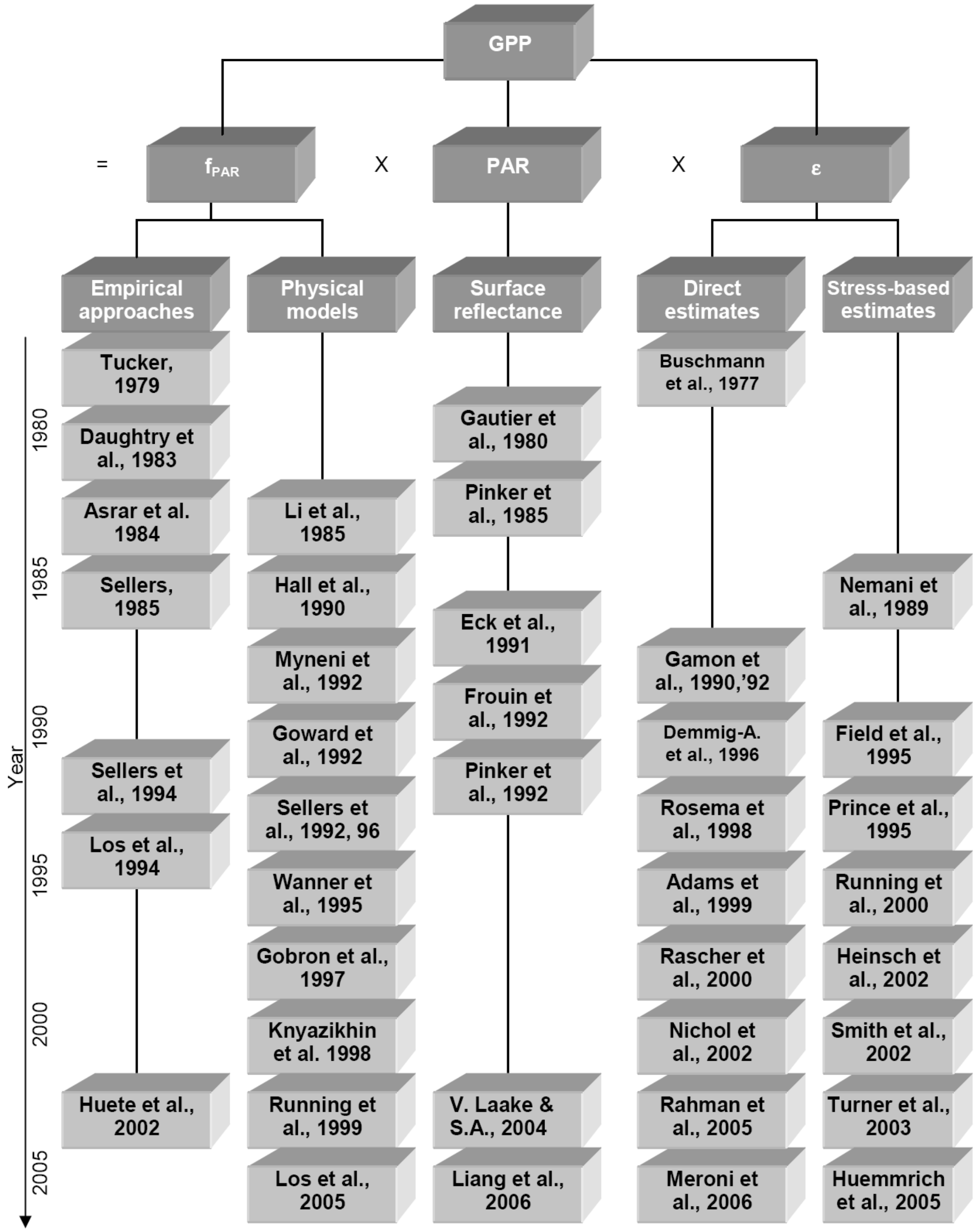

Figure 2: Illustration of approaches to assess GPP from remote sensing. PAR is generally derived from Top of Atmosphere (ToA) reflectance, techniques inferring f_{PAR} from remote sensing can be divided into empirical empirical approaches and physical models. ε can either be determined directly or indirectly through stress factors. Some examples of key literature to each approach are given.

4. Validation approaches

Validation and operationalization of the light use efficiency approach is currently underway at a number of spatial and temporal scales. At the stand level, eddy covariance data (EC) exhibit a key role for studying the temporal and spatial variability of GPP (Turner et al., 2006). EC measurements facilitate continuous estimates of net carbon accumulation, also referred to as net ecosystem production (NEP), from flux towers measuring CO_2 mixing ratios of up and down-moving eddies (Baldocchi, 2003), thereby using the covariance between the vertical velocity (w) and the mole-mixing ratio of CO_2 (sc) to estimate carbon fluxes (F_c),

$$F_C = \overline{\rho_a}\,\overline{w's_c'} \qquad (6)$$

where $\overline{\rho_a}$ is the mean molar density of dry air and $\overline{w's_c'}$ is the covariance between the vertical velocity (w) and the mole-mixing ratio of CO_2 (s_c). The spatial scale of an EC flux tower is about 1 km^2 (Kljun et al. 2004) and the temporal resolution is given by the integration of high frequency data, usually at a half hourly basis (Morgenstern et al., 2004). GPP can be determined from EC data by adding estimates of ecosystem respiration (R) to measured NEP values, and ε can be obtained from additional measurements of f_{PAR} and PAR using radiation sensors above and below the canopy (Humphreys et al., 2006). Remotely sensed estimates of stand level GPP have been correlated with EC flux data from ground based (Cheng et al., 2006; Sims et al., 2006), tower based (Filella et al., 1996; Stylinski et al., 2002), airborne (Nichol et al., 2000; 2002) and spaceborne platforms (Running et al., 1999; Drolet et al., 2005; Coops et al., 2007). Also, to bridge the spatial gap existing between near surface and airborne remote sensing platforms, Chen and Vierling (2006) tested a tethered balloon mounted platform to evaluate canopy reflectance of a grassland conifer forest ecotone. Networking approaches, such as the recently established SpecNet initiative (Gamon et al., 2006) attempt to link these observations with existing global fluxtower sites to further the understanding of relationships existing between biophysical processes and spectral reflectance data, thereby trying to overcome the fundamental scale mismatch between estimates obtained from eddy flux and remote sensing (Running et al., 1999; Rahman et al. 2001; Cheng et al. 2006; Gamon et al., 2006). Other objectives of this network are the exploration of temporal matters, derivation of flux components and the validation of satellite data products (Gamon et al., 2006).

At the landscape level, verification of GPP estimates has been undertaken in various broad scaled field studies comparing ground based estimates to remotely sensed data. One of the first projects designed to coordinate data collected by satellites, aircraft, and ground instruments in order to improve the understanding of carbon and water cycles, was FIFE (First ISLSCP (International Satellite Land Surface Climatology Project) Field Experiment), undertaken in the prairies of central Kansas from 1987 through 1989 (e.g. Hall et al., 1991; 1992; Sellers and Hall., 1992; Walthall, et al., 1993). The objectives of FIFE were to improve the understanding of interactions between the atmosphere and the vegetated land surface and to investigate the use of satellite observations to infer climatologically significant land surface parameters (Sellers and Hall., 1992). While remotely sensed estimates of f_{PAR} were found to be accurate within a range of 10%, key issues identified for remote sensing of photosynthesis were stress related factors such as soil moisture and saturation deficit (Hall et al., 1992; Charpentier and Groffman, 1992).

One of the largest projects aiming to improve our understanding of terrestrial carbon cycling and other biosphere-atmosphere interactions was the Boreal-Ecosystem-Atmosphere Study (BOREAS), undertaken between 1993 and 1997. Specifically designed to bridge a wide range of spatial scales (e.g. Kharouk et al., 1995; Sellers et al., 1995; 1997; Potter et al., 1999; Goetz et al., 1999), BOREAS integrated repeated leaf scale, flux-tower, airborne, and spaceborne observations to investigate issues of up-scaling local observations to landscape levels (1000x1000km) (Sellers et al., 1997). The study, located at multiple boreal forest sites in Saskatchewan and Manitoba (Canada), substantially improved the use of remote sensing for definition of vegetation structure and land cover for assessment of the surface–atmosphere exchange of mass and energy, nature and variability of surface albedo and radiation budgets, and the regional carbon balance (Gamon et al., 2004).

Most recently, validation of the MODIS GPP product was undertaken using the BigFoot approach, scaling field observations to global, satellite based estimates of GPP. BigFoot relied on ground measurements, EC-flux tower data, remote sensing data, and ecosystem process models to represent CO_2 fluxes for different biome types. Nine BigFoot study sites spanned eight major biomes, from desert to tundra, to tropical forest (Running et al., 1999). Validation of the MODIS GPP product was mainly undertaken in form of time series comparisons between GPP estimated from eddy covariance flux tower data and GPP from MODIS for one or more 1-km^2 cells surrounding the tower (Turner et al., 2003a,b; Xiao et al., 2004). While some of these comparisons have shown reasonable agreement between tower based estimates of CO_2 fluxes and MODIS land cover products, also numerous limitations were found and issues identified for further research: The largest error associated with the land cover classification is the simplifying assumption that each 1x1 km pixel only contains a single land cover class (Heinsch et al., 2006). This assumption generally fails to reflect the spatial heterogeneity in land cover, stand age, soil type and canopy structure for most biomes (Goulden et al., 1996). The use of a simple lookup table approach to determining ε from biome-specific parameters which do not vary in space and time (Running et al., 2000; Heinsch et al., 2002; Turner et al., 2003a), and distinguish only between 11 different vegetation types (Turner et al., 2003a; Heinsch et al., 2006) has been identified as the weak point of the GPP product as it greatly simplifies the existing spatial and temporal variability in $\underline{\varepsilon}$. In addition, assigning values of $\underline{\varepsilon}$ on the basis of biome type assumes between-biome variability to be greater than within biome variability, which is often not realistic (Goetz and Prince, 1996; Landsberg et al., 1997). A further serious limitation is the degree to which the GCM derived inputs represent realistic estimates of climate variables because of the coarse scale of the GCM model outputs (~100 km) (Turner et al., 2003a,b). These issues, together with errors related to propagation from other underlying MODIS products (Heinsch et al., 2006), have been identified as potential sources of the differences found between satellite-based GPP estimates and field measurements for some biomes (Running et al., 1999; Coops et al., 2007).

5. Requirements and direction for future studies

The ability to acquire primary production from remotely sensed data has increased considerably over the last few decades. However, from the reviewed literature, it is apparent that accurate modeling of GPP over large areas remains an active area of research with issues remaining to be solved on the leaf, stand, and landscape level.

5.1. Leaf level

Arguably, the use of remote sensing to detecting photosynthesis at the leaf level is relatively established, however many gaps remain our in understanding of the biochemical mechanisms that invoke and relax photo-protection and chlorophyll fluorescence. To date, an energy dependent component, likely induced by low pH values in the thylakoid membrane of the chloroplast (Demmig-Adams and Adams, 1996) and an energy independent component, relaxing only very slowly after more severe stress situations such as droughts or winter stress, have been identified (Adams et al., 1999). While the energy dependent component is reasonably well understood, less is known about the processes driving the energy independent component (Demmig and Winter, 1988). Additionally, the role of the Lutein cycle (Bungard et al., 1999) in photosynthetic efficiency is largely unexplored. Comprehensive understanding of these biochemical mechanisms driving the photochemical reaction process across a wide range of species is a key requirement for upscaling leaf level estimates to stand and global levels.

5.2. Stand level

At the stand level, uncertainty remains in understanding the temporal dynamics involved in photosynthetic efficiency and the contributions of shaded and sunlit parts of the canopy (Demmig-Adams et al., 1998). To improve the understanding of stand level GPP, modeling requires observation of vegetation canopies in a continuous mode and under varying illumination and environmental conditions. Accurate algorithms are required to distinguish the reflectance signals obtained from such observations between physiologically and physically induced components. The application of bi-directional reflectance distribution functions (BRDF)(e.g. Wanner et al., 1995; Li and Strahler, 1995) can help in this regard. Separation of reflectance signals however, is not trivial, as the high physiologically induced variability in canopy reflectance especially with respect to ε makes acquisition of BRDF-parameters from inversion of semi-empirical algorithms difficult (Los et al., 2005).

Possible ways to address these issues include spectral measurements from permanently established, near surface remote sensing devices, facilitating intensive and continuous studies of canopy level reflectance. At present, relatively few spectral datasets have been acquired using radiometers mounted on canopy cranes (Mariscal et al., 2004) or towers (Leuning et al., 2006; Hilker et al., 2007). Future research would benefit from integrated, tower based approaches to intensify measures of reflectance properties and temporal variability of GPP at networked sites, which can then be linked directly to CO_2 fluxes determined using the eddy covariance technique. Based on physical reflectance properties studied on the stand level using near surface remote sensing, mathematical models can be developed which, when calibrated from high resolution satellite platforms on a daily and fully spatially basis, may facilitate detailed estimates of photosynthetic flux from space. Hence, the success for estimating carbon fluxes at broader levels will heavily depend on our understanding of the dynamics and interrelations of spectral reflectance obtained at the stand scale.

5.3. Landscape level

At the landscape scale, research focused on the complex interactions between the biosphere and atmosphere targeting issues of upscaling from site observations to ecoregion, biome, and global levels is underway and must be actively pursued, with major challenges evident in the areas of modelling and minimising signal distortions, due to both the atmosphere and directional reflectance effects. Our understanding of bidirectional reflectance, radiative transfer modeling, and interactions between reflectance and forest stand structure has benefited greatly from multi-angle instruments, including the POLDER (Polarization and Directionality of Earth Reflectance) (Deschamps et al., 1994) and MISR (Multi-angle Imaging Spectrometer) (e.g. Lyapustin et al., 2007) sensors, specifically designed to address BRDF characteristics of the Earth surface from space (Leroy et al. 1997; Gamon et al., 2006). However, several challenges related to atmospheric effects remain, primarily caused by water vapor and aerosols, as these, even though they are well understood, are difficult to correct due to their high temporal and spatial variability (Hall et al., 1995).

Direct approaches regarding global prediction of ε from remote sensing, using both xanthophyll related pigment changes in the visible spectrum and fluorescence measurements in the near infrared region show promise to facilitate precise estimation of $\underline{\varepsilon}$ over large areas thereby overcoming a number of issues related to indirect approaches using stress related factors. Global estimation of vegetation stresses, however, provides valuable information that can help understanding the physiological responses of plant canopies observed. Satellite sensors providing high spectral and spatial resolution hold promise to facilitate acquisition of detailed stress maps of plant canopies which will allow mutual validation of $\underline{\varepsilon}$ acquired from direct and indirect approaches in a spatially comprehensive mode.

Currently there is an absence of spaceborne sensors available with wavebands narrow enough to obtain reflectance measurements specifically in the PRI region. EO1-Hyperion was the first hyperspectral sensor in space with a contiguous spectral bandwidth of 10 nm. However, being designed as a demonstration instrument, this sensor is limited in its signal to noise ratio and calibration accuracy (Datt et al., 2003; Khurshid et al., 2006). The MODIS sensor, such as on AQUA, provides wavebands close to the PRI region (Drolet et al., 2005), however, initial results indicate that the approach at this stage does not sufficiently account for the spatial heterogeneity of the landscape. Additionally, there is a lack of algorithms available for processing the full suite of MODIS Aqua spectral bands over land surfaces which limits the routine application of the approach. Future generation satellite sensors, data processing streams, and resultant data products can combine to help address and eventually overcome these issues.

The large area characterization of primary production depends on comprehensive testing and continued efforts of land surface validation, requiring coordinated scientific networking to meaningfully combine findings and results representative of a range of spatial scales. Networking approaches such as the Fluxnet community have greatly improved our knowledge on interactions of plant physiological responses to changing environmental conditions in the past. Intensified and networked research efforts are required for improved understanding of physically and physiologically induced reflectance properties of various vegetation types to facilitate modeling of GPP estimates representative of large areas. The ability to characterize GPP over a range of scales will greatly benefit from interdisciplinary communication and networking for both development of algorithms and product validation.

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