Chapter 29

From Leaves to Ecosystems: Using Chlorophyll Fluorescence to Assess Photosynthesis and Plant Function in Ecological Studies

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Summary

Photosynthesis is a critical parameter in ecological research. Not only does it drive productivity at the ecosystem scale, but at the level of species and the individual plant it is functionally related to growth and a suite of co-evolved traits that are critical to plant function, including hydraulic conductance, leaf lifespan, specific leaf area, and leaf nitrogen content. Chlorophyll (Chl) fluorescence provides a useful, direct, and integrated measure of photosynthetic function and plant stress making it a valuable tool for plant ecologists for use at the leaf level to the ecosystem level. At the leaf and whole plant level, the most useful parameters for ecological use in tracking photosynthetic performance and stress in plants are the potential quantum efficiency of photosynthesis, calculated from the ratio of two fluorescence parameters Fv (variable Chl fluorescence) /Fm (maximum Chl fluorescence) in a dark adapted leaf, and the quantum yield, $\Delta F/Fm'$, where ΔF is variable Chl fluorescence and Fm' is maximum Chl fluorescence in an illuminated leaf. The ratio of electron transport rates (ETR) to carbon assimilation rate, A (ETR/A) may also be an increasingly useful and easily measured parameter. Other parameters, including the ratio of UV excited blue fluorescence (BF) to Chl fluorescence, (BF/ChlF),

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are also becoming more widely used for the detection of plant stresses in response to various environmental factors. At the ecosystem level, reflectance indices of vegetation and carbon flux data from eddy correlation towers are currently used in large-scale productivity models. Chl fluorescence from vegetation can provide a direct measure of radiation use efficiency (RUE), making it promising for use in ecosystem level models, given continued development of technology for remote measurements. The role of individual species, which respond in contrasting ways to environmental disturbance, is critical to ecosystem dynamics. Remote measurement of fluorescence parameters may eventually be able to distinguish different species or functional groups within an ecosystem allowing species composition to be taken into account in large-scale models. This would allow a mechanistic understanding of ecosystem processes and provide a greater ability to predict changes in ecosystem function from perturbations that differentially affect species.

I. The Role of Photosynthesis in Ecological Research

Photosynthesis is one of the most important and widely measured physiological parameters in plant ecological research (Field et al., 1989; Schulze and Caldwell, 1996; Mooney and Ehleringer, 1997). This chapter highlights the importance of measuring photosynthetic parameters in ecological research and the use of chlorophyll (Chl) fluorescence to measure plant stress and productivity at different scales. Techniques for measuring plant fluorescence will become increasingly applicable and useful in tracking large-scale carbon fluxes and monitoring perturbations due to global changes at multiple scales. We first discuss the importance of photosynthesis from an ecological perspective and provide definitions of fluorescence parameters most useful for ecologists. We then seek to summarize the existing and future applications of Chl fluorescence for ecological studies. This includes a general overview of the application of Chl fluorescence techniques in detecting plant responses to various kinds of environmental stress. Finally, we explore the potential role of fluorescence techniques in large-scale ecosystem studies.

Numerous reviews have been written on the significance of photosynthesis in plant function and ecological performance (see for example, Pereira, 1995; Schulze and Caldwell, 1996). Here we focus on several aspects of photosynthesis that are relevant to understanding species' differences in relation to their environment and the relationship of photosynthesis to other functional traits of plants. Plant growth and ecosystem primary productivity are ultimately dependent on photosynthesis. A general relationship between photosynthesis and relative growth rate has been shown empirically and theoretically (Pereira, 1995), although the relationship is sometimes weak. Among individuals of ten species of oaks grown in a common garden, we have found a general relationship between photosynthetic rate and relative growth rate (Fig. 1; J. Cavender-Bares and F.A. Bazzaz, unpublished). Differences in how plants allocate resources can change the ratio of photosynthesis to relative growth rate. Hence the relative amount of photosynthetic tissue, in addition to photosynthetic rate, is critical in determining growth (Lambers and Poorter, 1992).

Beyond the link to growth and productivity, photosynthetic rate is also thought to be one of a constellation of co-evolved traits that vary together across species in relation to contrasting environmental conditions (Reich et al., 2003). Photosynthetic rate is coupled to stem hydraulic conductance and water transport capacity of plants (Fig. 2A; Brodribb and Field, 2000). Across species from different biomes around the globe, there are strong positive correlations between photosynthetic rates, leaf nitrogen content, and specific leaf area, and a strong negative correlation between photosynthetic rate and leaf lifespan

Abbreviations: A – assimilation rate; APAR – absorbed photosynthetically active radiation; BF – blue fluorescence; C_a, C_i – ambient and intracellular CO_2 concentration; Chl – chlorophyll; DTT – 1,4-dithiothreitol; ETR – electron transport rate; F_0, F_S – initial and steady state levels of Chl fluorescence; F_{APAR} – fraction of absorbed photosynthetically active radiation; FGVI – fluorescence global vegetation index; F_m, $F_{m'}$ – maximum levels of Chl fluorescence in a dark adapted leaf and in an irradiated leaf; FRF – far-red fluorescence; GEE – gross ecosystem exchange; GPP – gross primary productivity; NDVI – normalized difference vegetation index; NIR – near infrared; NPP – net primary productivity; NPQ – non-photochemical quenching of excited Chl; PAR – photosynthetically active radiation; PRI – photochemical reflectance index; PS – Photosystem; Q_A, Q_A^- – primary quinone acceptor of PS II in an oxidized and a reduced state; qE – energetic quenching of excited Chl; qI – irreversible quenching of excited Chl; qN – non-photochemical quenching of excited Chl; qP – photochemical quenching of excited Chl; qT – state II transition of excited Chl; RF – red fluorescence; Ψ_{leaf} – leaf water potential; ε – radiation use efficiency

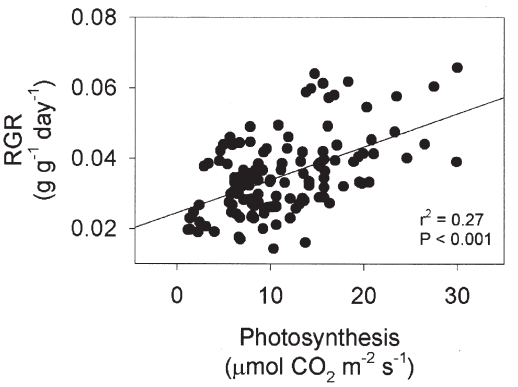

Fig. 1. Plot of relative growth rate (RGR; g g^{-1} day^{-1}) as a function of the rate of photosynthesis for ten species of oaks grown in a common garden. Each point represents an individual plant.

(Figs. 2B-D; Reich et al., 1997), indicating consistent trade-offs among these trait relationships. Such relationships highlight the utility of photosynthetic capacity in predicting other plant functional traits as well as whole plant strategies for resource use.

Chl fluorescence is directly related to the activity of Chl in the photosynthetic reaction centers, and can thus be used to measure photosynthetic efficiency (Genty et al., 1989). As a result, fluorescence provides a useful, direct, and integrated measure of photosynthetic function and plant stress. A list of the most useful fluorescence parameters in ecological studies is presented in the next section.

II. Definition and Explanation of Fluorescence Parameters

The following is a list of the most useful Chl fluorescence parameters and abbreviations for use in ecological studies with brief explanations of how they are calculated and how they may be interpreted. For a comprehensive list, see Mohammed et al (1995) (also see list of abbreviations in this chapter).

F_0 : minimal fluorescence level (dark); initial intensity of Chl fluorescence with all Photosystem II (PS II) reaction centers open while the photosynthetic membrane is in a non-energized state , i.e. in a dark adapted leaf (qP = 1; qN = 0).

F_S : fluorescence in steady state (light); intensity of Chl fluorescence at steady state in an irradiated leaf .

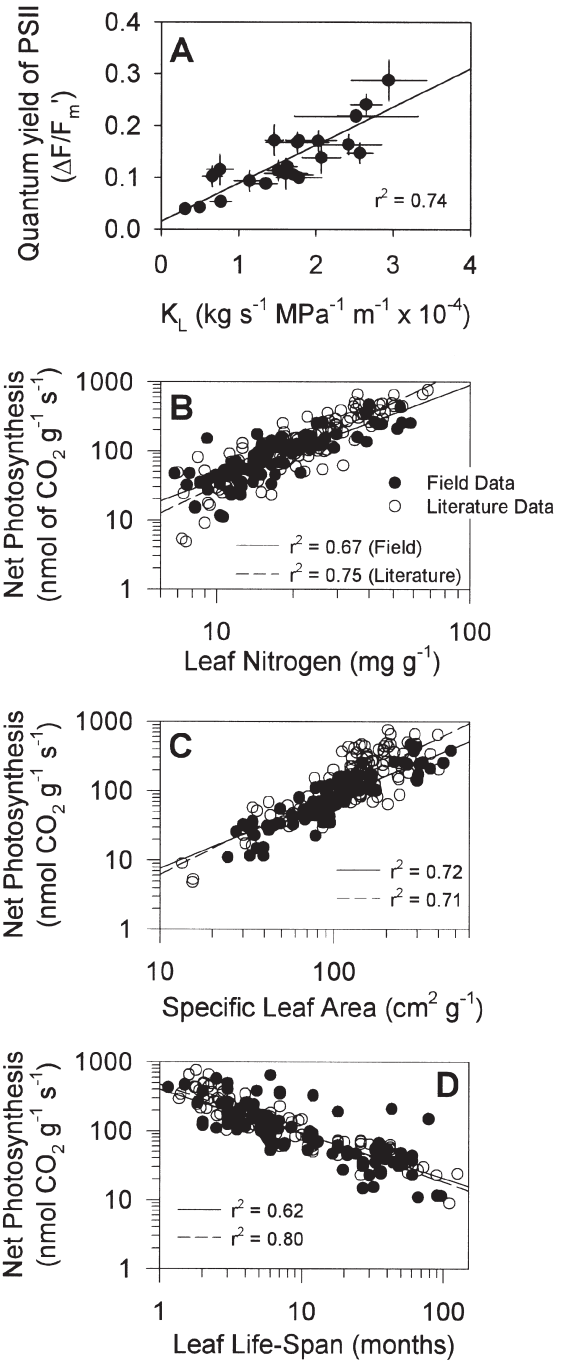

Fig. 2. (A) Quantum yield of photosynthesis in relation to leaf-area specific hydraulic conductivity (K_L) of stems from seven conifers and 16 angiosperms measured in full sun. Error bars are ± 1SE (n = 4). Data are redrawn from Brodribb and Field (2000). (B ,C and D) Net photosynthesis per unit dry leaf mass as a function of leaf nitrogen (B), specific leaf area (C), and leaf life-span (D) for species from six biomes; adapted from Reich et al. (1997). Regression lines are for field data (solid) and literature data (dashed).

F_m: maximal fluorescence level (dark); maximum intensity of Chl fluorescence in a dark adapted leaf with all PS II reaction centers closed; photochemical quenching is at a minimum (qP = 0) and all non-photochemical quenching processes are at a minimum (qN = 0).

F_m': maximal fluorescence level (light); maximum intensity of Chl fluorescence in an irradiated leaf with PS II reaction centers closed (qP = 0; qN > 0).

F_v: variable Chl fluorescence (dark); $F_m - F_0$; maximum variable Chl fluorescence when all non-photochemical processes are at a minimum.

F_v/F_m: related to the quantum efficiency of PS II (dark); quantum efficiency or potential quantum yield of PS II in a dark adapted leaf.

$\Delta F/F_m'$: yield of photosynthesis (light); ($\Delta F = F_m' - Fs$)/ F_m'; yield of photosynthesis in an irradiated leaf.

NPQ: non-photochemical quenching of excited Chl; NPQ is calculated as $(F_m - F_m')/F_m'$ (Stern-Volmer relationship) and is a good indicator of excess light energy because it reflects heat dissipation of excitation energy in the antenna system. (The calculation of NPQ may have an advantage over qN for ecologists because the data are normally distributed. Values of qN will always be between 0 and 1 and need to be transformed prior to statistical analysis.)

qN: non-photochemical quenching of excited Chl; calculated as $(F_m - F_m')/(F_m - F_0)$ representing non-radiative pathways of de-excitation of incoming light energy, mainly through heat and redistribution of excitation energy from PS II to PS I (Schreiber et al., 1986; Chapter 11, Schreiber).

qP: Photochemical quenching; calculated as $(F_m' - F_s)/(F_m' - F_0)$, is caused by energy transformation at PS II reaction centers (Schreiber et al., 1986; also see Chapters 11, Schreiber; and 18, Krause and Jahns).

F_v/F_m and $\Delta F/F_m'$ are potentially the two most useful parameters for ecologists doing measurements in the field. F_v/F_m gives the potential quantum yield or potential quantum efficiency of the leaf (Butler and Kitajima, 1975) and is thus an indicator of plant health (Chapter 12, Strasser et al.). A healthy terrestrial plant will almost always have a dark adapted F_v/F_m value close to 0.8. A decrease from this indicates a stress (either short-term or long-term) and the presence of a quenching mechanism. $\Delta F/F_m'$ is a measure of the effective quantum yield of photosynthesis under illumination (Genty et al., 1989). It may also be thought of as the photosynthetic rate per photon. When multiplied by the number of photons absorbed by PS II, it gives a measure of the electron transport rate. In the absence of stomatal limitation to photosynthesis, this value is almost always correlated with the CO_2 assimilation rate, although it includes all electron transport including electron flow to oxygen and detoxication of oxygen radicals as well as nitrogen assimilation. Similar to photosynthetic rate measured by carbon uptake (Fig. 1), F_v/F_m has been demonstrated to be a good predictor of growth rate particularly when adverse environmental conditions are limiting growth. Strong correlations between plant growth and F_v/F_m have been reported in a number of studies (see a review by Ball et al., 1995).

The relationship between rates of electron transport and photosynthesis (ETR/A), which is easily measured in the field, has the potential to be another important parameter in ecological studies as it can give an indication of the capacity of plants to protect PS II from oxidative damage (Lovelock and Ball, 2002). For example, photorespiration and the Mehler-peroxidase reactions utilize electron flow from PS II, and have been shown to protect against photooxidative damage (Wu et al., 1991; Lovelock and Winter, 1996). The relationship between ETR and photosynthesis is dependent on leaf temperature and light level as well as other factors that influence stomatal opening (Berry and Björkman, 1980; Osmond, 1981). When these variables are held constant, or factored out, species-level differences can be seen as a result of differences in the proportion of electron flow to competing sinks (Krall and Edwards, 1992). Figure 3 shows significant differences in the slopes of the relationship between electron transport rate and photosynthetic rate (CO_2 fixation) in three North American oak species grown under controlled environmental conditions (J. Cavender-Bares, unpublished). ETR values of these species exceed the theoretical minimum requirement for CO_2 fixation of four electrons per CO_2 and indicate a substantial flow of electrons to alternative electron acceptors.

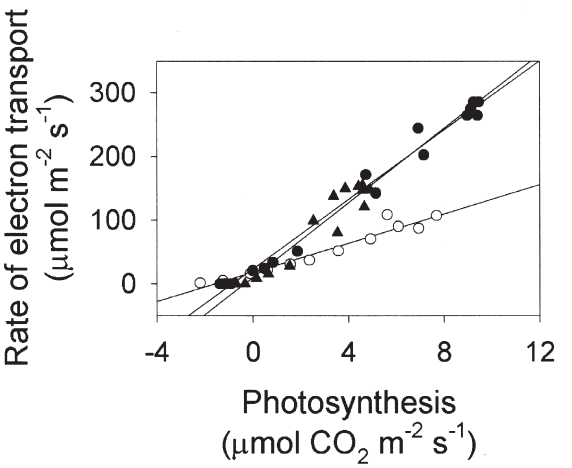

Fig. 3. The relationship between rates of electron transport and net CO_2 fixation for three species of oaks: *Quercus rubra* (open circles), *Quercus virginiana* (filled circles), and *Quercus michauxii* (filled triangles). (J. Cavender-Bares, unpublished.)

The fluorescence parameters discussed here are easily measured using commercially available fluorometers that excite PS II fluorescence. In interpreting the meaning of these parameters, however, it is important to understand something about the sources of variation in the Chl fluorescence signal. Variable Chl fluorescence is explained in numerous reviews, including Cerovic et al. (1999) and Van Kooten and Snel (1990). F_0, or minimum fluorescence in a dark-adapted leaf, is measured under very weak light. Under these conditions, the maximal amount of absorbed light energy is used for photochemistry at the highest efficiency and only a minimal fraction of the absorbed energy is re-emitted as chlorophyll fluorescence (F_0). Thus, the primary quinone acceptor (Q_A) of PS II is oxidized and the photochemical quenching (qP) is maximum (qP = 1). The intensity of Chl fluorescence can increase several fold when a dark-adapted leaf is suddenly illuminated. Upon illumination, fluorescence rises from a minimal level (F_0) up to a maximum level (F_m) and then decreases to reach a steady state level (F_s). This transient fluorescence induction (Kautsky effect; for a historical review, see Govindjee, 1995) reflects the photochemical activity of PS II. The level of variable Chl fluorescence is determined by both photochemical and non-photochemical quenching mechanisms (Cerovic et al., 1999). Under a dark to light transition using a saturating flash, all the Q_A molecules are temporarily reduced (Q_A^-) and the PS II photochemical reactions can no longer proceed. At this point, fluorescence is maximal (F_m) and qP is minimal (qP = 0).

A decline in F_v/F_m has often been interpreted as photoinhibition. This term is somewhat problematic because a decline in F_v/F_m may result from a number of different processes, some of which are readily reversible and not indicative of damage, and others which are slowly reversible and can be termed photodamage. Use of the word photoinhibition has led to confusion because in many studies, it has been used to describe decreases in F_v/F_m resulting from processes that include photoprotective non-photochemical quenching. Other authors reserve the term to indicate only slowly reversible non-photochemical quenching that can be interpreted as photodamage. A more reliable definition of photoinhibition would be a sustained depression in PS II efficiency. Difficulty arises in applying this definition in studies where it may not be possible to determine whether declines in F_v/F_m are resulting from readily reversible or slowly reversible processes or when this decline is a result of processes that include both photoprotection and photodamage in undecipherable proportions.

III. Detecting Stress in Plants at the Leaf and Whole Plant Level

Another important application of fluorescence in ecological research is its use as a tool in detecting and measuring stress in plants. Various fluorescence parameters have been used to detect different types of stress, including light stress, low and high temperature stress, nutrient stress, and water stress (see Chapters 3, Baker and Oxborough; 10, Kramer et al.; 12, Strasser et al.; 16, Moya and Cerovic; 18, Krause and Jahns; 20, Golan et al.; 22, Adams and Demmig-Adams; 23, Tevini; 24, Bukhov and Carpentier; 25, Joshi and Mohanty; 26, Papageorgiou and Stamatakis; and 31, Raven and Maberly). Photosynthetic rates may be reduced by stress conditions, which perturb or block photosynthetic electron transport and affect the photosynthetic apparatus. Increased dissipation of absorbed light energy by Chl fluorescence and heat emission can be diagnostic in detection of various stress factors. Detection of stress factors has been reviewed by Lichtenthaler and Rinderle (1988) and Méthy et al. (1994); also see Chapter 28, Lichtenthaler and Babani. In this section we present a brief overview of various fluorescence techniques that have been or could be useful in measuring plant stress under field conditions.

A. Light Stress

The problem of light stress in plants is discussed in several chapters in this volume. Light environments are highly dynamic in forests, with spatial and temporal variation in light quality and quantity forming a continuum from deep shade to full sunlight (Ball, 1995). Ball (1995) has reviewed the application of Chl fluorescence in identifying differences in the abilities of species to cope with light.

A decline in F_v/F_m has been used as an indication of light-stress in plants, and it may be the result of photodamage or of reversible non-photochemical quenching linked to photoprotective mechanisms, or a combination of the two (Demmig and Björkman, 1987; also see Chapter 22, Adams and Demmig-Adams). Within a canopy of a mature red oak tree, the top canopy leaves showed greater declines in F_v/F_m throughout the day, relative to subcanopy leaves, as a result of exposure to higher light intensities; Fv/F_m values readily recovered as light levels declined during a diurnal cycle (Fig. 4; J. Cavender-Bares, unpublished), indicating reversible non-photochemical quenching, probably the result of a photoprotective mechanism, in light-saturated canopy leaves.

Reversible declines in the quantum yield of photosynthesis after exposure to excess light energy has been attributed to a photoprotective mechanism involving the xanthophyll cycle (Demmig and Björkman, 1987; Demmig-Adams et al., 1995; Ruban and Horton, 1995; Barker et al., 1998; Logan et al., 1998; Demmig-Adams and Adams 2000; Chapter 22, Adams and Demmig-Adams). Intrinsic PS II efficiency (F_v/F_m) and the ratio of de-epoxidized xanthophyll pigments to the total pool of xanthophyll pigments (A+Z)/(V+A+Z), where A is antheraxanthin, Z is zeaxanthin, and V is violaxanthin) have been correlated both in the short term and long term. Data from Adams and Demmig-Adams (1994) shows that reversal of F_v/F_m matches the time course of the epoxidation of Z and antheraxanthin A to violaxanthin V in 8 plant species (Fig. 5). Increased capacity of xanthophyll cycle-dependent energy dissipation is thought to be a key component of the acclimation of leaves to a variety of different forms of light stress (Demmig-Adams et al., 1995)

In general, field studies have shown that species found in shady understory environments tend to have slower reversal of F_v/F_m after exposure to light stress than species that inhabit high solar radiation environments (Lovelock et al., 1994, 1998). Lovelock et al. (1998) found that species with leaves growing in high light environments (tree-fall gaps) had higher yields of PS II, higher non-photochemical quenching (NPQ) (Fig. 6) and more rapid recovery from photoinhibition than species with leaves growing in the shade. Similarly, Demmig-Adams et al. (1998) found leaves of *Schefflera arboricola* plants grown under low light to show pronounced photoinhibition of PS II after 24h exposure to high irradiance, requiring several days at low light levels to recover. Sun leaves, however, showed virtually no sustained effects on PS II.

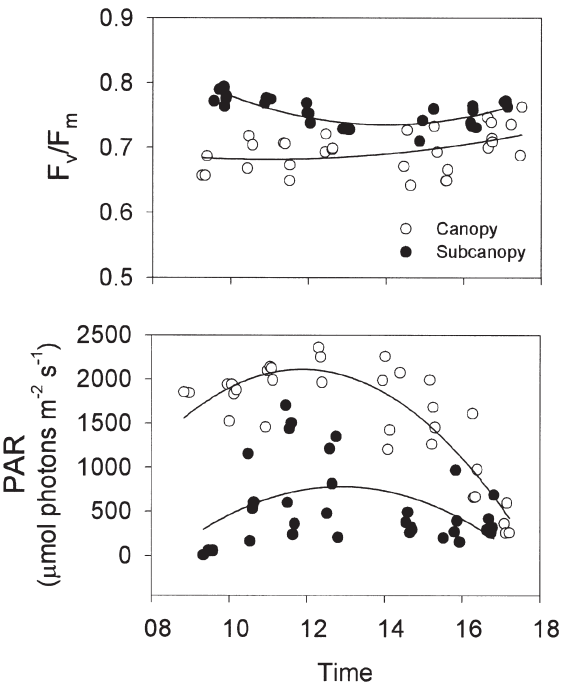

Fig. 4. Diurnal measurements of Photosystem II (PS II) potential quantum efficiency calculated as F_v/F_m (upper panel) and photosynthetically active radiation (PAR; bottom panel) in the canopy (open circles) and in the subcanopy (filled circles) for *Quercus rubra*. F_v/F_m measurements were taken after 15 minutes of dark adaptation. PAR was measured at the same time and on the same leaves as Chl fluorescence. (J. Cavender-Bares, unpublished.)

Sunflecks, which lead to large and rapid fluctuations in light levels, pose a particular problem for plants growing in the understory of forest canopies. The ability of plants to utilize light during sunflecks can be significantly limited both by photosynthetic capacity and by the induction requirement of photosynthesis (Pearcy, 1987). The latter results from declining metabolite pools, deactivation of the enzyme rubisco and stomatal closure during periods

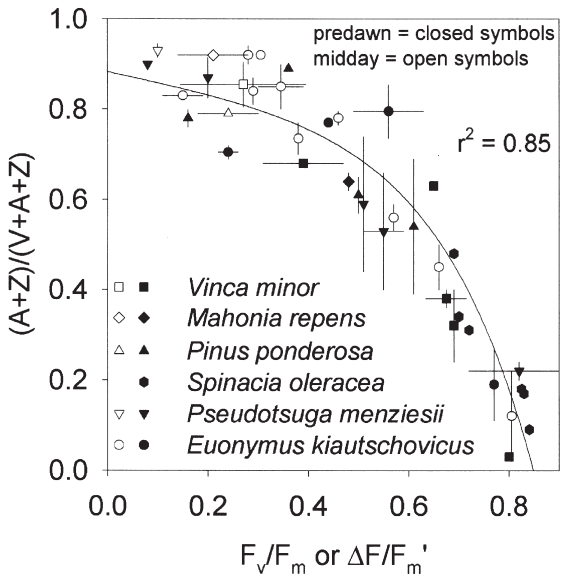

Fig. 5. The relationship between the level of antheraxanthin (A) + zeaxanthin (Z) per total xanthophyll cycle pool (violaxanthin (V) + A + Z) and the intrinsic PS II efficiency, measured as Fv/Fm in the dark and $\Delta F/F_m'$ in the daylight, adapted from Adams et al. (1994). Measurements made either on cold winter days prior to sunrise (closed symbols) or at mid-day during the summer (open symbols) when warm leaf temperatures were achieved, except for *Euonymus kiautschovicus*, with an intrinsic PS II photochemical efficiency below 0.2 that was sampled on a cold day in the winter. Species are listed in the figure. Error bars are ± 1SE (n = 3).

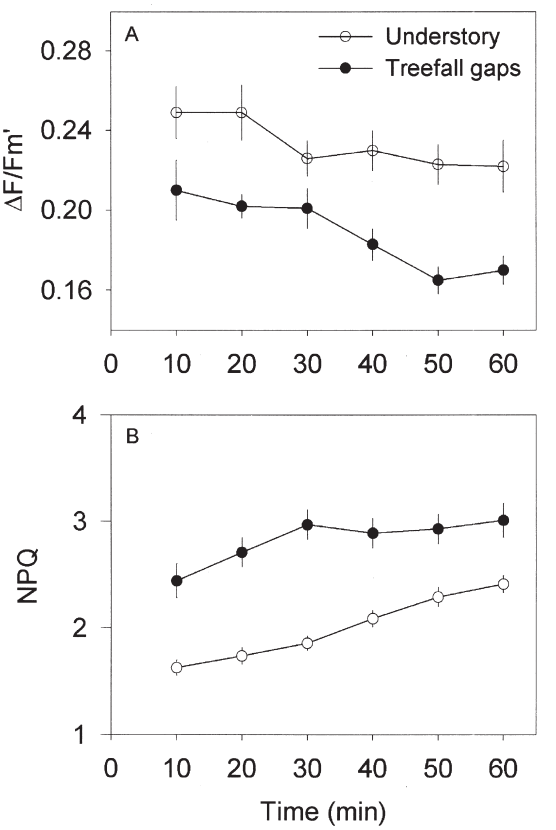

Fig. 6. (A) Mean quantum yield of PS II measured as $\Delta F/Fm'$ and (B) non-photochemical fluorescence quenching (NPQ) of leaf discs averaged for six species during exposure to 1000 μmol photons m^{-2} s^{-1} for 60 min, adapted from Lovelock et al. (1998). Filled circles are for leaves developed in the understory, while open circles are for leaves developed in tree-fall gaps. Error bars represent standard errors (n = 30 leaf discs). Species were: *Acalypha diversifolia*, *Alseis blackiana*, *Psychotria horizontalis*, *Hybanthus prunifolius*, *Andria inermis,* and *Piper aequale*.

of low light between sunflecks (Pearcy et al., 1994). These factors can result in leaves being exposed to higher light levels than can be accommodated by photochemical reactions during a sunfleck. In order to avoid over-excitation of the photosynthetic reaction centers, which could result in photodamage, leaves require photoprotective mechanisms capable of responding rapidly (Logan et al., 1997; Watling et al., 1997)

Watling et al. (1997) and Logan et al. (1997) found that in plants exposed to sunflecks in the field, F_v/F_m always returned to pre-sunfleck levels after return to low light levels by the end of the same day, indicating that no major photodamage had occurred during the sunfleck. However, Watling et al. (1997) found that light absorbance exceeded the capacity of the photosynthetic electron transport system to process it. Understory plants showed increases in qN, indicating increased thermal dissipation of light energy. This helps to protect PS II from over-excitation that could otherwise lead to photodamage, but it also brings about a decline in the quantum yield of PS II photochemistry. In their study, reduced PS II efficiency occurred as a result of exposure to saturation sunflecks in the field and was sustained in low light following sunflecks for close to two hours. Hence, there was a significant decline in photosynthesis in low light following a sunfleck. Watling et al. (1997) concluded that low assimilation rates and a low induction state could lead to high-light stress during sunflecks in understory plants. This is potentially a significant disadvantage for understory plants that are largely exposed to sub-saturating light levels. The exacerbation of high light stress due to a low induction state was thought to be most likely if sunflecks were infrequent (Watling et al., 1997). Logan

et al. (1997) did not find depressed PS II efficiency under low light levels following sunflecks, although in their study, maximum light levels during the sunfleck period (250 μmol photons m^{-2} s^{-1}) were much lower than in the study by Watling et al. (2000 μmol photons m^{-2} s^{-1}).

B. Low Temperature Stress

Photoinhibition induced by low temperatures has been recognized as a factor limiting photosynthetic efficiency and productivity of plants under field conditions (Ball, 1994; Ball et al., 1997). Increased levels of photoinhibition even under moderate light levels in the presence of low temperatures has been attributed to several factors, including the reduced utilization of excitation energy in carbon metabolism. This leads to an increased proportion of reduced Q_A in the steady state that results in an increase in excess excitation energy. Rates of repair via D1 protein turnover can be severely reduced as well (Krause 1994). Ball (1994) showed that photoinhibition was an important factor limiting regeneration of snow gum (*Eucalyptus pauciflora*) seedlings in southern Australia. She found the regeneration niche of snow gum seedlings to be limited to the east side of the understory shade trees where seedlings are protected from the simultaneous occurrence of freezing temperatures and intense morning light.

As with light stress alone, the ratio of variable to maximum Chl fluorescence (either F_v/F_m or $\Delta F/F_m'$) can be used as an empirical measure to determine the extent of stress under chilling conditions when exposed to even moderate light levels (Adams et al., 1990; Öquist and Huner, 1991; Ball, 1994; Krause, 1994; Adams et al., 1995; Ball et al., 1995). Figure 7A shows the decline in $\Delta F/F_m'$ in *Quercus virginiana* with increasing photosynthetically active radiation (PAR) under warm (24 °C) and chilling (5 °C) temperatures. The large decline in $\Delta F/F_m'$ under chilling temperatures relative to warm temperatures shows the increasing stress resulting from low temperatures as light level is increased. Significant decreases in electron transport rate are associated with this drop, resulting in lower CO_2 assimilation rates (Fig. 7B).

Lovelock et al. (1995) found reversible declines in F_v/F_m of Antarctic moss associated with freezing and thawing. They used dithiothreitol (DTT), which inhibits the formation of zeaxanthin, and found reduced levels of Z + A, and reduced non-photochemical quenching (qN). They attributed the reversible photoinhibition to a photoprotective mechanism associated with the xanthophyll cycle that prevents damage to the photosynthetic apparatus. The xanthophyll cycle and the photoprotective energy dissipation process associated with it appear to provide plants the flexibility required to deal with excessive levels of light absorption by Chl under a wide range of climatic conditions, including the low temperatures that give rise to winter stress (Adams et al., 1995; Chapters 21, Gilmore; and 22, Adams and Demmig-Adams).

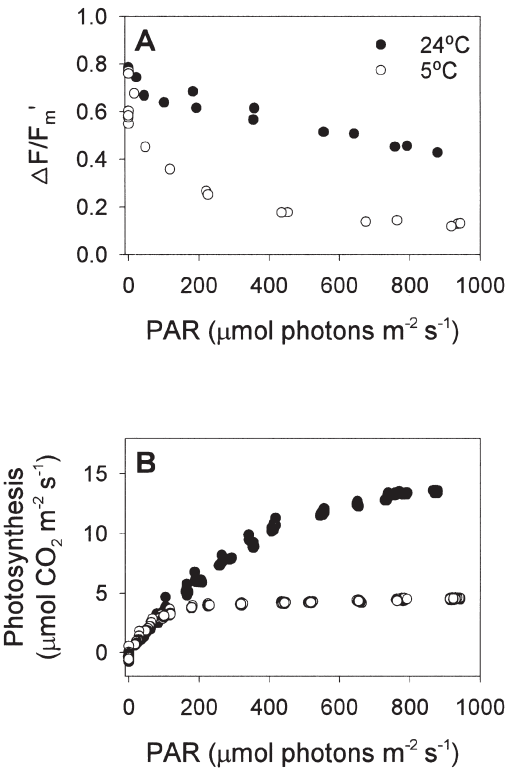

Fig. 7. Relationship between photosynthetically active radiation (PAR) and (A) PS II quantum yield measured as $\Delta F/F_m'$ and (B) the rate of carbon assimilation for *Quercus virginiana* under warm (24 °C) and chilling (5 °C) temperatures. Adapted from Cavender-Bares et al. (1999).

Following the method of Horton and Hague (1988), Cavender-Bares et al. (1999) compared the relaxation kinetics of non-photochemical quenching after exposure to light stress and chilling temperatures in an evergreen and a deciduous oak, and were able to identify differences among the two species in relative proportions of processes with different reversal rates. A rapidly reversible component (A_{fast}, half life on the order of seconds) has been interpreted as a energetic quenching (qE) or a photoprotective mechanism. An

essentially irreversible component of qN was identified (A_0), which can be interpreted as irreversible quenching (qI) associated with photodamage. An intermediate component (A_{slow}, half life on the order of minutes) was also apparent that has been associated with state I to state II transition and transfer of light harvesting complexes to PS I (qT) (Fig. 8). After simultaneous exposure to high light (1000 µmol photons m^{-2} s^{-1}) and chilling temperatures (5 °C) for one hour, the relaxation kinetics were measured after a return to warm temperatures and darkness. This experiment showed a higher proportion of qE in the evergreen oak, *Quercus virginiana*, that must deal with cold temperature stress compared to the deciduous species, *Quercus michauxii*, which drops its leaves after the onset of cold temperatures. There was also a trend toward higher qI, interpretable as photodamage, in the deciduous species. (For further definition of the various components of NPQ, see Chapter 18, Krause and Jahns; and for a detailed discussion of state changes, see Chapter 17, Allen and Mullineaux.)

In addition to more traditional measurements of F_v/F_m as indicators of cold-stress, Agati et al. (1996) used the ratio of Chl fluorescence measured at the two emission maxima (F685/F730) as a screening parameter for chilling tolerance. Lichtenthaler and Rinderle (1988) used a similar ratio, F690/F730, as a measure of stress in plants. Agati et al. (1996) found a decrease in this ratio in the chilling sensitive bean (*Phaseolus vulgaris*) but a slight increase in the ratio in the chilling tolerant pea plant (*Pisum sativum*). A second study attributed a decrease in this ratio (in this case, F685/F735) with chilling temperatures to a state I–state II transition that decreases PS II fluorescence and increases PS I fluorescence. Chilling temperatures apparently induced a modification in the thylakoid membranes, which altered the distribution of excitation energy between PS II and PS I (Agati et al., 2000). This fluorescence ratio has not yet been applied to field ecological studies.

Gilmore and Ball (2000) discovered a prominent component of the Chl fluorescence spectrum around 715 nm when measured at 77K in evergreen snow gum (*Eucalyptus pauciflora*) that coincides structurally with a loss of Chl and an increase in energy-dissipating carotenoids. It is associated with an increased capacity to dissipate excess light energy and prevent photo-oxidative bleaching and is likely to facilitate recovery of photosynthesis in the spring in overwintering evergreens (Gilmore and Ball, 2000). These innovative Chl fluorescence measurements have the potential to become important tools in detecting cold tolerance and cold stress under field conditions (also see Chapter 21, Gilmore).

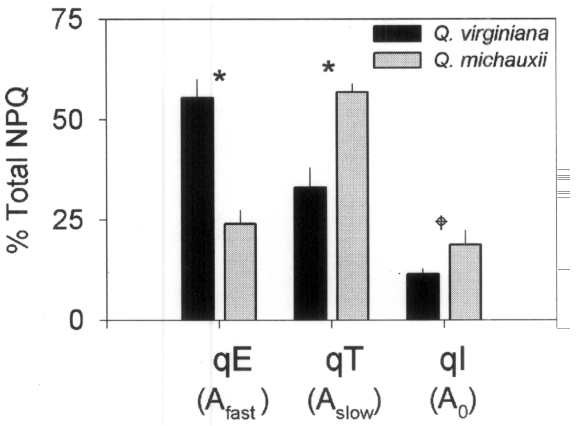

Fig. 8. A comparison of the kinetics of relaxation of the non-photochemical quenching NPQ of chlorophyll fluorescence for the evergreen and deciduous oak species, *Q. virginiana* and *Q. michauxii,* respectively. Total NPQ was calculated as: (dark adapted $F_m - F_m'$)/F_m' where F_m' is maximal fluorescence after 1 hr light. The relative amplitude (A) of components of NPQ relaxation were interpreted as qE, qT and qI such that qE corresponds to the rapidly reversible component (A_{fast}), qT to the slowly reversible component (A_{slow}), and qI to the irreversible component (A_0). Data are replotted from Cavender-Bares et al. (1999). Error bars are ± 1SE.

C. Nutrient Stress

A number of studies have shown that chlorophyll fluorescence parameters provide good indicators of nutrient deficiency (see for example, Subhash and Mohanan, 1994,1997; Kebabian et al., 1999; Werther and Havranek, 2000; Parkhill et al., 2001; Freedman et al., 2002). Perhaps one of the most useful indicators of nitrogen stress in plants is the ratio of UV excited blue fluorescence to Chl fluorescence (BF/ChlF) (Chappelle et al., 1984; Heisel et al., 1996; Lichtenthaler, 1996; Lichtenthaler et al., 1996; Corp et al., 1997; Buschmann and Lichtenthaler, 1998). Cerovic et al. (1999) have reviewed the use of UV-excited blue and red fluorescence in detecting nutrient deficiencies. They attribute an increase in BF/ChlF ratio in nutrient stressed plants to an accumulation of phenolic or flavonoid compounds in the leaf epidermis. These compounds absorb UV light and decrease UV transmittance through the epidermis, thereby decreasing the excitation of Chl molecules in the mesophyll by

UV light. The result is an increase in the BF/ChlF ratio (Cerovic et al., 1999).

According to the carbon/nutrient balance hypothesis, carbon fixed in excess by the plant relative to nutrient uptake stimulates the shikimate acid pathway and thus leads to the production of plant phenolics and other carbon-based compounds (Price et al., 1989; Waterman and Mole, 1994). These compounds can then serve an important function in the plant as anti-herbivore defenses. Empirical evidence supports the carbon/nutrient balance hypothesis as increases in phenolic compounds are generally found in nutrient deficient plants (Bryant et al., 1987; Price et al., 1989; Waterman and Mole, 1994).

Ounis et al. (2001) used dual-excitation fluorescence light detection and ranging (DE-FLIDAR to create a fluorescence excitation ratio using UV (355 nm) and visible (532 nm) radiation to determine epidermal UV absorption by Chl. The visible excitation wavelength was used as a reference and not absorbed by the epidermis. A dual fluorescence emission ratio of red fluorescence (RF) to far-red fluorescence (FRF) excited at 355 and 532 nm (RF_{ex532}/FRF_{ex355}) was found to be strongly positively correlated with Chl content, a result which was predicted by a model Ounis et al. had presented based on the Beer-Lambert Law. Hence, this ratio shows promise for detecting mineral deficiencies in plants. Similarly, Samson et al. (2001) used the ratio of UV excitation pulses at 360 nm to those in the blue at 440 nm to detect nutrient deficiencies in corn leaves. They found a very high positive correlation ($R^2 = 0.93$) between the fluorescence excitation ratio FRF_{ex360}/FRF_{ex440} and the nitrogen concentration of corn leaves.

D. Water Stress

Water availability is one of the most important limitations to photosynthesis and plant productivity (Kramer and Boyer, 1995). Chl fluorescence indices are important tools for measuring non-invasive parameters for remote sensing of plant photosynthesis and water status (Schmuck et al., 1992; Cerovic et al., 1996; Cornic and Massacci, 1996; Flexas et al., 2000). The effects of water stress on the photosynthetic efficiency of plants is discussed in Chapter 24 (Bukhov and Carpentier) and has been reviewed by Cornic and Massacci (1996).

A good correlation between rates of electron transport and assimilation rate has been found for C_4 plants, and the ratio of ETR/A is known to be consistent under a wide range of conditions (Edwards and Baker, 1993). For C_3 plants, however, this ratio can be quite variable, and the correlation between ETR and A can be lost altogether under conditions of water stress. When photosynthesis is limited by stomatal closure, which occurs during water stress, CO_2 availability in the chloroplast is reduced, increasing the ratio of O_2/CO_2. Electron flow toward oxygen thus increases, particularly through photorespiration (Cornic and Briantais, 1991; Krall and Edwards, 1992). Thus, changes in the relationship between ETR/A can be used as an indicator of water stress in plants (Flexas et al., 2002). Cerovic et al. (1996) also found that electron transport rates saturate at lower light levels in water stressed plants compared to well-watered plants. Electron transport rates and photochemical quenching (qP) decline with increasing water stress and stomatal closure because the photorespiratory cycle is a less efficient electron sink than carbon dioxide reduction (Stryer, 1988). As a consequence, a greater proportion of incoming light energy must be dissipated non-photochemically. In seven species of oaks grown across an experimental soil moisture gradient, we found higher non-photochemical quenching in water stressed plants than in plants that were not water-limited. For all species, there was a significant negative correlation between non-photochemical quenching (NPQ) and plant water status, measured as predawn leaf water potential (Ψ_{Leaf}) (two species are shown in Fig. 9A). This corresponded well to a decrease in intracellular [CO_2] (C_i) (plotted as the difference between ambient and intracellular [CO_2] ($C_a - C_i$) with decreasing predawn Ψ_{Leaf}, indicating stomatal closure (Fig. 9B) (J. Cavender-Bares, unpublished).

Other fluorosensing parameters have also been used to detect water stress. Cerovic et al. (1996) used mean lifetime and yield of remotely sensed Chl fluorescence to detect water stress in several crop species. They found decreases in the slope of the relationship between Chl fluorescence lifetimes and relative fluorescence yield in water stressed plants compared with controls. Flexas et al. (2000) found that the steady-state fluorescence parameter, Fs, was also useful in detecting water stress in plants. They found Fs to increase with light intensity in well-watered plants. As water stress was imposed, however, this relationship changed, and Fs actually decreased with increasing light intensity. In the study of oak species grown across an experimental soil moisture gradient under natural light conditions, we found Fs to decrease with decreasing predawn water potential (Fig. 9C). The possibility of using the simple Fs pa-

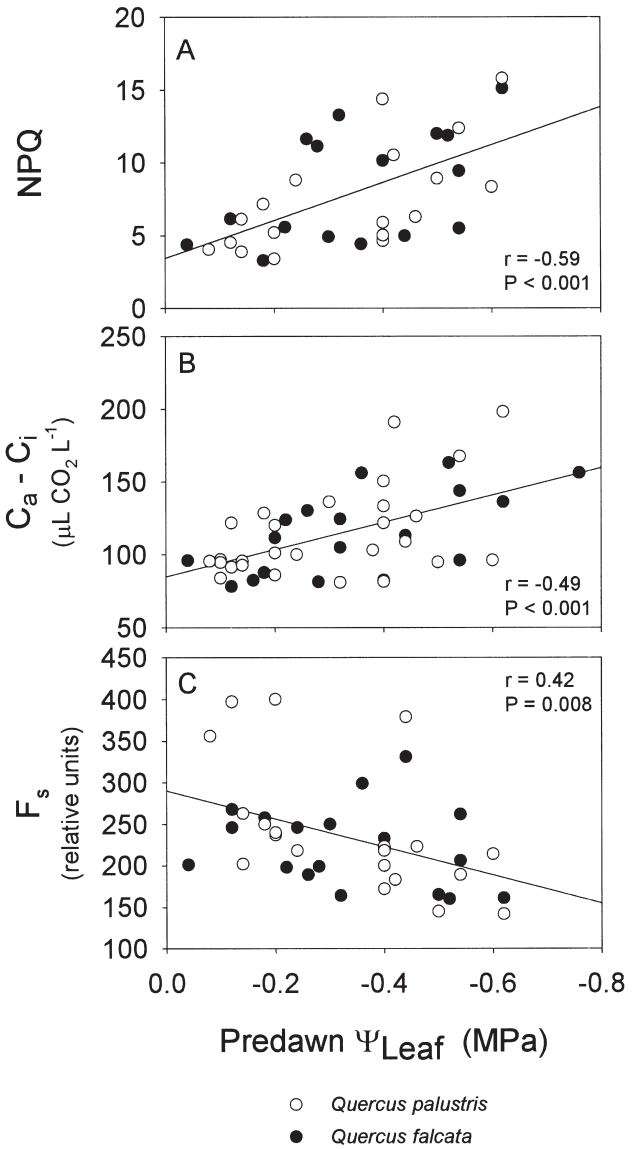

Fig. 9. Oak seedlings grown at low soil moisture have higher NPQ than those at higher soil moisture levels, as shown by the negative correlation between NPQ and Ψ_{Leaf} (A). This corresponds to a decline in the intercellular CO_2 concentration with increasing water stress (shown as $C_a - C_i$) indicating stomatal limitation to photosynthesis (B). An overall decrease in photochemical quenching (qP) is likely as the ratio of photosynthesis to photorespiration decreases with increasing water stress, resulting in an increase in NPQ. At the same time, steady state Chl fluorescence (Fs) increases with increasing water stress (C). (J. Cavender- Bares, unpublished.)

rameter, or the relationship of Fs and light level, as an indicator of water stress is particularly intriguing because Fs can be measured remotely with current technology (see Section IV.C).

IV. Measuring Productivity at the Ecosystem Level

There is a growing need to integrate ecological information across spatial and temporal scales in order to understand functioning of whole communities or ecosystems, particularly in relation to an array of human perturbations. The potential of Chl fluorescence and other fluorescence parameters to contribute to understanding community and ecosystem processes is increasing with the availability of new technologies that allow remote measurement of fluorescence parameters (Chapter 16, Moya and Cerovic).

Several approaches have been used to estimate

whole ecosystem fluxes and represent their dynamics, including i) estimating fluxes of carbon dioxide and other gases from ecosystems using eddy covariance measurements from towers and ii) linking satellite-based remote sensing of reflectance data to models of photosynthetic production. Looking forward, some fluorescence parameters could be measured from aircraft or satellite (Chapter 16, Moya and Cerovic) and coordinated with tower-based CO_2 flux measurements, improving the accuracy of photosynthetic production estimates. Additionally, in some cases, canopy measurements of gas exchange and fluorescence parameters could be incorporated to provide a mechanistic understanding of the dynamics of ecosystem processes and include, for example, the role of species composition in ecosystem productivity models. Incorporating remotely sensed measurements of Chl and leaf epidermal fluorescence into ecosystem studies could also be helpful in diagnosing stress factors that limit productivity.

A. Eddy Correlation Flux Towers

Eddy covariance flux towers have now been deployed in different biomes worldwide as a means of sampling net carbon fluxes over large landscapes. By integrating the high-frequency covariance between the concentration of atmospheric gases and vertical velocity, this method provides a direct means of sampling instantaneous landscape-level fluxes (Baldocchi et al., 1988; Verma, 1990). Gas fluxes are obtained by correlating the vertical wind component with the horizontal wind component, temperature, and gas density (e.g., CO_2 or H_2O). Infrared gas analysis is used to obtain carbon dioxide and water vapor densities. Estimates of ecosystem photosynthesis from eddy flux correlation measurements correspond fairly well with leaf level photosynthetic rates in canopies of mature trees that have been scaled up (Wofsy et al.,1993).

B. Models of Productivity using Reflectance Indices

Reflectance indices of vegetation from satellite data have been used to estimate whole ecosystem parameters, including net primary productivity (NPP). Vegetated and non-vegetated terrestrial areas can be readily distinguished based on their contrasting reflectance patterns in the red and near-infrared (NIR) spectral regions. Since photosynthetic pigments absorb in the red but not in the NIR, reflectance bands in these regions can be compared. The most commonly used vegetation index is the normalized difference vegetation index (NDVI):

$$NDVI = (R_{NIR} - R_{RED})/(R_{NIR} + R_{RED}) \quad (1)$$

where R_{NIR} is the reflectance in the NIR region, and R_{RED} is the reflectance in the red region. NDVI and other vegetation indices have limitations and need to be corrected to deal with interference from various sources that alter reflectance signals (Myneni and Williams, 1994; Sellers et al., 1996). Nevertheless, vegetation indices, such as NDVI provide a measure of the fraction of photosynthetically active radiation (F_{APAR}) absorbed by green vegetation. NDVI and F_{APAR} are causally related as both are strongly influenced by the amount of leaf area in a green vegetation canopy (Myneni and Williams, 1994). There is also empirical evidence showing that the two are linearly related (Kumar and Monteith, 1981; Hall et al., 1990).

Gamon and Qiu (1999) summarized several models of photosynthetic productivity, or carbon gain by vegetation, as follows:

$$\text{Photosynthetic rate} = APAR * \varepsilon, \quad (2)$$

where, APAR indicates the quantity of absorbed photosynthetically active radiation, and ε represents photosynthetic radiation-use efficiency—the efficiency of converting absorbed radiation to fixed (organic) carbon. If integrated over time and space, this equation can be expressed as:

$$\text{Primary productivity} = \Sigma APAR * \varepsilon, \quad (3)$$

where, primary productivity is often expressed as net primary productivity (NPP), typically equivalent to accumulated biomass within a growing season, Σ APAR is the absorbed PAR, or the annual integral of radiation absorbed by vegetation, and ε represents the average efficiency with which absorbed radiation is converted to biomass (Monteith, 1977). APAR can be further defined as the product of photosynthetically active radiation (PAR) and the fraction of that irradiance that is absorbed by vegetation (F_{APAR}). The fraction of PAR actually absorbed by the vegetation depends on the amount and distribution of photosynthetic biomass.

$$NPP = PAR * F_{APAR} * \varepsilon . \quad (4)$$

Respiration is not explicitly included in these models, but can be incorporated into the ε coefficient or a separate coefficient can be added. For a more thorough discussion of current modeling approaches and assumptions, see, for example, Cramer et al. (1999) and Beyschlag and Ryel (1998).

A number of authors have relied on the relationship between NDVI (or other reflectance indices) and F_{APAR} to estimate APAR, such that NPP can be expressed as a function *(f)* of NDVI, PAR and ε:

$$NPP = f(NDVI * PAR * \varepsilon). \quad (5)$$

The efficiency coefficient, ε, was initially assumed to be constant (Monteith, 1972; Kumar and Monteith, 1981) although it is known to vary with ecosystem type and with stresses from unfavorable levels of temperature, nutrients and water (Runyon et al., 1994; Joel et al., 1997). To account for this variation, ε is usually parameterized with field measurements as remote measures have been thought to be intractable (Field et al., 1998). Recently, however, the photochemical reflectance index (PRI), an index of xanthophyll cycle activity, which can detect changes in radiation use efficiency and can be measured remotely, was used to estimate ε (Nichol et al., 2000). PRI is often expressed as:

$$PRI = (R_{531} - R_{REF}) / (R_{531} + R_{REF}), \quad (6)$$

where, R_{531} represents reflectance at 531 nm (the xanthophyll cycle band) and R_{REF} indicates reflectance at a reference wavelength, generally in the yellow at 570 nm (Peñuelas et al., 1995; Gamon et al.,1997; Gamon and Surfus, 1999). Relationships have been shown between PRI and photosynthetic rates of canopy leaves, and thus for photosynthetic radiation use efficiency ε , for different species (Gamon et al., 1997; Nichol et al., 2000).

Based on these relationships, Rahman et al. (2001) recalculated the above equations as:

$$CO_2 \text{ uptake} = f(PRI * NDVI). \quad (7)$$

They combined CO_2 flux data from eddy covariance towers within the boreal forest of North America and found a strong correlation between gross CO_2 flux and (NDVI*sPRI), $R^2 = 0.82$ for nine tower sites, where sPRI is a scaled value of PRI ranging from 0 to 1 (Fig. 10).

C. Using Remote Sensing of Chlorophyll Fluorescence in Productivity Models

Remotely sensed measures of Chl fluorescence show promise for improving the accuracy of productivity estimates based on the NPP models described above. Moya et al. (2001) have proposed measuring Chl fluorescence at 740 nm (a wavelength at which light is not absorbed by the leaf) as an integrated measure of PAR * F_{APAR} (Chapter 16, Moya and Cerovic). This may be a more useful measure of absorbed radiation from vegetation than NDVI, or other indices based on reflectance, because fluorescence emission comes from the photosynthetic apparatus after absorbing light energy.

More significantly, Chl fluorescence parameters are likely to improve measurement of radiation use efficiency. Ultimately, $\Delta F/F_m'$ would be the ideal parameter to estimate ε as it is a direct measure of PS II radiation use efficiency (Genty et al., 1989). However, because an excitation light pulse is required to determine this ratio, it is still most usefully measured only at close range (<1m). The simple fluorescence parameter Fs may be a more practical alternative for estimating ε at large scales. Recent advances in technology allow remote sensing of the Fs parameter using sunlight excited Chl fluorescence via Fraunhoefer line discrimination (Moya et al., 1998; Kebabian et al., 1999). Fs has been shown to be correlated with photosynthetic rate (Freedman et al., 2002; Flexas et al., 2002) and with PRI (Moya et al., 2001). Freedman et al. (2002) demonstrated a strong negative correlation between the remotely sensed and sunlight excited steady state fluorescence ratio, F690/F760, and canopy photosynthetic rates of *Quercus hemispherica* exposed to differing levels of nutrient and carbon stress ($R^2 = 0.66$ for 12 plant canopies) (Fig. 11). Flexas et al. (2002) have also demonstrated strong relationships between Fs and photosynthetic rates as well as stomatal conductance rates. The ability to measure Chl fluorescence parameters remotely for use in ecosystem models should improve efforts to estimate CO_2 fluxes at large scales.

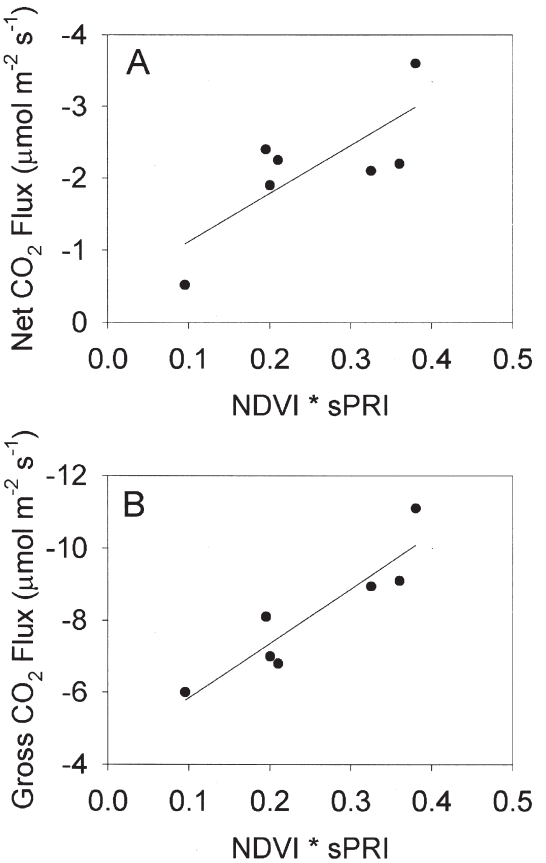

Fig. 10. Relationship between the net CO_2 flux (A) or gross CO_2 flux (B) and the product of the normalized difference vegetation index (NDVI) and a scaled value of the photochemical reflectance index (sPRI), adapted from Rahman et al. (2001). The correlation in (B) is significant ($r^2 = 0.82$, $P<0.002$), while that in (A) is not.

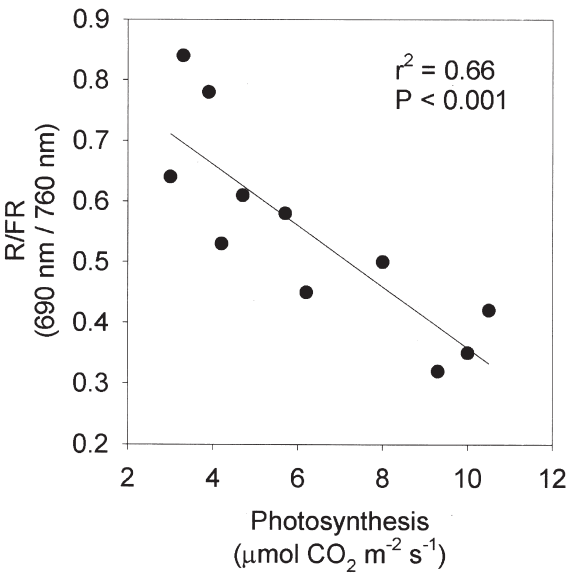

Fig. 11. The relationship between the ratio of red to far-red Chl fluorescence (690nm/ 760nm) to the CO_2 assimilation rate, measured remotely on canopies of *Q. hemispherica,* redrawn from Freedman (2002). Values of assimilation rate are the average of approximately five leaves per canopy.

V. Scaling from the Bottom Up — The Role of Species Composition in Ecosystem Dynamics

While remotely sensed Chl fluorescence parameters are likely to improve estimates of ecosystem productivity, other remotely sensed fluorescence measures may help elucidate the mechanisms of ecosystem response to changes in the environment. One limitation of ecosystem-scale modeling methods is that they try to capture the response of a unit of the landscape and integrate the response of all individuals present, regardless of differences among them. Such approaches do not specifically consider the individual behavior of various species in an ecosystem. The blue to red fluorescence ratio has been proposed as a general plant classification criterion (Cerovic et al., 1999) that may prove useful in tracking differences among species in response to the environment. The fluorescence global vegetation index (FGVI), described in Chapter 16 (Moya and Cerovic) and Cerovic et al. (1995, 1999), uses both red and blue fluorescence indices to identify individual species from fluorescence signatures as well as to detect stress. It thus provides the potential for mapping of individual species (with obvious limits to the spatial resolution) as well as remote detection of stress. The development of indices such as the FGVI will ultimately increase our ability to investigate ecosystem dynamics by scaling upward from species-level behavior. In turn, this will provide a greater ability to predict changes in ecosystem function from environmental perturbations that differentially affect species. The following is an example from a forest ecosystem of the northeastern United States, which makes clear the importance of species-level differences in the gross ecosystem exchange of carbon.

Within a New England mixed Hardwood forest, Bassow and Bazzaz (1998) showed that various environmental factors affect gas exchange rates of individual forest canopy species differently. Bassow and Bazzaz (1998) and Catovsky and Bazzaz

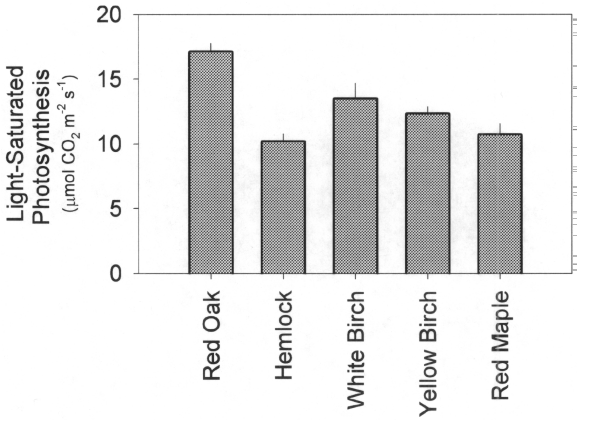

Fig. 12. Estimated maximal rates of photosynthesis for five tree species found in a mixed hardwood forest in New England, adapted from Bassow and Bazzaz (1998) and Catovsky and Bazzaz (2000).

(2000) showed significant differences in leaf-level photosynthetic rates of co-occurring species at the Harvard Forest (Fig. 12), with red oak (*Quercus rubra)*, consistently having the highest photosynthetic rates and hemlock (*Tsuga canadensis*) the lowest. When scaled up, interspecific variation in leaf-level photosynthesis gives rise to significant differences in canopy carbon uptake rates throughout a growing season such that red oak is estimated to have up to two-fold higher uptake rates than hemlock (Catovsky and Bazzaz, 2000). It is known that among the dominant species in this ecosystem, red oak with its deep rooting (Lyford, 1980) is less affected by severe drought in terms of gas exchange and other factors than other co-occurring species, such as birches, or maples (Auge et al., 1998; Caspersen and Kobe, 2001; Turnbull et al., 2002). The response of the whole ecosystem to environmental perturbations, such as severe drought, is likely to be influenced by the fact that the Harvard Forest canopy consists of 60–70% red oak. Goulden et al. (1996) showed that gross ecosystem exchange of carbon dioxide, as measured from eddy correlation flux towers, experienced only a 10% decrease during a severe drought year. Respiration that year, however, decreased by 30% due to decreased soil moisture (compare soil water content in 1995 to 1996, Fig. 13A) so that the net result was an increased downward flux of CO_2. During that same drought year, canopy photosynthetic rates of red oak showed little decline in photosynthesis relative to the wet year (Fig. 13B) (Cavender-Bares and Bazzaz, 2000). The trends in these photosynthetic data

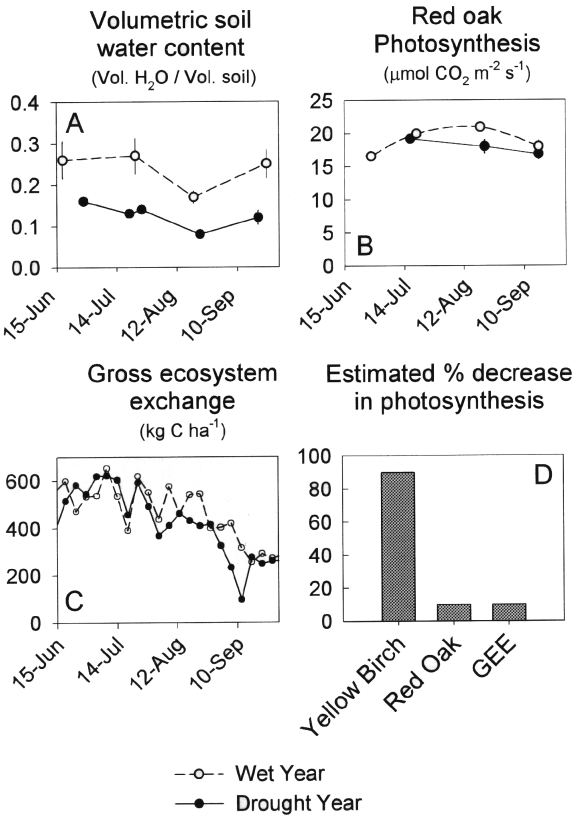

Fig. 13. (A) A comparison of soil moisture in a drought year (1995, closed circles) and a wet year (1996, open circles) (data courtesy of K. Newkirk). (B) Photosynthetic rate of canopy leaves of red oak (*Quercus rubra),* the dominant canopy tree in the Harvard Forest ecosystem, during the drought and wet years. (C) Gross ecosystem exchange (GEE) of carbon dioxide as determined from eddy correlation measurements for the Harvard Forest ecosystem in the drought and wet years (data courtesy of S. Wofsy). (D) Red oak showed a relatively small decline in photosynthetic rate during the drought year relative to yellow birch (*Betula papyrifera*). The small decline in photosynthetic rate of *Q. rubra* corresponds closely to the decrease in GEE. All three values are estimated declines calculated for peak summer months. Panels A and B are replotted from Cavender-Bares and Bazzaz (2000).

compare well to those of gross ecosystem exchange (GEE) determined during the same summer period for both the drought and wet years (Wofsy, 2000) (Fig. 13C). In contrast, yellow birch showed dramatic declines in photosynthetic rates resulting from a high degree of leaf wilt and damage during the drought. Red oak was able to maintain high gas exchange rates during the drought due in part to increases in water use efficiency as well as maintenance of high predawn water potentials most likely resulting from the ability of this species to root deeply and access deep water reserves (Cavender-Bares and Bazzaz,

2000). Had the canopy been composed of species incapable of avoiding drought, such as yellow birch, the net downward flux of carbon dioxide would likely have been lower.

Thus, in such mixed forests, future changes in species composition could have substantial impacts on forest carbon dynamics, both as a result of differences in abilities of species to sequester carbon as well as differences in stress tolerances of species. Ecosystem photosynthesis in this forest is likely to be lower if oak regeneration continues to decline and other canopy species with lower photosynthetic rates become more dominant (Catovsky and Bazzaz, 2000). Ecosystem response to perturbation is also likely to change if species composition changes, as species can have markedly different responses to changing environments (Bazzaz, 1996). This speaks to the need for incorporating mechanistic analyses of factors contributing to ecosystem processes, including the role of individual species and species composition, into models that use remote measurements to estimate large scale fluxes. An important step toward this goal is the further development of the FGVI (discussed above) and other species-level indices that rely on fluorescence signatures (Tyystjärvi et al., 1999) that can provide the basis for remote detection of species composition. Such indices, combined with other remote sensing techniques that allow estimation of whole ecosystem fluxes, should promote mechanistic analyses of changes in ecosystem processes in response to disturbance.

VI. Concluding Remarks

Fluorescence provides a rapid, non-destructive means of studying photosynthetic and other physiological processes of plants under field conditions. Measurements of Chl fluorescence parameters are becoming increasingly useful in ecological studies of whole plant photosynthesis and plant function, providing insights about mechanisms of plant responses to environmental stress, and responses of whole ecosystems to environmental change.

It is important to have diverse tools for monitoring photosynthesis, productivity and stress for assessment of plant and ecosystem health, crop monitoring, global change monitoring, and collecting baseline data for modeling of global processes. The need for such tools is made clear by recent comprehensive efforts to assess ecosystem health at large spatial scales (Heinz Center, 2002). Combining techniques is likely to improve reliability and accuracy. Remote fluorescence measurements show promise for improving or validating currently used methods for assessing ecosystem health and productivity at large-scales, such as measurement of gas fluxes and satellite measurement of reflectance indices. In addition, integrating ecosystem flux data with information on species composition, based on fluorescence signatures that allow identification and mapping of individual species, may allow a mechanistic determination of how climate change and other disturbance factors affect ecosystem function.

Acknowledgments

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