Potentials and limitations for estimating daytime ecosystem respiration by combining tower-based remote sensing and carbon flux measurements

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Potentials and limitations for estimating daytime ecosystem respiration by combining tower-based remote sensing and carbon flux measurements

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Abstract

Vegetation carbon uptake and respiration constitute the largest carbon cycle of the planet with an annual turnover in the order of 120 GT. Currently, neither ecosystem carbon uptake (through photosynthesis) nor ecosystem carbon release (through respiration) can be measured directly during the daytime. Instead, flux-tower measurements rely on nighttime respiration based on the assumption of zero carbon uptake which are then projected to daytime using an exponential relationship to soil temperature at shallow soil depth. As an alternative to this approach, R could possibly also be determined from combining daytime eddy covariance measurements of net ecosystem production (NEP) and spectral observations of gross primary production (GPP). In previous work, we have shown that multi-angular observations can be used to determine GPP from the absorbed photosynthetically active radiation (APAR) and spectrally obtained observations of light-use efficiency ($\varepsilon$). The difference of NEP and GPP suggests that daytime respiration is greater and more dynamic than conventional estimates derived from nighttime flux values. Our findings also suggest that an accelerated ecosystem metabolism results in an exponential increase in respiration which eventually diminishes net ecosystem production. Respiration was also closely related to air and soil temperature. We conclude that tower-level spectral measurements provide considerable new insights into ecosystem fluxes as they allow independent yet complementary measurements of different aspects of the carbon and energy cycle.

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1. Introduction

Net ecosystem productivity (NEP) is the difference between gross primary production (GPP) and the sum of autotrophic and heterotrophic respiration (R), also known as ecosystem respiration (Trumbore, 2006). As both GPP and R are much greater fluxes than NEP, comprehensive understanding of these components is essential for determining the response of ecosystems to global change and related carbon feedbacks (Janssens et al., 2001; Valentini et al., 2000). Currently, it is not possible to measure R directly in the presence of photosynthesis (Desai et al., 2008). Instead, most stand-level estimates of respiration rely on nighttime flux measurements of NEP, based on an assumption of zero GPP (Reichstein et al., 2005). These nighttime flux observations are extrapolated to daytime measurements using relationships between nighttime R ($R_N$) and various environmental drivers; most commonly, an exponential relation between $R_N$ and soil temperature ($T_s$) is used (Morgenstern et al., 2004):

$$R = R_0 (T_s - 10)/10$$

where $R_0$ is the nocturnal ecosystem respiration ($\mu$mol m$^{-2}$ s$^{-1}$) at a reference temperature of 10 °C, $T_s$ is the soil temperature at a shallow depth (e.g. 5 cm) and $Q_{10}$ is the factor by which R increases for a 10 °C increase in temperature (Lloyd & Taylor, 2014). Methods based on $Q_{10}$ estimates of $R_N$ are widely applied across different scales (Beer et al., 2010; Mahecha et al., 2010); but limitations have also been documented. First, low friction velocity ($u^*$) during calm nocturnal periods can result in insufficient turbulent mixing (Van Gorsel et al., 2009) and, consequently, a systematic underestimation of fluxes has been observed during those times (Goulden, Munger, Fan, Daube, & Wofsy, 1996;
Lavigne et al., 1997). Second, the use of the relationship between nighttime NEP versus temperature to calculate daytime R (RDP) ignores the light inhibition of respiration (Janssens et al., 2001). Finally, different transport mechanisms of heat and momentum at leaf level (Belcher, Finnigan, & Harman, 2008) result in faster changes in the wind profile through the canopy than of the temperature profile (Van Gorsel et al., 2009). Reichstein et al. (2005) found a 25% difference in daytime R depending on whether observations were derived from short term or long term temperature sensitivities.

As a complementary approach to extrapolation of night time flux measurements, this paper explores the potentials and limitations for using remotely sensed estimates of GPP to obtain RDP by computing the difference between GPP and NEP derived from eddy covariance fluxes. Using a flux-tower based, automated, multi-angle spectro-radiometer (AMSPEC) (Hilker, Nesic, Coops, & Lessard, 2010), we have shown in previous work that stand-level GPP may be obtained from multi-angle reflectance as product of the fraction of absorbed PAR intercepted by the canopy (APAR) and the photosynthetic light use efficiency, ε (Monteith & Moss, 1977). GPP estimates based on this approach could potentially provide an independent method for determining stand-level respiration without having to resort to night-time observations. Estimates of APAR have long been derived from vegetation indices, and work by Chen, Rich, Gower, Norman, and Plummer (1997) and Ryu et al. (2011) has demonstrated that angular retrievals of spectral reflectance effects (Los, North, Grey, & Barnsley, 2005). In other words, this paper explores the potentials and limitations for using remotely sensed estimates of GPP to obtain RDP by combining tower-based remote sensing and eddy flux observations.

The objective of this work is to investigate and compare the temporal dynamics, similarities and differences of the described method as opposed to deriving RDP conventionally as a (Q10) function of TS. Based on results from different forest stands spanning a range of biophysical and spectral characteristics, we conclude that tower-based spectral observations can be a vital tool for improving estimates of carbon fluxes in terrestrial ecosystems, and provide new opportunities to scale estimates of carbon fluxes in space and time.

2. Methods

2.1. Site description

Five research sites were selected to cover a variety of temperate and sub-arctic forest stands; including a coastal Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.)) dominated stand on Vancouver Island (DF49), an Aspen (Populus tremuloides Michx.) dominated forest in Central Saskatchewan (SOA) and three mountain pine beetle (Dendroctonus ponderosae Hopk.) affected lodgepole pine (Pinus contorta Doug. ex. Loud var. latifolia Engl.) stands in Northern British Columbia. Table 1 contains an overview, references and site description for each individual stand and the dates that the spectral data were acquired.

2.2. Eddy covariance measurements

Simultaneous flux measurements and multi-angular spectral data were acquired as part of the Canadian Carbon Program. Net ecosystem exchange (NEE) was determined as the sum of the half-hourly EC fluxes of CO2 and the rate of change in CO2 storage in the air column between ground and EC-measurement height. At DF49 and SOA, EC fluxes were measured using a three-axis sonic anemometer–thermometer (Model R3, Gill Instruments Ltd., Lymington, UK) and a closed-path CO2/H2O infrared gas analyzer (IRGA) (LI-6262 or LI-7000, LI-COR Inc., Lincoln, NE, USA) (Barr et al., 2004; Jassal et al., 2007). At the Northern BC sites, a three-axis sonic anemometer–thermometer (Model CSAT3, Campbell Scientific Inc, Logan UT, USA) and an open-path CO2/H2O IRGA (Model LI-7500, LI-COR Inc.) were used (Brown et al., 2010). The rate of change in CO2 storage in the air column was calculated from the half-hour average CO2 concentrations obtained at EC measurement height (Morgenstern et al., 2004). Incident and reflected PAR [µmol m−2 s−1] was measured using upward and downward looking quantum sensors (model 190 SZ and 190 SA, LI-COR Inc.) above and below the canopy and fPAR was derived at each site from the incident and reflected total PAR measured above and below the canopy, leaf area index, and the solar zenith angle (θ) at the time of measurement.

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<th>Table 1 Study site descriptions and acquisition dates.</th>
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<td>Site, reference</td>
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<tr>
<td>Campbell River (DF49) (Morgenstern et al., 2004)</td>
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<td>Kennedy Siding (MPB-06) (Brown et al., 2010; Hilker et al., 2009)</td>
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<td>Crooked River (MPB-03) (Brown et al., 2004)</td>
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<td>Summit Lake (MPB-09)</td>
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<td>Southern Old Aspen (SOA) (Barr et al., 2004)</td>
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NEP was calculated as $-\text{NEE}$ (net ecosystem exchange).

Conventional daytime estimates of respiration (REC) were calculated using the annual exponential relationship between nighttime NEE and soil temperature ($T_s$) at the 5-cm depth (Jassal et al., 2007). As the scatter of the relationship between nighttime NEE and $T_s$ varies with temperature (heteroscedasticity), ordinary least squares regression is not suitable to fit these data, because it assumes a normal distribution. Instead, a logarithmic transformation was used to determine the increase in respiration with temperature as follows (Morgenstern et al., 2004):

$$\ln R_E = \ln (R_{\text{ref}} Q_{10}^{T_s/T_{\text{ref}}}) + \ln Q_{10} \frac{T_s}{10}$$  \((2)\)

where $R_{\text{ref}}$ is the respiration at reference temperature $T_{\text{ref}}$. If $T_{\text{ref}}$ is set to 10, Eq. (2) yields

$$\ln R_E = \ln (R_{10} Q_{10}^{T_s/10}) + \ln Q_{10} \frac{T_s}{10}.$$  \((3)\)

The threshold friction velocity ($u_{th}$) was set to 0.3 m s$^{-1}$ (Morgenstern et al., 2004). Conventional GPP (GPP$_E$) was calculated as NEP + REC (Humphreys et al., 2006).

Continuous automated chamber measurements were available at the DF49 site (Gaumont-Guay et al., 2006; Jassal et al., 2007) and obtained for the observation period (Table 1). The system consists of an IRGA (model LI-800, LI-COR), a diaphragm pump (model TD-4X2N, Brailsford Co., Rye, NY, USA), a storage module (model SM192, CSI) and an opaque PVC chamber (i.d. 10.8 cm, volume 1426 cm$^3$), which is equipped with a temperature and relative humidity sensor (model HMP35CF, CSI). A more detailed description of the soil chamber measurements can be found in Gaumont-Guay et al. (2006).

### 2.3. Tower based spectral data

Canopy spectra were acquired from an automated, multi-angular spectroradiometer, Amspec I (Hilker, Coops, Nesis, Wulder, & Black, 2007) and Amspec II (Hilker, Nesis, et al., 2010) mounted on top of the flux towers at each site during different seasons between 2006 and 2010. Amspec II features a pan-tilt unit which allows the sensor head to be oriented at any view zenith angle ($\theta_v$) between 43° and 78° and azimuth ($\phi_v$) between 0 and 360°. Measurements before 2009 were made using the prototype version, Amspec I, operating at a fixed vertical zenith angle of 62° (Chen & Black, 1992). To allow sampling under varying sky conditions, canopy spectra were obtained from simultaneous measurements of solar irradiance and radiance, sampled continuously from sunrise to sunset at a 5° angular step width (horizontally and vertically), with the full rotation completed every 15 min. The spectroradiometer used is a Unispec-DC (PP Systems, Amesbury, MA, USA) featuring 256 contiguous bands with a nominal band spacing of 3 nm and a nominal range of operation between 350 and 1200 nm. The upward pointing probe is equipped with a cosine receptor (PP-Systems) to correct sky irradiance measurements for varying solar zenith angles.

### 2.4. Deriving PRI' and GPP from spectral reflectance

Amspec provides spectral observations over a large range of viewing geometries. While these observations could be used to infer PRI' directly, this is not necessarily desirable because 1) levels of background reflectance will vary depending on where the sensor is pointing and 2) a
modeled reflectance based on the bidirectional reflectance distribution (BRD) of a significantly reduced set of observations obtained from different locations around the tower should be more representative of stand level conditions, which is critical, especially if shadow fractions are being modeled in a non-spatially explicit fashion. For a limited time interval (<60 min), stand level $\varepsilon$ (and therefore PRI at a fixed view and sun angle) can be considered constant. During this time interval, multi-directional PRI will change only as a function of $\alpha_s$ (Hall et al., 2008). For any given sun/observer geometry, PRI can be modeled from AMSPEC data as a linear combination of isotropic, geometric and volumetric scattering components (Roujean, 1992):

$$\text{PRI}(\theta_v, \theta_s, \Delta\varphi) = k_i F_i(\theta_v, \theta_s, \Delta\varphi) + k_g F_g(\theta_v, \theta_s, \Delta\varphi) + k_v F_v(\theta_v, \theta_s, \Delta\varphi)$$ (4)

where $\theta_s$ and $\Delta\varphi$ are the view zenith and azimuth angles, respectively; $k_i, k_g$ and $k_v$ are the isotropic, geometric and volumetric scattering coefficients, and $F_i$ and $F_v$ represent the geometric and volumetric scattering kernel functions, respectively.

For the same geometry, $\alpha_s$ can be modeled using the Li–Strahler approach (Li and Strahler, 1985) and $\delta \varepsilon / \delta \alpha$ can be determined. The Li–Strahler model requires inputs of stand density, surface topography and crown geometry, which were available from previous field campaigns (Hilker et al., 2009) and published values (Brown et al., 2010; Chen et al., 2006). Hall et al. (2011) derived the theoretical relationship between PRI' for a range of shadow fractions and relative light use efficiency $\Delta \varepsilon$ (scaled between 0 and 1 with 1 being an unstressed canopy):

$$\Delta \varepsilon = \frac{\max \Delta - \min \Delta}{\max \Delta}$$ (5)

where $\Delta$ is the decrease in reflectance at 531 nm, relative to an unstressed plant canopy ($\min \Delta$). As a result, $\varepsilon$ can be determined from PRI' independently of flux measurements when the maximum light use efficiency ($\varepsilon_{\max}$) is known (Hall et al., 2011). In this study, $\varepsilon_{\max}$ was approximated using the maximum $\varepsilon$ observed during the study period and $\varepsilon$ was calculated as the first derivative of PRI with respect to $\alpha_s$ for each 1 hour interval (note that while $\varepsilon_{\max}$ is scaled using EC data, the functional shape between PRI' and $\varepsilon$ is still independent of EC based estimates, it’s parameters are described in detail in Hall et al. (2011).

GPP_{Amspec} was calculated as hourly mean using spectrally derived $\varepsilon$ and tower-based observations of incident and reflected PAR measured above and below the canopy, leaf area index, and the solar zenith angle ($\theta$) at the time of measurement (Chen, 1996).

3. Results

Fig. 1 shows a panoramic view the selected research sites; the mosaics were observed by Amspec’s webcam (Hilker, Nesic, et al., 2010). In the case of the MacKenzie site, no webcam images were available; instead three photographs (Fig. 1E) illustrate the progressive decline of this site during the 2008 mountain pine beetle infestation (Hilker et al., 2009). The figure illustrates the structural and phenological differences of the selected research sites. Despite large differences in structure, and variation in background reflectance, $\varepsilon$ was successfully
described by PRI using the same relationship (Hall et al., 2011) across all examined vegetation types (Fig. 2). The largest range of $\varepsilon$ values was found at DF49 and SOA, whereas the mountain pine beetle affected Kennedy Siding and Crooked River sites showed consistently low $\varepsilon$ values throughout the observation period. Light-use efficiency was notably higher at the harvested Summit Lake site, due to the much lower $f_{\text{PAR}}$ resulting from a low leaf area (Fig. 1).

Fig. 3 shows the new respiration estimates obtained from GPP$_{\text{Amspec}}$ – NEP$_{\text{EC}}$ (R$_{\text{Amspec}}$) in relation to air and soil temperature as well as canopy photosynthesis. R$_{\text{Amspec}}$ was non-linearly related to $T_{\text{air}}$ (Fig. 3A), and $T_{\text{s}}$ (Fig. 3B). The figure shows that R$_{\text{Amspec}}$ was relatively insensitive to temperature changes below 10 °C but sensitivity increased exponentially to a maximum R$_{\text{Amspec}}$ of about 35 $\mu$mol $m^{-2}$ s$^{-1}$ for $T = 25$ °C. Similar patterns were also observed for the relationship between R$_{\text{Amspec}}$ and GPP$_{\text{Amspec}}$ (Fig. 3C): R$_{\text{Amspec}}$ was mostly insensitive to GPP$_{\text{Amspec}}$ below 10 $\mu$mol $m^{-2}$ s$^{-1}$ but showed a sharp non-linear increase thereafter. By definition, the difference between the observations and the 1:1 line shown in Fig. 3 is NEP acquired from the eddy covariance measurements. In cases where the observation point is close to the line, at low or high levels, little or no carbon is accumulated. The carbon uptake during periods when GPP$_{\text{Amspec}}$ was low was mostly balanced by a minimum required respiration component; however, when GPP$_{\text{Amspec}}$ was high, R$_{\text{Amspec}}$ increased exponentially, thereby also eliminating the effect of the enhanced carbon uptake.

Fig. 4 presents the dependence of REC and R$_{\text{Amspec}}$ on $T_{\text{s}}$ and GPP$_{\text{Amspec}}$ across all 5 sites. The solid surface describes the Amspec derived respiration (R$_{\text{Amspec}}$), the semi-transparent surface shows the corresponding value for REC. As could be expected, both estimates were dependent on $T_{\text{s}}$ and GPP$_{\text{Amspec}}$. The relationship between R$_{\text{Amspec}}$ and $T_{\text{s}}$ was non-linear. The shape of the relationship between R$_{\text{Amspec}}$ on $T_{\text{s}}$ and GPP$_{\text{Amspec}}$ was similar across all sites, however, the magnitude of the respiration component varied considerably and ranged from 4 $\mu$mol $m^{-2}$ s$^{-1}$ at the Summit Lake site to more than 20 $\mu$mol $m^{-2}$ s$^{-1}$ at the highly productive DF-49 site.

A comparison between the diurnal variations in REC and R$_{\text{Amspec}}$ is illustrated in Fig. 5A–E. We are also plotting variations in rel. humidity, soil temperature and PAR for comparison. To minimize the effects of varying day length over time, all data is presented as hourly averaged observations acquired over a 30-day period between June and July. REC is a direct function of $T_{\text{s}}$, resulting in low REC values in the mornings and high values later in the day. Nonetheless, the variation in REC was relatively small, especially at the DF-49 site, at which the soil is sheltered from direct sunlight by a dense canopy. Amspec estimates of GPP and therefore R$_{\text{Amspec}}$ followed the pattern of $T_{\text{air}}$ more closely, lagging PAR by up to several hours. This lag was most pronounced at the site with the highest biomass (DF49 site) and least pronounced at the partially harvested (Summit Lake) site. Diurnal variations R$_{\text{Amspec}}$ were substantially higher than EC-derived respiration fluxes (REC). Across all sites, the correspondence between hourly REC and R$_{\text{Amspec}}$ was significant but moderate in strength ($R^2 = 0.39 p < 0.01$), as a result of the differences in diurnal dynamics.

The differences in dynamics of daytime respiration can also be seen in Fig. 6, which illustrates diurnal variations in GPP$_{\text{Amspec}}$ and R$_{\text{Amspec}}$ for a day with high and low temperatures, respectively (here for the DF-49 site). Fig. 6A shows a warm summer day with high $T_{\text{air}}$, but low NEP. During this day, R$_{\text{Amspec}}$ followed GPP$_{\text{Amspec}}$ closely in the morning and dominated carbon fluxes in the afternoon, thereby reducing the overall amount of carbon accumulated. Fig. 6B shows a day with low NEP and low temperatures. During this day, R$_{\text{Amspec}}$ did not lag GPP$_{\text{Amspec}}$ and low NEP simply resulted from the small difference found between GPP$_{\text{Amspec}}$ and R$_{\text{Amspec}}$. The patterns were also similar for days with high NEP (Fig. 6C and D): In a situation where air
temperature was relatively high, a lag was observed between GPP_{Amspec} and R_{Amspec} (Fig. 6C), whereas GPP_{Amspec} and R_{Amspec} peaked at the same time of day, when the temperature was relatively low.

4. Discussion

This study introduced an alternative approach for estimating daytime ecosystem respiration by combining optical remote sensing (of GPP) and flux-tower measurements of NEP. Our findings are based on previous theoretical (Hall et al., 2008, 2011) and experimental work (Hilker, Gitelson, Coops, Hall, & Black, 2011; Hilker, Gitelson, et al., 2011; Hilker, Nesic, et al., 2010), in which we have demonstrated that multi-angle spectral observations can be used to robustly infer photosynthetic light-use efficiency (\(\varepsilon\)), GPP (Hall et al., 2011; Hilker, Hall, et al., 2010) and heat fluxes (Hilker et al., 2013). These findings are confirmed by results presented in Fig. 2, which demonstrate PRI' as indicator of \(\varepsilon\), despite the considerable differences in vegetation structure, phenology and physiology observed at the selected sites (Fig. 1).

Measurements of daytime respiration are not currently possible in the presence of photosynthesis and as a result, direct validation of estimates from both the \(Q_{10}\) extrapolated night-time observations and the approach introduced in this paper is difficult. Confidence in AMSPEC derived GPP estimates independently of EC-measured CO2 fluxes may be obtained from the link between latent heat fluxes (\(\lambda E\))...
and GPP via the Ball–Berry relationship (Collatz, Ball, Grivet, & Berry, 1991). For instance Hilker et al. (2013) showed a strong correlation between λE modeled from AMSPEC derived GPP and the difference between net radiation (Rn), soil heat fluxes (G) and sensible heat fluxes (H) across the same sites as presented in this study. The work also showed good agreement with direct measurements of turbulent energy fluxes. While these results provide experimental confidence in AMSPEC-based estimates of GPP, it is acknowledged that a direct quantification of uncertainties in R is not currently possible due to a lack of independent observations.

The higher variability of R found in this study is supported by a number of independent measurements of respiration components, for instance from soil chambers (Gaumont-Guay et al., 2006). Aboveground respiration is closely linked to photosynthesis, as increased GPP will also require an increased ecosystem metabolism and maintenance respiration, which should result in a larger autotrophic respiration component (Jassal et al., 2007, Fig. 3). When GPP is small, the minimum respiration required for the basic ecosystem metabolism will consume most of the carbon accumulated by photosynthesis (Fig. 3C). While respiration is relatively low for an intermediate level of GPP, R will increase exponentially with GPP. Consequently, higher GPP does not necessarily result in higher NEP, because an increased metabolism may consume most of the energy produced. This finding also provides an additional rationale for down-regulation of the photosynthetic apparatus (Demmig-Adams & Adams, 1996), as pacing the photosynthetic machinery to an intermediate level will help optimizing the NEP output. For the DF-49 site, our results suggest that the optimum net carbon accumulation is at an intermediate GPP rate of ≈ 20 μmol m⁻² s⁻¹. Minimum respiration rates should vary with living biomass, as lower biomass systems should also result in lower respiration costs to maintain the ecosystem metabolism.

An important finding of Fig. 5 is the considerably larger diurnal range of R_Amspec compared to R_EC, which suggests higher daytime fluxes of GPP and R and therefore a greater potential for changes in these fluxes with changes in climate and forest degradation. These results are consistent with previous reports of underestimation of daytime carbon fluxes (Gaumont-Guay et al., 2006; Hermle, Lavigne, Bernier, Bergeron, & Paré, 2010) and suggest that soil temperature alone may not always adequately reflect diurnal fluxes of plant respiration. This interpretation is supported by the significant, but relatively weak relationship between R_Amspec and T_s (Fig. 3B), which suggests that on a daily timescale, dynamics in R_Amspec may largely be driven by GPP (which in turn is dominated by PAR) and T_Air, at least in areas where daytime fluxes are dominated by autotrophic respiration component.

This study has demonstrated that nighttime independent estimates of daytime respiration could provide considerable insights in ecosystem carbon fluxes and help solve some of the most pressing issues of vegetation carbon feedbacks and ecosystem resilience to climate change. A constellation of remote sensing and EC-flux measurements could therefore be a vital approach to address these questions as it allows independent yet complementary measurements of different aspects of the carbon (Hilker et al., 2008) and energy (Hilker et al., 2013) cycle. A major limitation to (any) respiration estimates is its validation at stand level scales. While current difficulties in verifying the components of ecosystem fluxes are certainly acknowledged, progress may be made through combination of branch level optical sensors (Garrity, Vierling, & Bickford, 2010) and chamber measurements. Further uncertainties include mismatches in measurement footprints (Hilker et al., 2008), productivity losses resulting from photorespiration (Ogren, 1984) and the non-linear character of the PRI' ε relationship diminishing measurement sensitivity at high ε levels.
Nonetheless, given the potential of multi-angular optical measurements not only for the determination of GPP and R, but also for canopy biochemistry and leaf pigments (Hilker, Coops, et al., 2011; Hilker, Gitelson, et al., 2011) and heat fluxes (Hilker et al., 2013), AmSpec-like systems could be a vital part of a standard instrumentation of tower-based scientific networks (Baldocchi, 2003; Papale & Valentini, 2003) and other terrestrial ecosystem research. Such observations could complement existing EC-flux measurements by providing linkages between observed fluxes and changes in plant biochemistry as observed from spectral data. While this would require upgrading of existing instrumentation, it would provide additional evidence independent of the current measurement standards and also provide unique opportunities for scaling stand level observations to satellite data.

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