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Remote sensing of photosynthetic-light-use efficiency of a Siberian boreal forest

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ABSTRACT

The relationship between a physiological index called the photochemical reflectance index (PRI) and photosynthetic light-use-efficiency (LUE) of a Siberian boreal forest during the winter–spring transition, or green-up period, was investigated in 2000. During this time the photosynthetic apparatus was considered under stress as a result of extremes of temperature (from −20 to 35 °C) coupled with a high radiation load. Reflectance measurements of four stands were made from a helicopter-mounted spectroradiometer and PRI was calculated from these data. Eddy covariance towers were operating at the four stands and offered a means to calculate LUE. A significant linear relationship was apparent between PRI, calculated from the helicopter spectral data, and LUE, calculated from the eddy covariance data, for the four sites sampled. Reflectance measurements were also made of a Scots pine stand from the eddy covariance tower. Needles were also sampled during the time of spectral data acquisition for xanthophyll pigment determination. Strong linear relationships were observed among PRI, the epoxidation state of the xanthophyll cycle (EPS) and LUE over the green-up period and the diurnal cycle at the canopy scale.

1. Introduction

Elucidating the role of terrestrial ecosystems in the global carbon cycle and understanding short- and long-term dynamics is a matter of high practical and scientific importance. Tackling such an issue requires the collection of data at spatial scales ranging from the local (forest stand) to global. Remote sensing offers a powerful and non-invasive tool which is capable of sampling over this range of scales.

Remote sensing of photosynthesis to date has made heavy use of the Normalised Difference Vegetation Index (NDVI) (Goward et al., 1994; Gamon et al., 1995). Fundamentally NDVI is related to the leafiness of the canopy and saturates when the ground is fully covered by leaves. NDVI does not probe the physiological processes of photosynthesis, which can change from hour to hour and from day to day. There is thus a pressing need to explore and utilise other methods that are sensitive to changes in the photosynthetic process itself.

The reflectance spectrum of leaves contains a physiological signal that is directly related to photosynthetic light-use efficiency (LUE) (Gamon et al., 1992, 1997; Nichol et al., 2000). This signal arises from a close coupling between photosystem II (PSII) and the photoprotective pigments of the xanthophyll cycle. When leaves absorb more light than they can use in photosynthesis, the xanthophyll cycle pigment violaxanthin is converted into related forms antheraxanthin and zeaxanthin. The excess light is then safely dissipated as heat by transfer to zeaxanthin, causing the efficiency

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of photosynthesis to decrease (Demmig-Adams and Adams, 1992; Gilmore and Yamamoto, 1993; Pfundel and Bilger, 1994; Demmig-Adams et al., 1996; Osmond et al., 1999; Niyogi., 1999). As a consequence of this conversion of the xanthophyll cycle pigments, the reflectance around 531 nm is measurably changed and thus is a sensitive optical indicator of changing photosynthetic efficiency (Gamon et al., 1992; Penuelas et al., 1995; Fillela et al., 1996; Gamon et al., 1997; Nichol et al., 2000). To allow for variations in reflectance arising from other optical effects, the 531 nm reflectance signal has been expressed relative to a reference wavelength by means of a normalised difference index called the Photochemical Reflectance Index or PRI. PRI has been shown to be strongly correlated with leaf-scale and small-plot-scale photosynthetic LUE (Penuelas et al., 1995; Fillela et al., 1996; Gamon et al., 1997). The functionality of this index remains to be tested over further canopies in a number of other ecosystems that may be subject to a variety of stress factors.

Conifers must endure severe stress in the form of sub-zero temperatures combined with high photon flux densities, especially in early Spring. Under these conditions photosynthetic consumption of excitation energy is blocked but leaves must retain their capacity to photosynthesise when favourable conditions return. This combination of high light and low temperatures causes severe inhibition of photochemical efficiency of PSII (Martin et al., 1978). Extreme photoinhibition at sub-zero temperatures during winter and early spring is well documented for conifers growing in the field (Öquist and Ögren, 1985; Hallgren et al., 1990; Ottander and Öquist, 1991; Ottander et al., 1995).

This study addresses the utility of PRI as an indicator of LUE in four contrasting Siberian boreal forest canopies. It specifically focuses on the transition from late winter into spring and summer when the canopy moves from severe photoinhibition to full photosynthesis.

Extensive canopy spectral reflectance measurements were thus made over the late winter/spring period from a helicopter platform. Eddy covariance systems measured the gas exchange over four Siberian sites continuously during May–June 2000. These data provided the opportunity to investigate the relationship between PRI and LUE when the forest was making the transition from winter dormancy to the physiologically active state during this period.

2. Materials and methods

2.1. Site characteristics

The sites are located on the east and west sides of the Yenisei river in Siberia near Zotino (60°44′N, 89° 09′E). Vegetation types within the area were subjects of an ongoing field experiment into the carbon balance of the region and are outlined here.

Scots Pine stand. The *Pinus sylvestris* L (Scots pine) stand lies about 40 km west of the Yenisei river (60°45′N, 89°23′E, elevation 90 m) at the eastern edge of the west Siberian lowland. The mean canopy height is 16 m. The forest occurs on alluvial sand dunes surrounded by sphagnum peat bogs and river meanders. The canopy is open with a leaf area index (LAI) of 1.5. The pine canopy has been described in detail by Wirth et al. (1999), where the stand is identified as "200_{ld}." Understorey characteristics are described by Shibistova et al. (2002).

Bog. The bog lies 30 km west of the Yenisei river (60°45′N, 89°23′E, elevation 80 m) at the eastern edge of the west Siberian lowland. The surface vegetation is located in distinct hummocks and hollows. The vegetation is described in detail by Kurbatova et al. (2002).

Mixed stand. The mixed stand lies on the east side of the Yenisei river on loam to clay-rich soil (61°87′N, 89°47′E, elevation 160 m). The terrain is essentially flat with a mix of *Abies siberica* (Siberian fir), *Picea abies* (Norway spruce), *Pinus siberica* (Siberian pine), *Sorbus aucuparia* (Rowan) and *Betel pendula* (Silver birch). Canopy height is approximately 22 m. The LAI was measured using an LAI-2000 plant canopy analyser (LICOR, Lincoln NE, USA) on 5 May and 25 June, and was estimated at 2.3 and 3.3, respectively. The site is described in detail by Röser et al. (2002).

Pole stand. The pole stand lies on the east side of the Yenisei river on loam to clay-rich soil (61°87′N, 89°46E, elevation 150 m). The terrain is essentially flat with mainly *Abies siberica* (Siberian fir), and intermittent *Picea abies* (Norway spruce) and *Pinus siberica* (Siberian pine). The mean canopy height is 22 m. The canopy LAI was 1.87, 2.97 and 2.85 on 5 and 10 May and 25 June, respectively. The site is described in detail by Röser et al. (2002).

2.2. Canopy spectral reflectance data

Helicopter measurements. A portable spectroradiometer (GER-1500, Geophysical & Environmental

Table 1. *Summary of the dates and reflectance data acquisition with the range of temperature and solar radiation experienced during the observation period*[a]

Site	Instrument	Obs date	Temp. range	PPFD range	SZA	Azimuth
Scots pine	GER-1500	05/05/00	6.37–6.67	1450–1456	44	169
		13/05/00	9.96–10.40	1415–1450	42	167
		14/06/00	24.70–24.75	1546–1549	39	153
		15/05/00	–	–	50	115
		15/05/00	–	–	38	193
Mixed	GER-1500	05/05/00	6.07–6.12	1430–1467	44	174
		13/05/00	5.9–6.2	1219–1303	42	181
		14/06/00	24.02–24.28	1565–1577	38	163
		15/06/00	26.09–27.06	1344–1433	48	120
		15/06/00	28.55–29.24	1421–1385	38	199
Pole	GER-1500	05/05/00	6.85–7.04	1332–1339	44	183
		13/05/00	5.9–6.2	1219–1303	42	181
		14/06/00	24.28–24.33	1561–1577	38	166
		15/06/00	27.06–27.79	1433–1529	47	124
		15/06/00	28.59–29.24	1385–1391	39	202
Bog	GER-1500	13/05/00	10.15–10.6	1309–1402	42	189
		14/06/00	25.3–25.50	1549–1554	39	157
		15/06/00	–	–	49	117
		15/06/00	–	–	38	195

[a]Measurements were made around midday ±2 h of solar noon. Missing data points indicated with a dash. SZA is the solar zenith angle in degrees. Solar azimuth angle is also given in degrees. "Obs" date is observation date and temperature range is in °C. The PPFD range is in μmol m^{-2} s^{-1}.

Research Corp., Milbrook, NY) was flown on a helicopter with the fibre optic probe mounted at nadir orientation on a steel mount through a hatch in the bottom of the helicopter. A twin axis spirit level was fixed to the mount as a visual level to aid manoeuvres during measurement. The fibre optic had a 23° instantaneous field of view (IFOV) and yielded a ground resolution of 122 m at the 300 m altitude. The GER-1500 has a useable spectral range from 350 to 1050 nm, with data being reported in 512 spectral bands.

Data were acquired on clear cloud-free days whilst the helicopter hovered at each site for 1–2 min for each observation (Table 1). Reflectances were calculated by normalising the canopy radiance by the radiance of a 99% calibrated reflectance standard (Spectralon, Labsphere, North Sutton, NH) measured immediately before each flight. Measurements were made around ±2 h of solar noon (consisting of an average of 32 scans). Observations were made from 5 May to 15 June, when the canopy moved from negligible photosynthesis (the winter condition) to full photosynthesis. Spectral calibration procedures were performed before and after the field season to check for changes in sensor response.

Tower spectral measurements. Measurements of the reflectance spectra of the Scots pine forest canopy were acquired from the north, south, east and west sides of the tower. The same open-ended fibre optic probe used in the helicopter measurements was attached to the GER-1500 and positioned at the top of the tower (26 m, 8 m above the canopy) at an angle of 45° to the normal so as to minimise the sensor "seeing" the flux tower. This yielded a (elliptical) spatial resolution of about 27 m. An average of four spectral scans using this configuration was made for each measurement. Diurnal measurements were made on clear cloud-free days or when there was cloud below 20° on the horizon.

PRI from the GER-1500 data was formulated as follows:

$$\mathrm{PRI} = (R_{570} - R_{530})/(R_{570} + R_{530})$$

where R_{570} (the reference waveband) and R_{530} (the xanthophyll waveband) are the reflectances in the spectral bands 570 and 530 nm, respectively. This differs slightly (by 1 nm) from that used in previous studies, but still lies within the range of wavelengths acceptable for the calculation of PRI (Gamon et al., 1993)

To follow the development of the canopy "greening up" from winter into spring, a (broadband) normalised difference vegetation index (NVDI) was also calculated from the helicopter data. To evaluate this change in greenness, an AVHRR-equivalent NDVI is defined as:

$$\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{VIS})/(\mathrm{NIR} + \mathrm{VIS})$$

where NIR is the reflectance in the wavebands of the near-infrared and VIS is the reflectance in the visible wavebands. This vegetation index is typically employed with AVHRR observations. The AVHRR equivalent VIS and NIR were derived from the spectra by averaging across appropriate wavelengths. The VIS AVHRR channel is computed from spectral data between 580 and 680 nm. The NIR AVHRR channel is computed from spectral data between 725 and 900 nm (described in Goward et al., 1994). The spectral data acquired by the GER-1500 were averaged to these waveband intervals, and NDVI calculated. This approach was taken to facilitate a later comparison with actual AVHRR computed NDVI values for the region.

2.3. Eddy covariance measurements of fluxes

Half-hour fluxes of momentum, sensible heat, water vapour and carbon dioxide (and meteorological variables) were measured continuously at all four sites using tower-mounted eddy covariance systems operated by scientists from the Max-Planck Institute for Biogeochemistry in Jena and Institute of Forest in Krasnoyarsk. Full details of instrument set-up and theory are presented elsewhere (Arneth et al., 2002; Lloyd et al., 2002; Röser et al., 2002). At the Scots pine site, a second eddy covariance system was set up on the forest floor. Half-hour average fluxes of under canopy momentum, sensible heat, water vapour and carbon dioxide were measured continuously (Shibistova et al., 2002).

2.4. Estimates of stand photosynthesis

Mixed stand, pole stand and bog. The CO_2 flux was partitioned into photosynthesis and respiration by estimating daytime ecosystem respiration as functions of air temperature. Following the procedure described in Nichol et al. (2000) night-time windy ($u^* > 0.2$) CO_2 fluxes were plotted against air temperature and an exponential function fitted:

$$A = c\mathrm{e}^{bT_\mathrm{s}}$$

where A is carbon dioxide flux, T_s is soil temperature, c and b are constants and e is the base of the natural logarithm. Daytime ecosystem respiration was then calculated using this function and daytime air temperatures. This was done for each month's flux data for May and June for the bog, mixed and pole stands.

Scots pine stand. For the Scots pine stand, the ground eddy covariance system provided continuous data on soil respiration. Estimates of canopy photosynthesis were made as the daytime half-hour CO_2 fluxes after the respiration component had been removed.

Light-use efficiency (LUE). Half-hourly values of canopy photosynthesis and incident PPFD were averaged during the period of the helicopter overflight for all four sites (which was between 1230 and 1430 h). Therefore, photosynthesis and PPFD were averaged for this period, and an average canopy LUE was computed from these averages generating a midday average LUE value. This was calculated as follows:

$$\text{Canopy light use efficiency} = \frac{\text{Canopy photosynthesis}\left(\mu\text{mol CO}_2\ \text{m}^{-2}\ \text{s}^{-1}\right)}{\text{Incident PPFD}\ (\mu\text{mol photons}\ \text{m}^{-1}\ \text{s}^{-1})}$$

2.5. Xanthophyll cycle pigments

Top canopy needles of Scots pine (*Picea sitchensis*) were sampled for xanthophyll pigment analysis. Using a shotgun, top branches in full sunlight were removed from three trees. One year old needles were selected and ground in liquid nitrogen using a mortar and pestle and then immediately transferred to liquid nitrogen. The samples were then freeze dried and stored in the dark at $-20\ ^\circ$C. The growth of new needles in Scots pine began around the beginning of May and terminated at the end of June. The samples were analysed for pigment concentrations at the Research School of Biological Sciences, Australian National University.

Pigments were extracted in acetone with a mortar and pestle. The separation and quantification were by HPLC (Gilmore and Yamamoto, 1991). Relative concentrations of violaxanthin (V), antheraxanthin (A) and zeaxanthin (Z) were used to calculate the epoxidation state (EPS) of the xanthophyll cycle after Thayer and Bjorkman (1990) as

$$\mathrm{EPS} = (\mathrm{Z} + \mathrm{A})/(\mathrm{V} + \mathrm{A} + \mathrm{Z}).$$

The samples collected for pigment analysis were taken at the same time spectral data were being collected from the top of the tower.

3. Results

3.1. Seasonal variation in landscape scale LUE – a helicopter study

All spectra exhibited the typical characteristics of vegetated canopies with the characteristic peak in the visible, with the sharp increase into the near infrared at 700 nm (Fig. 1). Decreasing PRI_{HELI} from the onset of snowmelt was apparent at all four sites (Fig. 2). These changes in PRI_{HELI} were mirrored in the calculated values of canopy light use, LUE, which showed an inverse relationship to PRI_{HELI}. An increase in canopy LUE was observed in all four canopies from 5 May to 14 June (Fig. 2). $NDVI_{HELI}$ (hereafter "canopy greenness") increased from 5 May to a plateau in June (Fig. 3).

Top canopy PRI_{HELI} was moderately correlated with canopy LUE ($R^2 = 0.50, p < 0.01$) when the data from the four sites were combined (Fig. 4, bold line). However, the Scots pine stand in particular exhibited a flat response between PRI_{HELI} and LUE, with PRI_{HELI} varying by only 0.01 for a change in LUE of 0.003 mol CO_2 per mol PPFD. Collating the PRI:LUE data set from the Canadian boreal forest with the data from the Siberian boreal forest indicated two separate relationships (Fig. 4, dashed line). The LUE values for the Siberian stands decreased within the same range as the LUE values in Canada but had lower values of PRI. A significant difference also existed between the two regression lines ($p = 0.01$).

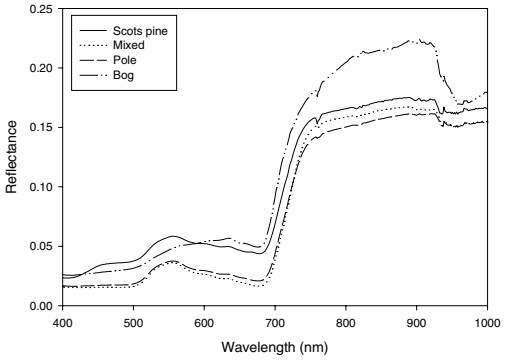

Fig. 1. Mean reflectance spectra of four Siberian boreal forest canopies acquired on 14 June by a helicopter-mounted spectroradiometer (GER-1500). Each curve is the mean of 32 spectral scans.

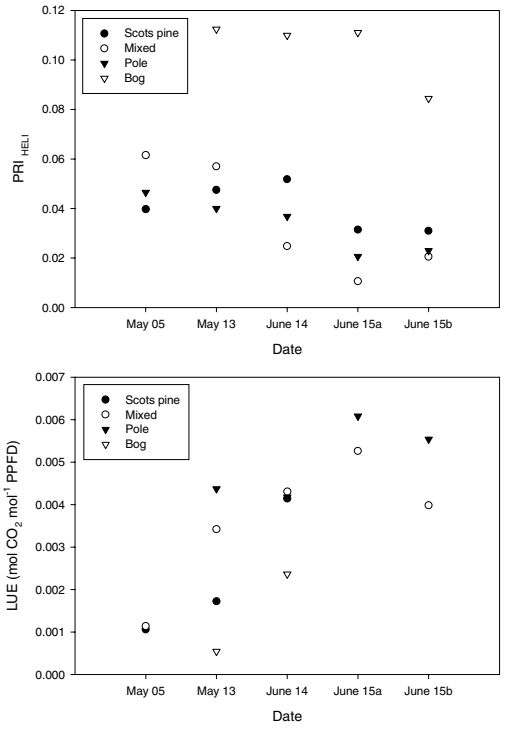

Fig. 2. Trend in PRI during the winter–spring transition in four Siberian boreal forest canopies and canopy LUE over the same period. Missing points denote missing CO_2 flux data. June 15a represents measurements at 11am and June 15b represents measurements at 2.30pm.

The relationship between canopy LUE and $NDVI_{HELI}$ is shown in Fig. 5, where a significant relationship is apparent between these two variables ($R^2 = 0.64, p < 0.001$).

3.2. Seasonal change in Scots pine LUE and xanthophyll cycle pigments – a tower study

Needles sampled in full sunlight on the 15 April, when temperatures were around -10 °C, showed a maximal value of $(Z + A)/(V + A + Z)$ of 0.993 (Fig. 6). By the beginning of May, the relative quantities of xanthophyll cycle pigments in the de-epoxidised state fell from 0.916 to 0.698 on 13 May. This decrease was paralleled by a steady increase in

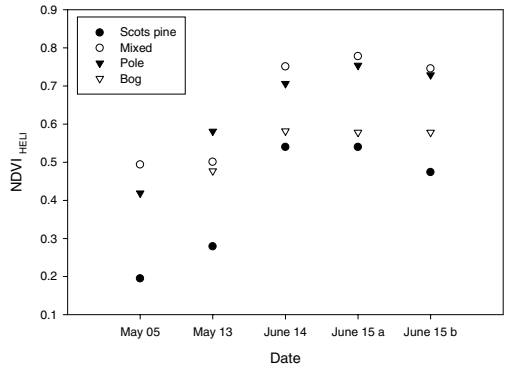

Fig. 3. Seasonal change in the NDVI for four Siberian boreal forest canopies. June 15a represents measurements at 11am and June 15b represents measurements at 2.30pm.

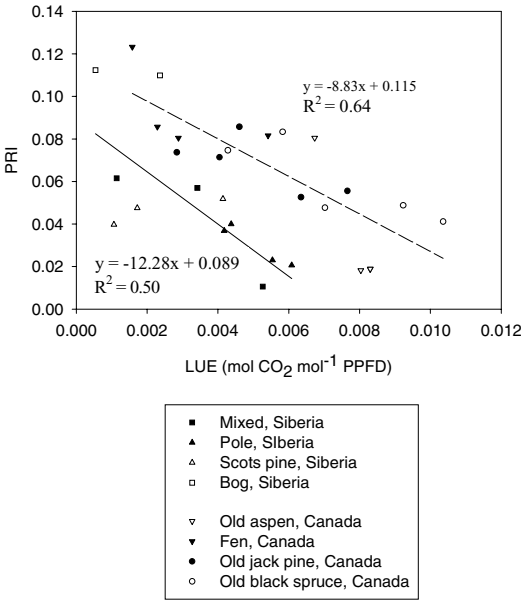

Fig. 4. Relationship between PRI and LUE in four Siberian boreal forest canopies sampled in full sun (dark line), Each point is the average of 32 spectral scans and 3 h of eddy covariance data. Relationship between PRI and LUE in Canadian boreal forest (dashed line). Each point is an average of 20–25 spectral scans and 4 h of eddy covariance data.

canopy LUE (Fig. 6B), with the relation between the two being linear and significant (Fig. 6C, $R^2 = 0.64$, $p < 0.05$). A plot of the relationship between PRI and $(Z + A)/(V + A + Z)$ showed an underlying positive relationship (Fig. 7).

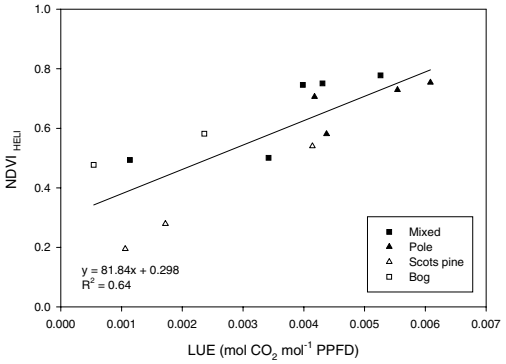

Fig. 5. Relationship between NDVI and LUE in four Siberian boreal forest canopies sampled in full sun. Each point is the average of 32 spectral scans and 3 h of eddy covariance data.

3.3. Diurnal change in Scots pine PRI and LUE

Photosynthesis increased with incident PPFD until noon and subsequently declined with a decreasing LUE (Fig. 8). LUE continued to fall as the ratio of photosynthesis to PPFD decreased through the afternoon. PRI_{TOWER} again followed an inverse relationship to LUE. The relationship between PRI_{TOWER} and LUE over the diurnal cycle was linear and highly significant ($R^2 = 0.97$, $p < 0.001$).

4. Discussion

4.1. Seasonal responses of PRI, LUE and NDVI

The results presented here are the second application of PRI to measurements of photosynthetic light use efficiency of boreal forest. The first study by Nichol et al. (2000) focused on a boreal forest canopy in Canada and demonstrated that PRI, also measured from a helicopter platform, correlated well with estimates of LUE from eddy covariance measurements. The PRI was also recently examined in boreal forest in a study by Rahman et al. (2001). Strong relationships between modelled photosynthesis (based on PRI and NDVI) and actual carbon fluxes across multiple BOREAS tower sites were also obtained.

The study takes a further step by focusing on boreal forest in Siberia during a critical period where the climate, forest structure and understorey were changing rapidly during spring. Previous studies have shown that the xanthophyll cycle works at its highest

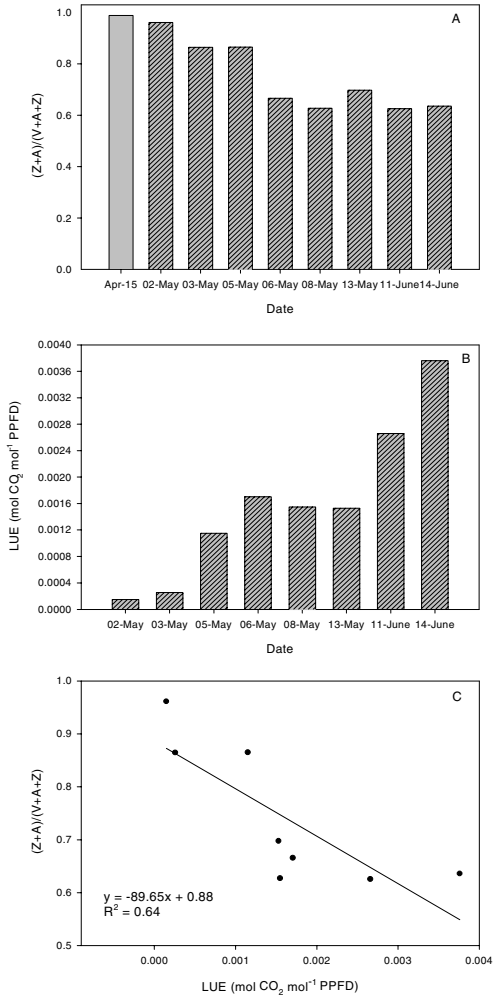

Fig. 6. The seasonal change in (A) the epoxidation state of the xanthophyll cycle $(Z + A)/(V + A + Z)$ (measured from one year old needles) (B) photosynthetic light-use-efficiency (LUE) and (C) the relationship between the epoxidation state and LUE during the winter spring transition in a Siberian Scots pine forest canopy. Each LUE value is calculated from a half-hour value of PPFD and CO_2 flux data.

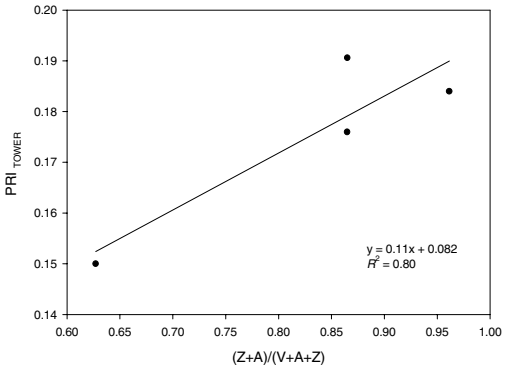

Fig. 7. Relationship between the epoxidation of the xanthophyll cycle $(Z + A)/(V + A + Z)$ and the PRI calculated from tower measurements of Scots pine spectral reflectance. Each point is an average of four spectral scans. Each LUE value is calculated from a half-hour value of PPFD and CO_2 flux data.

capacity during winter dormancy in evergreen species, including conifers (Ottander and Öquist, 1991; Adams et al., 1994; Ottander et al., 1995; Verhoeven et al., 1996; Vogg et al., 1998; Verhoeven et al., 1999). During this time cellular structure changes dramatically and the xanthophyll cycle remains almost entirely in its de-epoxidised state (i.e. with maximum quantities of zeaxanthin) to dissipate all of the absorbed energy as heat. The winter sample taken of the needles at the Scots pine site (Apr-15, Fig. 7) supports this point. The value of $(Z + A)/(V + A + Z)$ was 0.99, which is the highest value recorded for epoxidation of the xanthophyll cycle (Osmond, personal communication). Further winter samples were taken by Ensminger et al. (2001) during the winter/spring period in Siberia during 2001, and similar high values of EPS were also recorded. Ottander et al. (1995) reported winter values of 0.1 in *Pinus sylvestris* [EPS expressed as $(0.5A + V)/(V + A + Z)$], demonstrating that the xanthophyll cycle was maintaining very high concentrations of zeaxanthin. Adams et al. (1994) also studied the winter dynamics of the xanthophyll cycle in overwintering leaves of *Pinus ponderosa*, and reported EPS values of around 0.9, indicating major photoprotection and energy dissipation. Such high (or low) values of EPS have also been found in other conifer species during the winter (Verhoeven et al., 1996; Verhoeven et al., 1999).

The rapid change in PRI_{HELI}, LUE and $NDVI_{HELI}$ measured from the helicopter (Figs. 2 and 3) and tower PRI_{TOWER}, LUE and $(Z + A)/(V + A + Z)$ of the Scots pine stand (Figs. 6 and 7) showed the four sites emerging from winter dormancy. The main stimulus for recovery during post-dormancy is a combination of temperature and water status, and in stands of Scots pine such recovery typically occurs during April–May (Ottander and Oquist, 1991; Ottander et al., 1995). As long as the water supply in the soil is frozen and unavailable, no active reaction centres of PS II are found

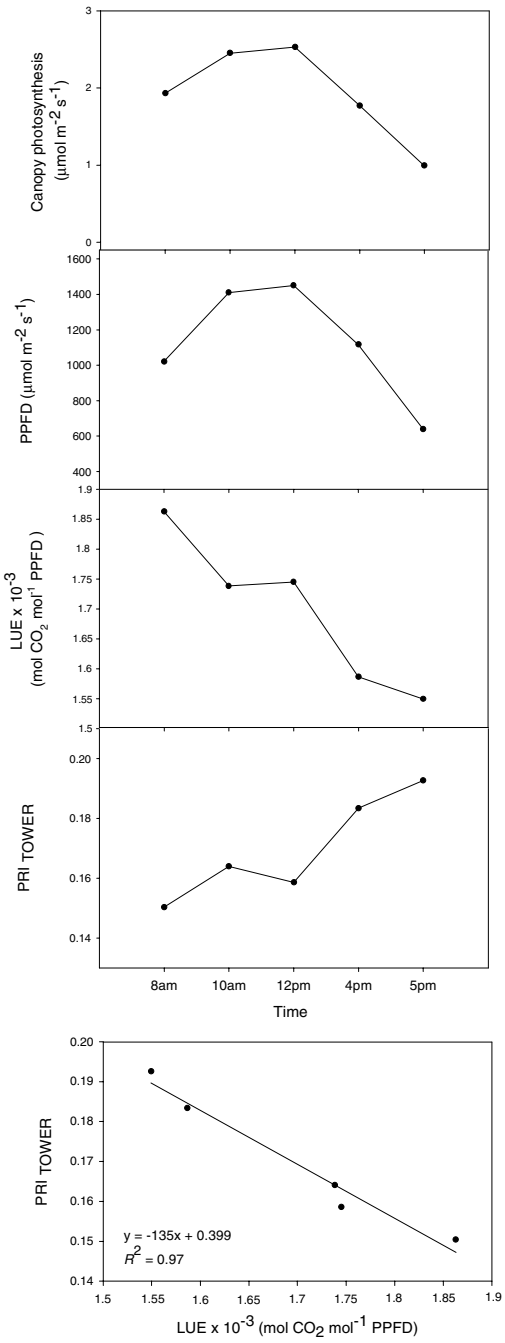

Fig. 8. Diurnal light response of canopy photosynthesis, incident PPFD, LUE and PRI of a Scots pine canopy. Each spectral measurement is an average of four spectral scans with each LUE value being calculated from a half-hour value of PPFD and CO_2 flux data.

in Scots pine (Tsel'niker and Chetverikov, 1988). Although favourable temperatures can stimulate the recovery of spring gas exchange, strong solar radiation at this time continues to promote daytime photoinhibition, which would explain why the changes in $(Z + A)/(V + A + Z)$ are not dramatic and still high over this period. Part of this slow recovery is probably also due to the de novo synthesis of photosynthetic pigments and damaged proteins of PS II (Greer et al., 1986).

Although NDVI increased rapidly in the sites studied here, the growth of the new year's needles was not complete until the end of June, and thus cannot explain the trend in "greenness." The increase in concentration of chlorophyll in current year needles is also slow, as mentioned, typically beginning in March and reaching a maximum in June (Ottander et al., 1995). Therefore the increase in $NDVI_{HELI}$ is probably attributed to slowly increasing green leaf area and melting of snow underneath the canopies also probably being important.

In agreement with the findings from Nichol et al. (2000) a linear relationship between PRI_{HELI} and LUE was also apparent for the four sites studied here, although the strength of the relationship was clearly weaker.

4.2. Canadian and Siberian boreal forest PRI and LUE

When the results from the boreal forests were collated, the slope of the relationship between PRI and LUE was different (Fig. 4). Although the actual range of LUE values between Canada and Siberia (for the same time of year) were similar their corresponding values of PRI were very different. This is likely to be the result of a combination of factors. Of the canopies studied in Siberia, one (Scots pine) was relatively open with a bright understorey whose spectral characteristics were markedly different to that of the overstorey. Viewed from above the scene was a mixture of green canopy (with relatively low LAI) and a bright understorey of lichen. The results showed that the scene PRI was closer to that of lichen than green vegetation (data not shown). The bog, whilst dominant in green mosses and shrubs (flowering was absent), was still flooded in places and had high reflectance in the visible, with almost no difference in reflectance between the two wavebands. Thus the response of PRI to LUE was flat. A more detailed examination of the influence of stand structure and background reflectance is underway and

is the subject of a separate publication (Nichol et al., in preparation).

A number of factors could have caused the difference between tower and helicopter-measured PRI values. An important consideration for remote sensing is the robustness of a calculated vegetation index to atmospheric perturbation. The influence of the atmosphere on any remotely sensed observation is the result of a delicate balance between aerosol and molecular scattering and absorption by aerosols and atmospheric gases. Molecular scattering and absorption can be accounted for satisfactorily and is given by Rayleigh's formulation (for details see Asrar, 1989). Barton and North (2001) demonstrated in their modelling study that top-of-the-atmosphere PRI differed from top-of-the-canopy PRI when Rayleigh scattering was not corrected for. This may in part explain why the tower-measured PRIs were lower than the helicopter PRI values. However, the look angle differed between the tower and helicopter measurements (nadir for the helicopter and 45° for the tower), which could also explain the differing PRI values between these scales. Firm conclusions cannot be drawn.

Aerosol scattering is the main variable component of the atmospheric effect for dark surfaces (i.e. the visible for vegetation), whilst aerosol absorption is important for bright surfaces (i.e. vegetation in the NIR) (Asrar, 1989). However, knowledge of the surface reflectance and the optical properties of the atmosphere must be known to determine whether the atmospheric aerosols have influenced the spectral measurements.

A further potential source of error which could have contributed to the lack of agreement between Canadian and Siberian datasets may have arisen in the calibration of the spectroradiometers used for collecting the reflectance data. Whilst the equipment set-up and measurement protocol were identical and calibration tests were performed on both instruments during the campaigns, differences in wavelength position between the two instruments cannot be ruled out, as the instruments were not intercalibrated.

4.3. Diurnal variability in Scots pine PRI and LUE

The diurnal measurements made of the Scots pine canopy clearly showed a close tracking of sun angle induced variation in canopy LUE by PRI_{TOWER}. This has also been found on smaller plots (Gamon et al., 1992) and from modelling studies Barton and North (2001). First thing in the morning, incident PPFD is utilised with a higher degree of efficiency. As the sun's zenith increases towards solar noon the intensity increases and the efficiency of photosynthesis decreases, with the de-epoxidised status of the xanthophyll cycle increasing. Thus, a greater proportion of the pool size of $V + A + Z$ remains as zeaxanthin. This is evident from the change in PRI_{TOWER}.

In addition to tracking changing xanthophyll cycle activity itself, PRI may to a degree also be reflecting changes that are occurring in chlorophyll/carotenoid ratios that occur upon winter/spring transition, or with senescence. The correlation between PRI and the chlorophyll/carotenoid ratio (data not shown) was significantly weaker than the relationship between PRI and $(Z + A)/(V + A + Z)$. Firm conclusions cannot be drawn from such a small sample size, and would merit further investigation with a larger data set than the one presented here.

One further consideration comes with the calculation of the LUE term. In this study LUE was calculated using incident rather than absorbed PPFD. It is conceivable therefore that PRI could have been affected to some degree by the changing absorptance, and the resulting PRI–LUE relationship could be driven in part by changing light absorption as the snow melts and as the canopies green due to chlorophyll synthesis and leaf development. Thus some of the PRI–LUE relationship could be attributed to this, and not just to the changing LUE from the canopies emergence from photoinhibition.

5. Summary

This work demonstrated that the helicopter-measured PRI_{HELI} was linearly related to photosynthetic LUE when the data from four Siberian boreal forest canopies were combined, although the relationship was weaker than that found in similar boreal forest canopies in Canada. It is likely that a number of factors, including stand structure, instrument calibration, understorey reflectance features, pigment composition and the atmosphere, all played a role by introducing variation in the observed relationship between PRI_{HELI} and LUE at the canopy scale.

The spectral measurements made of the Scots pine canopy from the tower indicate, however, that a high portion of the PRI signal can be attributed to the changing canopy LUE and proportions of the xanthophyll cycle pigments in the de-epoxidised state over the spring period. This confirms the role of the xanthophyll

cycle in photoprotection, and its measurement using remote sensing.

The work presented here and by Nichol et al. (2000) addresses important questions concerning the remote sensing of physiological processes. The ability to probe directly the processes of photosynthesis using the spectral information at 530 nm will undoubtedly continue to offer possibilities for measuring landscape processes.

However, as the results presented here demonstrate, PRI cannot (yet) be used as a direct predictor of photosynthetic efficiency until a number of confounding issues, including those outlined above, can be resolved. A sound understanding of the factors that influence PRI will also pave the way for refining this index such that its application can span across ecosystems and vegetation types.

The deployment of new hyperspectral satellite sensors will provide data that could be useful for calculating a meaningful PRI at the landscape and larger scales. However, applications at such scales will require careful attention to the above-mentioned confounding. Ultimately, extending small-area techniques to large areas involves a number of challenges that can only be addressed with both theoretical and empirical studies at a range of scales.

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