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Investigating light-use efficiency across a jack pine chronosequence during dry and wet years

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Summary Light-use efficiency (LUE) is the ability of vegetated canopies to use light for photosynthesis. Together with remote sensing estimates of canopy cover and meteorological inputs, LUE provides a physical basis for scaling carbon uptake processes from the stand to the global scale. A better understanding of the factors that control LUE will result in improved global estimates of carbon uptake from the terrestrial biosphere. To examine factors that control variability in LUE in stands of different ages during dry and wet conditions, we measured LUE in a chronosequence of four jack pine stands (recent clearcut (age 1–3), regenerating (age 8–9), immature (age 29–30) and mature (~90 years old)) during one normal (2002), one very dry (2003) and two very wet (2004, 2005) growing seasons in Saskatchewan, Canada. Cumulative CO_2 fluxes decreased significantly at all sites during the drought year of 2003, as did mean LUE. Canopy foliage at the recently regenerating jack pine site increased by 19% between 2002 and 2003. Foliage growth rate was reduced by 6% between 2003 and 2004, and foliage biomass decreased by 6% from 2004 to 2005. Over the four years studied, LUE was greatest at the mature jack pine site and lower, but similar, at the other three sites. Mean growing-season LUE varied with mean soil water content at each site, except at that of the newly regenerating stand where soil water had little influence. Mean daily vapor pressure deficit typically had the greatest influence on variability in LUE at all sites. Diffuse versus direct radiation also had significant but varying effects on LUE in jack pine stands of different ages.

Keywords: climate anomalies, eddy covariance, forest, gross primary production, MODIS, radiation use, remote sensing.

Introduction

Light-use efficiency (LUE; g C MJ^{-1}), defined as the ratio of gross primary production (GPP; g C m^{-2} day^{-1}) to absorbed photosynthetically active radiation (APAR; MJ m^{-2} day^{-1}), describes the ability of vegetation to use light for photosynthesis. Although LUE changes instantly with changes in GPP and radiation, it is typically estimated over averaging periods of 30 min or individual days. Dewar et al. (1998) summarized three generalizations from the literature about ecosystem LUE: (1) LUE is constant during vegetation growth when water supply is non-limiting; (2) the use of carbon for gross photosynthesis (carbon-use efficiency; CUE) is constant across species; and (3) APAR is positively correlated with increased leaf nitrogen. These generalizations enable aggregation of LUE and vegetation productivity (for example, net primary production (NPP) and GPP) from local to global scales by remote-sensing-based land-cover types and ecosystem models (Turner et al. 2002, Running et al. 2004, Drolet et al. 2005).

The eddy-covariance (EC) method provides a direct measurement of net ecosystem exchange (NEE), where –NEE is equal to net ecosystem production (NEP). This can be used to estimate ecosystem respiration (R_e) and GPP, which is needed to calculate LUE. Numerous studies have shown that LUE varies both linearly and nonlinearly with changes in air temperature (T_{air}), vapor pressure deficit (VPD) and soil water content (θ), depending on vegetation type, age and structure (e.g., Turner et al. 2003, Leuning et al. 2005, Schwalm et al. 2006). This indicates that LUE is not a simple function of meteorological driving mechanisms, or species type, and therefore functional convergence among many species is unlikely. Lack of functional convergence of LUE will affect the accuracy of models of vegetation productivity. Further, the use of varying definitions and methods for calculating LUE has led to mixed and non-comparable results in the literature (Gower et al. 1999, Schwalm et al. 2006).

Few studies have examined controls on the variability in LUE in different ages of the same species or during anomalous meteorological conditions. The purpose of our study was to determine how LUE varied in jack pine stands of different ages, under different radiation conditions (cloudy, partly sunny and sunny) and dry and wet periods over up to four years per site. The influences of meteorological driving mechanisms and different methods for estimating LUE, including those used in remote sensing-based models, are also discussed.

Materials and methods

Study sites

A chronosequence of four jack pine (*Pinus banksiana* Lamb.) stands was examined during the growing season (June 1 to September 30) over 4 years (2002 to 2005), where data were available. Stands included a mature jack pine forest of ~90 years of age (OJP) (examined years 2002–2005), an immature jack pine forest (HJP75) (examined years 2004–2005, age 29–30), a rapidly regenerating young jack pine forest (HJP94) (examined years 2002–2003, age 8–9) and a recently clearcut and scarified site with jack pine seedlings (HJP02) (examined years 2003–2005, age 1–3). The jack pine sites are located within 6 km of each other in the lower part of the White Gull watershed (53°54′ N, 104°39′ W, ~490 m a.s.l.), north of Prince Albert, Saskatchewan, Canada. Both OJP and HJP75 were studied extensively during the Boreal Ecosystem–Atmosphere Study (BOREAS) (e.g., Baldocchi et al. 1997*a*, 1997*b*, Gower et al. 1997). During our study, all sites were operating as part of Fluxnet-Canada (Barr et al. 2006, Coursolle et al. 2006), under the Boreal Ecosystem Research and Monitoring Sites (BERMS) project. The BERMS research project concentrates on species and disturbance-induced differences in carbon and water exchanges in the same climatic region (e.g., Barr et al. 2006, Kljun et al. 2006). Individual sites tend to be relatively flat, varying by less than 12 m in elevation (Chasmer et al., unpublished). Soils are sandy, coarse textured and well drained (Baldocchi et al. 1997*b*). Each site has extensive meteorological and CO_2, water and energy flux measuring equipment in accordance with Fluxnet-Canada protocols (www.fluxnet-canada.ca), as well as mensuration information, site characteristics and temporal and high-resolution remote sensing data.

Forest stand characteristics are described in Table 1 (OJP, HJP75 and HJP94), based on measured forest stand data from eight, eight and six forest mensuration plots per site, respectively. At OJP, HJP75 and HJP94, forest mensuration plots were 11.3 m in radius, and were located 100 and 500 m from the EC flux station (OJP and HJP75), and in 250 m at HJP94. Foliage gap fraction estimates were made at individual plots during diffuse conditions in May and August 2005 by digital hemispherical photography (DHP) set to two F-stops below default exposure (Zhang et al. 2005). The DHP system was set at five photographs (four photographs each at a distance of 11.3 m from the center photograph) per plot. The gap fraction estimates were converted to leaf area index (LAI) by the thresholding method of Leblanc et al. (2005). The LAI was adjusted to account for site-specific canopy clumping, woody:total area ratios and needle:shoot area ratios (Chen et al. 2006). Estimates of LAI were slightly lower than those of Chen et al. (2006) at OJP, although comparisons with effective LAI were almost the same, indicating possible differences in allometric woody:total and needle:shoot area ratios used. Differences in DHP-estimated LAI may also be associated with instrumentation, heterogeneity in leaf area and structural variability throughout the site. Table 2 contains mensuration information from four 2-m-wide × 25-m-long transects of 1 m^2 plots (50 plots per transect) measured in late May 2005 at HJP02.

During the study (2002–2005), there were large differences in yearly cumulative precipitation, providing a unique opportunity to study LUE over a range of soil water (i.e., dry to wet) contents. Figure 1 illustrates cumulative precipitation measured at OJP from 2001 to 2005. The year 2001 is included because drought occurred during and before 2001 and lasted until 2003, leading to significant water shortages for periods of greater than one year (e.g., Kljun et al. 2006).

Site instrumentation

Site instrumentation has been discussed by Coursolle et al. (2006), Kljun et al. (2006) and Barr et al. (2006). Briefly, the EC method was used at all sites throughout the growing season to measure CO_2 fluxes averaged over 30-min periods. Net ecosystem production ($\mu mol\ m^{-2}\ s^{-1}$) was measured by the EC system where NEP = –NEE ($\mu mol\ m^{-2}\ s^{-1}$). Positive NEP indicates that CO_2 from the atmosphere was used for photosyn-

Table 1. Mean vegetation characteristics at OJP, HJP75 and HJP94 for 22 plots. The values in parenthesis are standard deviations (SD). Abbreviations: *n*, number of trees sampled; DBH, tree bole diameter at breast height (1.3 m above ground); and LAI, leaf area index.

Site	*n*	Stem density (stems m^{-2})	Tree height (m)	DBH (cm)	LAI[1]	Canopy depth (m)	Crown diameter (m)	Other species
OJP	381	0.11 (0.001)	14.2 (3.5)	9.33 (4.55)	1.6 (0.1)	8.3 (2.7)	2.0 (1.0)	Alder, bearberry, reindeer lichen, blueberry, cranberry
HJP75	1447	0.59 (0.19)	6.3 (1.6)	5.69 (3.49)	2.8 (0.42)	3.5 (1.3)	0.9 (0.4)	Grasses, reindeer lichen, bearberry
HJP94	2081	0.86 (0.56)	1.6 (0.7)	2.31 (1.05)	1.1 (0.2)	1.6 (0.7)	0.7 (1.1)	Grass, blueberry, alder, raspberry, bearberry, reindeer lichen

[1] LAI measurements from Chen et al. (2006) differ from LAI observed in our study.

Table 2. Mean vegetation characteristics at HJP02 for 200 plots (each 1 × 1 m) along four transects. Mean percent cover does not add up to 100% (averaged between four transects) because some plots have more or less of individual cover types. Values in parentheses are standard deviations (SD). Abbreviations: *n*, number of trees (in 200 1 m^2 plots); and LAI, leaf area index.

n	Tree height (m)	Tree cover (%)	Grass cover (%)	Reindeer lichen cover (%)	Soil cover (%)	Wood debris cover (%)	Herb cover (%)	Estimated LAI
37	0.19 (0.12)	9 (11)	21 (18)	23 (30)	32 (18)	26 (24)	8 (15)	0.29

thesis, whereas negative NEP indicates that the site was releasing more CO_2 into the atmosphere than it was using for photosynthesis. Each site has undergone the same measurement and data processing protocol whereby daily R_e (μmol m^{-2} s^{-1}) was modeled based on the relationship between nighttime R_e and soil temperature (Barr et al. 2004). Gross primary production (GPP; μmol m^{-2} s^{-1}), defined as the uptake of CO_2 by the ecosystem through photosynthesis, was estimated from measured NEP and modeled R_e: GPP = NEP + R_e. We measured CO_2, H_2O and friction velocity with a sonic anemometer (CSAT3, Campbell Scientific, at OJP and HJP02; Gill R3-50, Gill Instruments, at HJP75; SAT-550, Kaijo, at HJP94) combined with a closed-path infrared gas analyzer (LI 6262, Li-Cor) (Barr et al. 2006). The EC systems have been installed above the canopy at heights of about 28, 17, 3 and 2 m above the ground surface at OJP, HJP75, HJP94 and HJP02, respectively. The 30-min mean CO_2 fluxes were determined from 20, 20, 10 and 20 Hz measurements at the OJP, HJP75, HJP94 and HJP02 by block averaging. Any gaps in the 30-min fluxes were filled by a moving-window regression approach (Barr et al. 2006, Kljun et al. 2006). Because of inherent problems with the EC technique (e.g., Massman and Lee 2002), data were quality controlled based on a minimal surface friction velocity of 0.35 m s^{-1}. Inaccuracies in R_e and GPP may exist in this analysis; however, averaging over 30 min minimizes the influence of errors in the data. Further processing of EC data is discussed in Kljun et al. (2006) and Barr et al. (2006).

Light-use efficiency was determined for daytime periods, defined as the period when incoming above-canopy shortwave radiation exceeded 1.0 W m^{-2}. Net radiation (R_n) was measured with a four-component net radiometer (W m^{-2}) (CNR1, Kipp and Zonen), and was used with above-canopy PAR to estimate variations in foliage growth at HJP94 and HJP02 (discussed below). Above- and below-canopy PAR (μmol m^{-2} s^{-1}) was converted to MJ m^{-2} per 30 min and per day based on a conversion of 0.25 and adjusted for daytime minutes. We measured PAR with a Li-Cor Model LI190 at OJP and HJP75 and an Eko Model ML-020P (Eko Instruments) at HJP94 and HJP02. Above-canopy incident and reflected PAR sensors were installed on booms at heights of 28, 17, 3 and 2 m above the ground at OJP, HJP75, HJP94 and HJP02, respectively. Below-canopy incident PAR measurements were made at OJP and HJP75 at a height of ~1 m. Below-canopy PAR measurements were unavailable for HJP94 or HJP02.

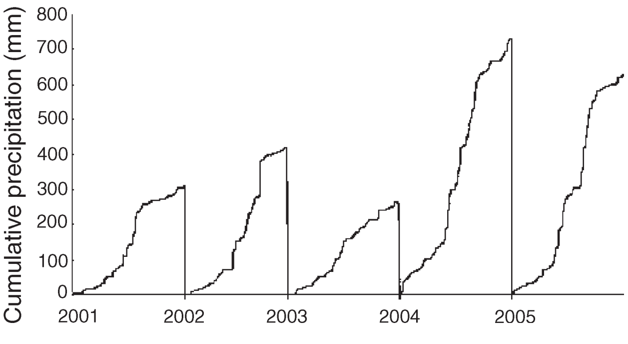

Figure 1. Cumulative precipitation measured at OJP for 2001–2005 illustrating dry (i.e., 2001 and 2003) and wet years (i.e., 2004 through 2005). Year 2002 may be considered normal because the cumulative precipitation approximated the 30-year mean annual cumulative precipitation (~450 mm) measured by Environment Canada at a nearby weather station (Waskesiu, Saskatchewan).

We related meteorological driving mechanisms to LUE to determine their interaction at each sites. Mean daily T_{air} and VPD were derived from measurements made with top-of-canopy air temperature and relative humidity sensors (Model HMP45C, Vaisala). At each location, θ (m^3 m^{-3}) was measured at depths of 0–15, 1–30, 30–60, 60–90, 90–120 and 120–150 cm with soil moisture probes (CS615, Campbell Scientific). Soil temperature was measured with soil temperature probes (CS107b, Campbell Scientific) placed at depths of 2, 5, 10, 20, 50 and 100 cm in the soil column.

Calculation of light-use efficiency

We calculated APAR, which was used in the estimation of LUE, as:

$$\mathrm{APAR} = (\mathrm{PAR}_{\mathrm{AC}\downarrow} - \mathrm{PAR}_{\mathrm{AC}\uparrow}) - (\mathrm{PAR}_{\mathrm{BC}\downarrow} - \mathrm{PAR}_{\mathrm{BC}\uparrow}) \quad (1)$$

where $\mathrm{PAR}_{\mathrm{AC}\downarrow}$ is above-canopy incoming PAR, $\mathrm{PAR}_{\mathrm{AC}\uparrow}$ is above-canopy reflected PAR, $\mathrm{PAR}_{\mathrm{BC}\downarrow}$ is incoming below-canopy PAR after interception with branches and leaves, and $\mathrm{PAR}_{\mathrm{BC}\uparrow}$ is the reflected PAR from the ground surface (Gower et al. 1999). Because $\mathrm{PAR}_{\mathrm{BC}\uparrow}$ was not measured at any of our sites, it was omitted from the estimation of APAR. Reflected ground surface PAR albedo ($\mathrm{PAR}_{\mathrm{BC}\uparrow}$) is 6% at OJP and HJP75 (Chen 1996), and contributed little to the reduction in APAR at these sites.

There was only one PAR sensor measuring $\mathrm{PAR}_{\mathrm{BC}\downarrow}$ at OJP and HJP75. Each sensor was compared with 40 DHPs per site at distances of 100 and 500 m from each tower to assess the representiveness of the OJP and HJP75 $\mathrm{PAR}_{\mathrm{BC}\downarrow}$ sensors. The mean fraction of PAR absorbed by the canopy (fPAR) measured by the PAR sensors was 0.61 (OJP) and 0.70 (HJP75) in 2005. Mean fPAR from DHP was 0.54 (SD = 0.06) (OJP) and

0.55 (SD = 0.06) (HJP75). Green fPAR estimates of Chen et al. (2006) in 2005 were 0.49 (OJP) and 0.54 (HJP75) with TRAC (fractional cover was not provided). Results of Chen et al. (2006) were slightly lower than our estimates of fractional cover because Chen et al. (2006) removed the fraction of wood observed by the sensor as well as $PAR_{AC\uparrow}$ and $PAR_{BC\uparrow}$. Mean difference between DHP and PAR sensors at OJP was 11%, and at HJP75 it was 21%, indicating the $PAR_{BC\downarrow}$ sensors at OJP and HJP75 may have been located in areas with slightly more foliage than the average for the rest of the stand. The DHP methods are also prone to measurement errors and have been found to underestimate gap fraction by 8%, on average, at a number of sites when compared with other optical methods (Chen et al. 2006). Despite slight overestimation of fPAR by PAR sensors at HJP75, fPAR estimates were reasonable approximations of DHP measurements throughout the stand.

Because $PAR_{BC\downarrow}$ was not directly measured at HJP94 and HJP02, it was modeled for these sites based on Beer's Law:

$$\mathrm{APAR} = \alpha_s \, \mathrm{PAR}_{\mathrm{AC}\downarrow}(1 - e^{-k\,\mathrm{LAI}}) \qquad (2)$$

where α_s is canopy absorptivity ($1 - PAR_{AC\uparrow}/PAR_{AC\downarrow}$), and k is the extinction coefficient estimated as a constant 0.45 for simplicity (Chen et al. 2006). The LAI likely varies during the growing season and between years at HJP94 and HJP02. Because monthly measurements of LAI were not made at these sites, the normalized difference vegetation index (NDVI) was used at both sites to estimate mean monthly LAI as described by Wilson and Meyers (2007):

$$\mathrm{LAI} = -K \log\left(\frac{\mathrm{NDVI}_{\max} - \mathrm{NDVI}}{\mathrm{NDVI}_{\max} - \mathrm{NDVI}_{\min}}\right) \qquad (3)$$

where $NDVI_{max}$ is the maximum NDVI with dense vegetation, NDVI is measured for each month, $NDVI_{min}$ is the minimum NDVI with no vegetation and K is a scaling constant based on measured LAI (Tables 1 and 2). Mean monthly NDVI values were calculated from 30-min global shortwave radiation and incoming and reflected PAR between 0900 and 1500 h local time. Only data for clear days, when above-canopy incoming shortwave radiation was > 200 W m^{-2}, were included in the averaging procedure. Table 3 provides minimum and maximum NDVI values and estimated LAI minimum and maximum values from 2002 (2003 at HJP02) to 2005.

Beer's Law was used to model APAR at OJP for comparison with measured APAR. Figure 2 provides a comparison between APAR measured with radiation sensors and modeled results from Equation 2 at OJP. High correlations between APAR estimated by Beer's law and measured APAR at OJP indicate that modeled results at HJP94 and HJP02 will be comparable to the results of direct measurement.

Cloudy, partly sunny and sunny days were examined on a daily basis, per growing season, based on the ratio of measured incoming shortwave radiation (K_{in}) to the computed top-of-atmosphere shortwave radiation (K_{TOA}). Top-of-atmosphere incoming shortwave radiation was determined by the clear sky model of Bird and Hulstrom (1991) (http://rredc.nrel.gov/solar/models/clearsky/) adjusted for latitude, longitude and time zone of each site. The influences of solar zenith angle and leaf angle and area were reduced by averaging K_{in}/K_{TOA} between 1000 and 1400 h, local time. Cloudy days were defined as having a daily K_{in}/K_{TOA} between 0 and 0.33, partly sunny days as having a daily K_{in}/K_{TOA} between > 0.33 and 0.66 and sunny days as having a daily K_{in}/K_{TOA} between > 0.66 and 1.0.

Table 3. Values of normalized difference vegetation index (NDVI), leaf area index (LAI) and the scaling constant, K. Mean monthly minimum and maximum estimates are shown based on in situ measured LAI (Tables 1 and 2) during the last year of study (2005).

Site	Year	Summer NDVI		K	LAI	
		Min	Max		Min	Max
HJP02	2003	0.16	0.49	0.9	0.20	0.21
	2004	0.29	0.50	0.9	0.25	0.31
	2005	0.37	0.57	0.9	0.24	0.31
HJP94	2002	0.14	0.56	3.9	0.64	0.73
	2003	0.29	0.57	3.9	0.97	1.07
	2004	0.33	0.59	3.9	1.03	1.14
	2005	0.31	0.56	3.9	1.01	1.06

Statistical analysis

Comparisons were made to determine the influence of site age, radiation and drought versus wet years on LUE by analysis of variance (ANOVA) (Ebdon 1992). We did not use ANOVA to test hypotheses. Least squares (quadratic) regression methods were used to determine the relationships between LUE and

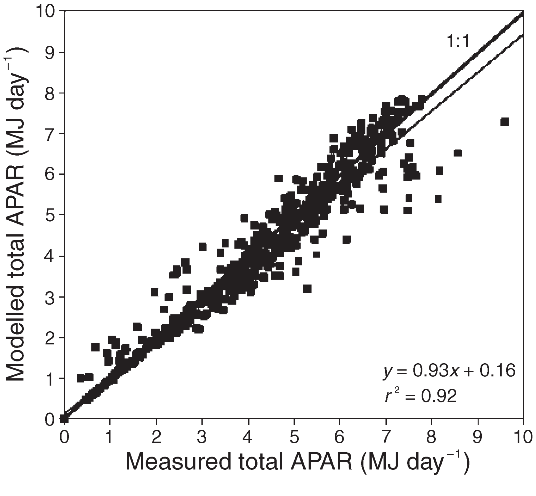

Figure 2. Relationship (thin line) between measured total daytime absorbed photosynthetically active radiation (APAR) and modeled APAR at OJP during the four years of study (n = 488). The relationship tends to follow the 1:1 line for most days, although during about 20 days, the modeled results tend to underestimate measured APAR. Outliers tend to occur near the start and end of the growing seasons each year.

meteorological driving mechanisms.

Results

Influences of dry, normal and wet years on LUE at individual sites

Large differences in meteorological driving mechanisms, CO_2 fluxes, GPP, NEP and R_e were found during dry, normal and wet years and among the sites studied (Table 4). The drought year of 2003 had a strong influence on meteorological conditions measured at each site, resulting in higher mean growing-season APAR, T_{air} and VPD. Mean θ was reduced by up to 40% at all sites. The wet years of 2004 and 2005 had greater than normal cumulative annual precipitation (~760 mm and 640 mm compared with 290 mm in 2003), higher θ, and lower mean growing-season T_{air}, APAR and VPD. The year 2002 had normal amounts of precipitation, and mean meteorology was similar to 2004 and 2005.

Table 4 presents cumulative totals of CO_2 fluxes and mean meteorological conditions during the growing season at each site from 2002 to 2005. Cumulative growing season increases in GPP, NEP and R_e are shown in Figure 3 for each site. Net ecosystem production did not vary greatly at OJP despite large differences in mean θ (varying by as much as 40%). Mean growing season GPP and R_e at OJP decreased from 2002 to 2003 by 9 and 8%, respectively, despite an early peak in GPP from June to early August. This was caused by a warm spring and a leaf flush that was about three weeks earlier than in 2002 (Kljun et al. 2006). Cumulative mid-growing season (July and August 2004) GPP remained low compared with 2002 and 2005 (Figure 3a). Fluxes of R_e decreased by 8% in 2003 and increased slightly in 2004 and 2005. At HJP75, measurements in 2004 and 2005 were similar, although mid-season CO_2 fluxes, GPP and R_e were lower in 2004 than in 2005 (Figure 3b). Comparisons with the drought year were not made at HJP75 because of lack of data. At HJP94 in 2003, mean growing-season GPP decreased by 5% and NEP increased by 12%, in proportion with a significant 17% decrease in R_e. Gross primary production was significantly greater in June and July 2003 than at the same time in 2004, likely because of increased air temperatures and an early spring. By the end of the growing season, NEP was only slightly greater in 2003 than in 2002 at HJP94. Fluxes at HJP02 were not measured in 2002, but became a greater source of CO_2 to the atmosphere from 2003 to 2004. The value of –NEP increased by 14% between 2003 and 2004, GPP increased by 30%, and R_e increased 24%. Increases in GPP by 22% and decreases in R_e by 16% from 2004 to 2005 resulted in a 66% reduction in –NEP.

Did the drought of 2003 reduce the LUE of jack pine stands of different ages? Light-use efficiency was lower at all sites in 2003 (Table 4). Strong correspondence between rising and falling LUE and mean θ per year was observed for most sites except HJP02, where LUE tended to increase over time, regardless of changes in mean θ (Figure 4). Changes in LUE were also a function of changes in mean APAR, especially during the drought year when both APAR and intercepted PAR (IPAR) were greater than during other years, resulting in lower LUE. Absorbed PAR was 11% greater in 2003 than in 2004 at OJP corresponding to a 20% decrease in LUE. Also, APAR was 28% greater at HJP94 in 2003 than in 2002, corresponding to a 29% decrease in LUE. However, at HJP02, APAR was re-

Table 4. Mean growing-season meteorological conditions, annual variability in canopy structure and CO_2 flux totals per site for up to four years of study. Abbreviations: T_{air} = air temperture (°C); VPD = vapor pressure deficit (Pa); T_{soil} = soil temperature (°C); θ = volumetric soil water content ($m^3\ m^{-3}$); fPAR = fraction of photosynthetically active radiation absorbed by the canopy; APAR = absorbed photosynthetically active radiation (MJ day^{-1}); IPAR = intercepted photosynthetically active radiation (MJ day^{-1}); LUE = light-use efficiency (g C MJ^{-1}); GPP = gross primary production (g C m^{-2}); NEP = net ecosystem production (g C m^{-2}); and R_e = ecosystem respiration (g C m^{-2}).

Site	Year	T_{air}	VPD	T_{soil}	θ	fPAR	Total APAR	Total IPAR	LUE APAR	LUE IPAR	Total GPP, Jun to Sep	Total NEP, Jun to Sep	Total R_e, Jun to Sep
OJP	2002	14.95	1.69	12.68	0.10	0.55	4.12	4.47	1.06	1.00	475	166	299
	2003	16.59	1.70	13.02	0.06	0.55	4.23	4.60	0.87	0.82	432	164	274
	2004	14.00	1.22	11.40	0.09	0.55	3.75	4.08	1.09	1.01	450	173	278
	2005	14.95	1.31	12.42	0.09	0.56	3.96	4.29	1.06	0.98	463	184	280
HJP75	2002	–	–	–	–		–	–	–	–	–	–	–
	2003	–	–	–	–		–	–	–	–	–	–	–
	2004	14.10	1.22	12.68	0.13	0.70	3.70	3.50	0.85	0.81	459	195	256
	2005	14.89	2.65	13.68	0.12	0.69	4.05	4.29	0.77	0.75	463	198	259
HJP94	2002	14.98	1.65	14.80	0.08	0.25	2.34	2.51	0.82	0.77	208	45	162
	2003	15.24	1.70	15.26	0.07	0.35	3.27	3.50	0.58	0.54	197	51	135
	2004	–	–	–	–	0.38	–	–	–	–	–	–	–
	2005	–	–	–	–	0.36	–	–	–	–	–	–	–
HJP02	2002	–	–	–	–		–	–	–	–	–	–	–
	2003	16.63	1.66	15.41	0.12	0.08	0.87	0.94	0.72	0.66	45	–51	100
	2004	13.93	1.21	14.19	0.14	0.18	0.94	1.01	0.73	0.68	65	–59	132
	2005	14.39	1.26	13.87	0.11	0.20	0.84	0.92	0.85	0.79	84	–20	111

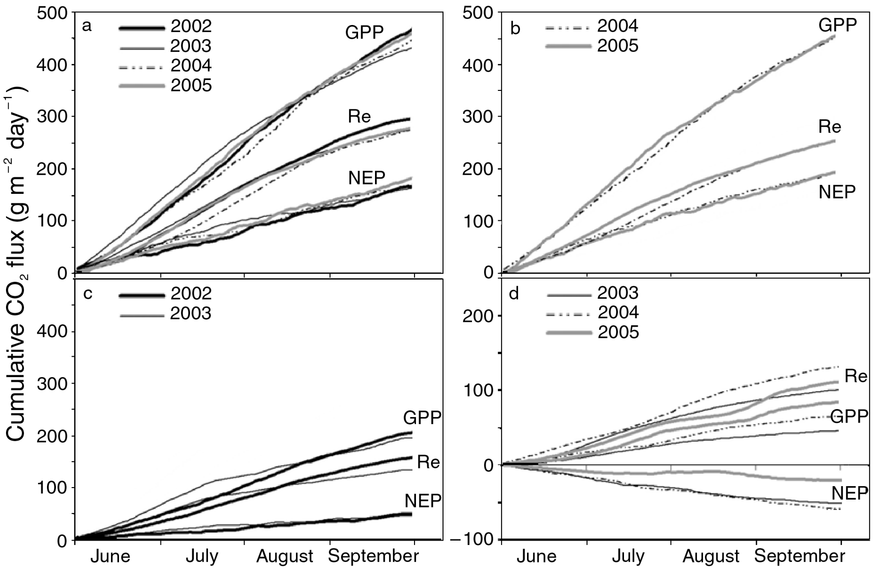

Figure 3. Cumulative growing season CO$_2$ fluxes estimated at (a) OJP, (b) HJP75, (c) HJP94 and (d) HJP02. Early spring temperatures in 2003 tended to increase CO$_2$ fluxes near the beginning of the growing season (June).

duced by only 7% in 2003 compared with 2004.

Comparisons between LUE in 2003 and 2005 were made by single factor ANOVA at OJP and HJP02, HJP75 and HJP94 were not included because of a lack of data for these years. Light-use efficiency was normally distributed in all cases, and variances in LUE in 2003 versus 2005 were similar at OJP. However, at HJP02, LUE varied by 30% between 2003 and 2005. Mean daily LUE varied significantly between the drought of 2003 and the wet period of 2005 at OJP ($P < 0.001$, $F = 11.75$, $F_{\text{critical}} = 3.88$); however, at HJP02, LUE remained relatively constant regardless of dry and wet conditions ($P = 0.27$, $F = 1.23$, $F_{\text{critical}} = 3.91$). A comparison for the years that were studied at HJP75 and HJP94 indicated that LUE at HJP75 decreased slightly with soil water content from 2004 to 2005, as did LUE at HJP94 from 2002 to 2003 (Figure 4).

Canopy structure varied slightly following the drought of 2003 at HJP94, and to some extent at HJP02. The NDVI at HJP94 (Table 4) increased by 19%, on average, from 2002 to 2003, but growth was stunted in 2004, increasing by only 6%. The NDVI decreased by 6% at HJP94 between 2004 and 2005, despite increased mean soil water content, indicating that foliage growth at HJP94 may have had a 1- to 2-year lagged response to the drought in 2003, or may have been negatively affected by lower growing season T_{air}. At HJP02, NDVI increased by 18% between 2003 and 2004, and 16% between 2004 and 2005. Canopy structure did not vary at OJP, and was not measured prior to the drought at HJP75. We did not assess variability in belowground (root) biomass.

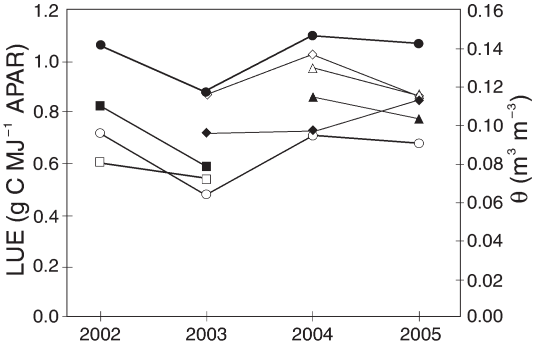

Figure 4. Growing season mean light-use efficiency (LUE; filled symbols) per year and mean volumetric soil water content (θ; open symbols) at each site (OJP: ●, ○; HJP75: ▲, △; HJP94: ■, □; and HJP02: ◆, ◇).

Meteorological influences on GPP and LUE

Meteorological drivers and the amount of solar radiation available for photosynthesis influenced the variability in GPP and LUE per growing-season year and per site (Figure 5). For all years studied, about 50% of the variability in VPD occurred because of changes in T_{air} ($P < 0.001$), whereas T_{air} and VPD had lesser influences on θ at all sites. Also, T_{air} and T_{soil} were autocorrelated ($r^2 = 0.35$, $P < 0.001$). Incoming PAR had the largest influence on GPP at OJP and HJP75 (Figures 5a and 5b), accounting for about (r^2) 28 and 36% ($P < 0.001$) of the variability in carbon uptake over the four years. Total daily GPP increased with total incoming PAR reaching a plateau of about 4.2 g C m^{-2} day^{-1} at 8 MJ of PAR at OJP and did not vary greatly from year to year. Vapor pressure deficit and T_{air} had less influence on GPP at OJP (VPD, $r^2 = 0.21$, $P < 0.001$; T_{air}, $r^2 = 0.14$, $P < 0.01$; Figure 5a). Optimal photosynthesis at OJP occurred at a VPD of 200 Pa and a T_{air} of 18 °C. Similar relationships were found at HJP75, where GPP saturated at about 4 g C m^{-2} day^{-1} but could withstand a higher incoming PAR of 10 MJ, on average. At HJP75, VPD and T_{air} had the greatest influence on GPP (VPD, $r^2 = 0.20$, $P < 0.001$; T_{air}, $r^2 = 0.20$, $P < 0.001$). Optimal rates of photosynthesis occurred at 350 Pa and a T_{air} of 18 °C. Variability in daily θ at OJP and HJP75 was small and did not correlate well with GPP on a daily basis.

Light-use efficiency was strongly affected by meteorologi-

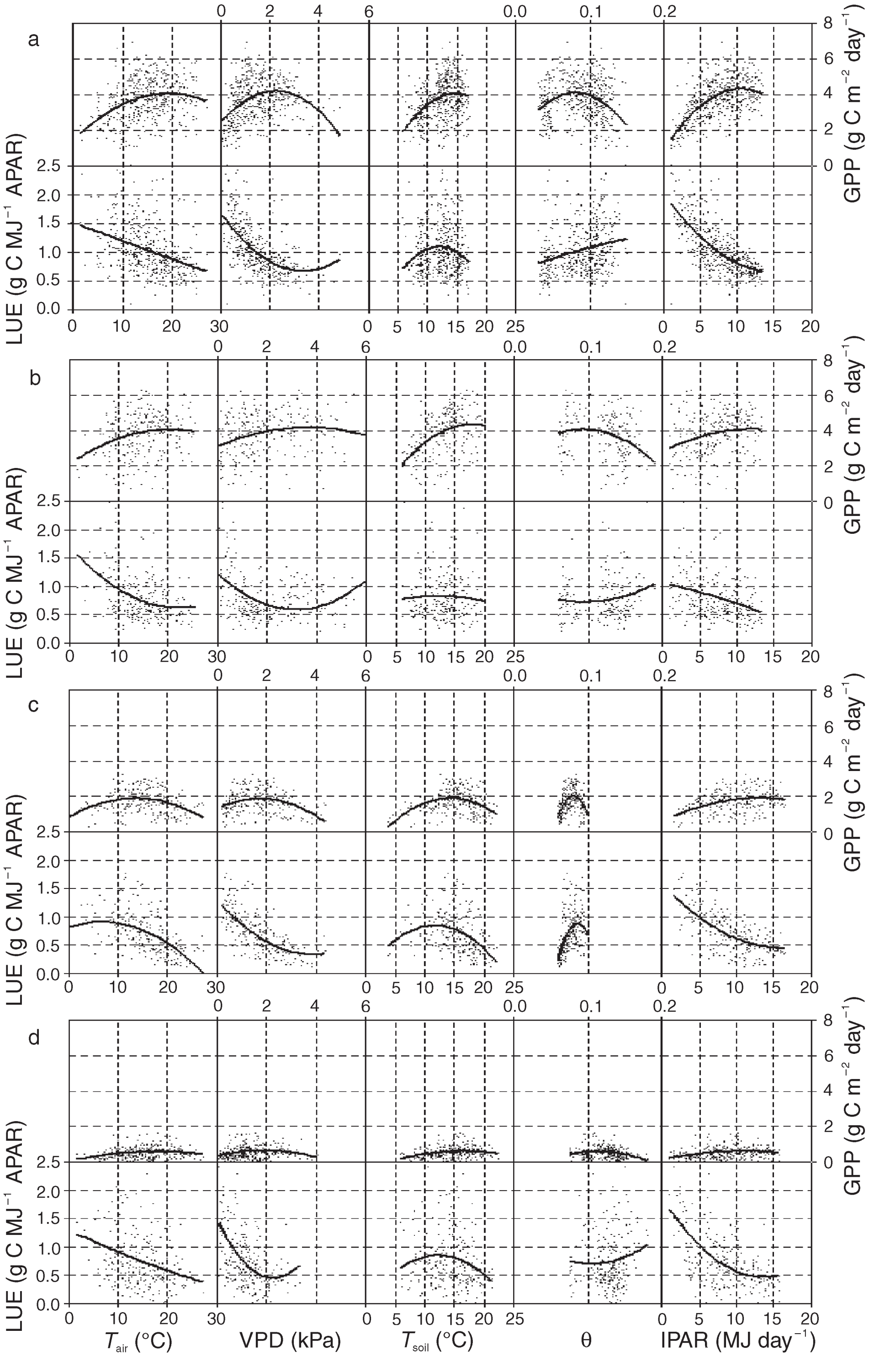

Figure 5. Daily mean meteorological driving mechanism influences on total daily gross primary production (GPP) and mean light-use efficiency (LUE) at (a) OJP and (b) HJP75 for the combined 2002–2005 growing seasons (where data exist). Quadratic regression lines ($y = b_0 + b_1x + b_2x^2$) provide the best fit of the data and illustrate where relationships exist between driving mechanisms and GPP and LUE. Mean daily meteorological driving mechanism influences on total daily GPP and mean LUE at (c) HJP94 and (d) HJP02 for the combined 2002–2005 growing seasons (where data exist). Abbreviations: T_{air} = air temperture; VPD = vapor pressure deficit; T_{soil} = soil temperature; θ = volumetric soil water content; and IPAR = intercepted photosynthetically active radiation.

cal driving mechanisms at OJP and HJP75 (Figure 5). At OJP, LUE decreased to 0.6 g C MJ^{-1} with increasing VPD to a maximum of 400 Pa when examined over all four growing seasons ($r^2 = 0.33$, $P < 0.001$). Light-use efficiency decreased with increasing T_{air} and was positively correlated with changes in θ. At HJP75, LUE was only weakly correlated with daily mean T_{air} ($r^2 = 0.13$, $P < 0.01$) in 2002 and 2003 and decreased at T_{air} greater than 20 °C (Figures 5a and 5b).

In the sites with the two younger stands, HJP94 and HJP02, daily mean meteorological driving mechanisms had no significant effects on GPP (Figure 5c and 5d). Light-use efficiency was strongly influenced by VPD at HJP94 ($r^2 = 0.47$, $P < 0.001$), with LUE decreasing below 0.5 g C MJ^{-1} at VPDs of about 400 Pa. Light-use efficiency was greatest at $T_{air,}$ = 10 °C, but decreased almost linearly above 10 °C. Because T_{air}, and VPD were strongly autocorrelated at HJP94 ($r^2 = 0.68$), relationships between LUE and T_{air} and VPD were similar. At HJP94, T_{soil} and θ had minimal influences on LUE on a daily basis. At HJP02, LUE decreased with increasing VPD ($r^2 = 0.19$, $P < 0.001$) to about 0.5 g C m^{-2} day^{-1} at 350 Pa. Strong controls by VPD at these sites may be associated with the low soil water content and limits to stomatal conductance (cf. Jenkins et al. 2007).

LUE differences between jack pine ages

To determine if the assumption of functional convergence holds over long periods of time and in different ages of trees, we examined daily mean LUE from all growing seasons at all sites simultaneously by multiple-factor ANOVA. Although LUE at each site was normally distributed, all sites had some interdependence, with correlations (r^2) of 0.27 (HJP02), 0.43 (HJP94) and 0.55 (HJP75) when compared with OJP for the entire four-year (growing season only) period. HJP75, HJP94, and HJP02 were more independent, with correlations (r^2) ranging between 0.10 and 0.15. Significant differences in LUE existed between OJP ($P < 0.001$, $F = 48.79$, $F_{\mathrm{critical}} = 2.61$) and sites HJP75, HJP94 and HJP02, whereas differences in LUE between HJP75 and HJP94 were less significant (OJP: $P = 0.07$, $F = 2.71$, $F_{\mathrm{critical}} = 3.01$). Within a site, LUE differed significantly between the drought year of 2003 and the other years examined ($P < 0.001$, $F = 11.75$, $F_{\mathrm{critical}} = 3.88$).

Differences in mean LUE between HJP94 and HJP02, and to a lesser extent, HJP75 were not significant (Figure 6). These results were biased because HJP75 included only the two wet years (2004 and 2005), whereas HJP94 included one normal (2002) and one drought (2003) year. Assuming that LUE is greater during wet years than dry years (as found for OJP), LUE at HJP75 could be biased toward slightly higher values, and HJP94 could be biased toward slightly lower values, which may increase similarity in mean LUE estimates per site.

Influences of radiation on LUE at individual sites

Figure 7 presents box plots of LUE during sunny, partly sunny and cloudy conditions for each site. A multiple-factor ANOVA was used to test differences in age-specific mean daily LUE for up to four growing seasons based on (1) radiation and (2) dry versus wet years (because these are inherent factors in all datasets). Significant differences in LUE were found at each site as a result of varying radiation; however, drought versus wet years did not have a significant effect on the use of diffuse versus direct radiation for photosynthesis. The largest differences in LUE occurred between cloudy and partly sunny conditions, and to a lesser extent partly sunny and sunny conditions at all sites. The differences in LUE between cloudy and partly sunny conditions were greatest at HJP02 ($P < 0.001$, $F = 40.86$, $F_{\mathrm{critical}} = 3.03$) where mean daily LUE during cloudy conditions was 0.55 g C MJ^{-1} APAR greater than during partly sunny conditions. Similar mean LUE differences of 0.49 and 0.47 g C MJ^{-1} APAR were found between cloudy and partly sunny conditions at HJP75 ($P < 0.001$, $F = 62.86$, $F_{\mathrm{critical}} = 3.03$) and OJP ($P < 0.001$, $F = 141.94$, $F_{\mathrm{critical}} = 3.01$). Among sites, the least difference in mean daily LUE (0.39 g C MJ^{-1} APAR) between cloudy and partly sunny conditions was at HJP94 ($P < 0.001$, $F = 58.22$, $F_{\mathrm{critical}} = 3.03$).

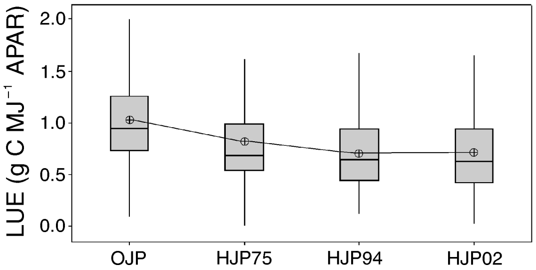

Figure 6. Box plot of mean light-use efficiency (LUE) over four growing seasons (June to September). Circle with cross hairs represents mean LUE, and the central line represents the median LUE. The box includes the 75th and 25th percentiles. The whiskers extend to the maximum and minimum values of LUE.

Small differences in mean LUE were found between partly sunny and sunny conditions. OJP had the greatest difference in mean LUE between partly sunny and sunny conditions (0.25 g C MJ^{-1} APAR). HJP75 and HJP02 had the same difference in mean LUE between partly sunny and sunny conditions (0.19 g C MJ^{-1} APAR), and HJP94 had the smallest difference (0.15 g C MJ^{-1} APAR). These results indicate that site age or canopy structure, or both, exhibit some influence on LUE, although results tend to be confounded. We might expect that the greatest effects of diffuse versus direct radiation would occur at OJP and HJP75 because of a reduction of shadow (e.g., Gu et al. 2002), but it appears that these differences were strongest at the site with the youngest stand.

Comparison of methods for estimating LUE

Examples of four methods for estimating mean growing-season LUE (from daily means) are illustrated for the jack pine sites over four years of study (Figure 8). In the first example (a), APAR is defined as: APAR = ($\mathrm{PAR}_{\mathrm{AC}\downarrow}$ – $\mathrm{PAR}_{\mathrm{AC}\uparrow}$) – ($\mathrm{PAR}_{\mathrm{BC}\downarrow}$) at OJP and HJP75, but was modeled by Beer's Law at HJP94 and HJP02, with the inclusion of $\mathrm{PAR}_{\mathrm{AC}\uparrow}$. In (b), IPAR was estimated as $\mathrm{PAR}_{\mathrm{AC}\downarrow} - \mathrm{PAR}_{\mathrm{BC}\downarrow}$, and was modeled by Beer's Law at HJP94 and HJP02. The example in (c) used incoming shortwave radiation (K_{in}) only at all sites. The LUE example in (d) was used in the MODIS GPP remote sensing context. It incorporates a constant maximum LUE (1.058 g C MJ^{-1} IPAR) determined per classified biome type and is linearly reduced when VPD exceeds 2500 Pa, and T_{air} freezes stomata closed (–8 °C) (Heinsch et al. 2006). Estimates of LUE in (d) are typically driven by meteorology from general circulation model (GCM) reanalysis, but in this case maximum LUE has been reduced with measured T_{air} and VPD at the tower.

The results in Figure 8 illustrate little difference between LUE estimated with APAR (Figure 8a) compared with IPAR (Figure 8b), even as canopies increase in openness. The above-canopy reflected component is about 3 to 7%. Ground-surface PAR albedo was measured by Chen (1996) at OJP and HJP75,

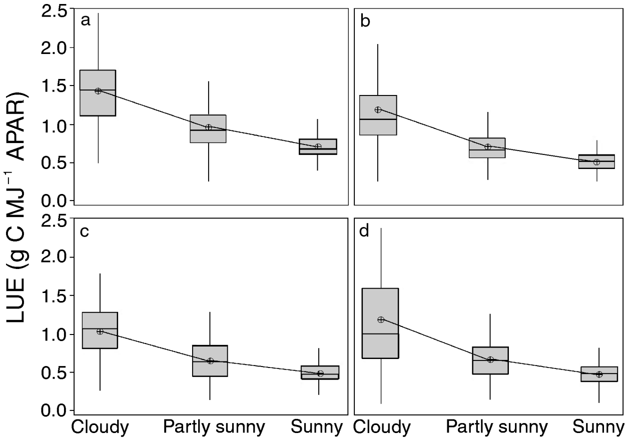

Figure 7. Box plots of mean light-use efficiency (LUE) over four growing seasons (June to September) for (a) OJP, (b) HJP75, (c) HJP94 and (d) HJP02. Each growing season has been divided into cloudy, partly sunny and sunny days. Circle with cross hairs represents mean LUE, and the central line represents the median LUE. The box includes the 75th and 25th percentiles. The whiskers extend to the maximum and minimum values of LUE.

and was about 6% of incoming above-canopy PAR. Inclusion of reflected PAR from the ground surface would increase $\mathrm{LUE}_{\mathrm{APAR}}$ by an additional 6% compared with $\mathrm{LUE}_{\mathrm{IPAR}}$. Use of incoming shortwave radiation only (Figure 8c), without removal of incident radiation below the canopy resulted in an overestimation of light and a strong decrease in LUE at all sites. Shortwave solar radiation is problematic for estimating LUE because much of the near infrared portion of the spectrum is strongly scattered and is not used in photosynthesis (Gower et al. 1999).

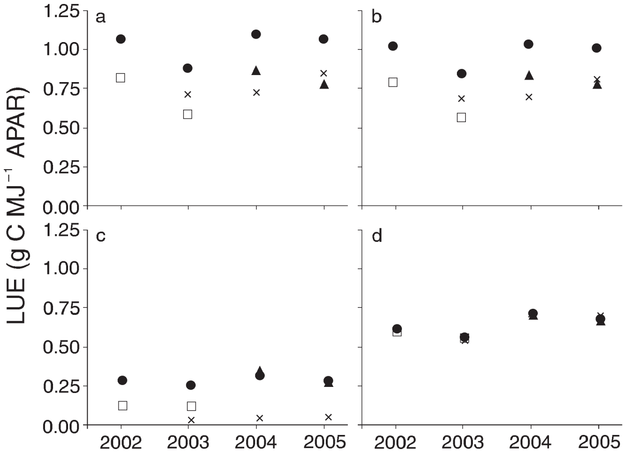

Figure 8. A comparison of four methods commonly used to estimate light-use efficiency (LUE): (a) LUE = GPP/APAR; (b) LUE = GPP/IPAR; (c) LUE = GPP/total intercepted solar radiation; and (d) LUE = 1.058 g C MJ^{-1} IPAR linearly reduced with VPD > 2500 Pa, and $T_{\mathrm{air}} < -8$ °C. Abbreviations: GPP = gross primary production; APAR = absorbed photosynthetically active radiation; IPAR = intercepted photosynthetically active radiation; VPD = vapor pressure deficit; and T_{air} = air temperature. Symbols: ●, OJP; ▲, HJP75; □, HJP94; and ×, HJP02.

The final method (Figure 8d), based on a biome-specific maximum LUE, follows mean growing-season trends in LUE observed at each site. Maximum LUE approximately matches mean LUE of OJP. This includes a reduction in LUE in 2003 followed by increased LUE in 2004 and 2005. Mean growing-season LUE used by MODIS to estimate GPP (with the inclusion of fPAR from MODIS) was underestimated by about 40% (OJP), 15% (HJP75), 14% (HJP94) and 16% (HJP02), on average. MODIS often overestimates fPAR (e.g., Heinsch et al. 2006) which is multiplied by LUE to estimate GPP. Low biome-specific LUE may be used to offset overestimates of fPAR by MODIS when used to calculate global GPP (e.g., Zhao et al. 2005, Heinsch et al. 2006, Turner et al. 2006). Inclusion of varying degrees of diffuse and direct radiation measured on a global basis per day with remote sensing satellites may also improve LUE estimates per biome-type applied to fPAR to estimate cumulative GPP.

Discussion

Dry and wet growing season influences on LUE

Mean LUE per site was about double that estimated by Schwalm et al. (2006) for the growing season of 2004 at the same sites. Schwalm et al. (2006) estimated mean growing-season LUE vaues of 0.5 g C MJ^{-1} APAR (OJP), 0.48 g C MJ^{-1} APAR (HJP75) and 0.11 g C MJ^{-1} APAR (HJP02), where APAR is estimated from measured LAI and the MODIS-based LAI product (HJP02) by Beer's Law. The LAI measurements in Schwalm et al. (2006) were about 25 to 35% greater at OJP and HJP75 and 75% greater at HJP02 compared with values obtained by Chen et al. (2006) and in our study. MODIS typically overestimates LAI at HJP02 because of mixed pixel influences in the site. Overestimates of LAI would result in underestimates of LUE if using a Beer's Law approach. Results of Turner et al. (2003) are similar to ours, where LUE varied from between 0.8 and 1.2 g C MJ^{-1} APAR between June and September at a northern boreal black spruce stand. Green et al. (2003) found that mean annual LUE for a jack pine forest was 0.71 g C MJ^{-1} IPAR, also in the range of results found in this study. Similarly, Lagergren et al. (2005) reported an LUE of 0.71 g C MJ^{-1} IPAR for a mixed conifer forest in Sweden.

We found that variability in LUE can be strongly affected by severe drought and wet years in jack pine of varying ages (Figure 4). Similar results have been reported by Pereira et al. (2007) for Mediterranean ecosystems (oak, eucalypts and grassland) and by Allen et al. (2004) for irrigated and non-irrigated sweetgum and sycamore stands. Pereira et al. (2007) found that drought reduced photosynthesis as a result of seasonal water deficits, and reduced saturation during periods of increased radiation (fewer diffuse radiation days) and T_{air}. They also mention that ground plants with shallow root systems die during droughts, and R_{e} is less affected than carbon uptake. Phillips and Riha (1993) suggest that drought causes increased partitioning of biomass to roots, thereby causing a reduction in LUE in older ecosystems. When GPP and R_e were compared at the jack pine sites during drought and wet years, we found that the magnitude of the reductions in GPP and R_e was dependent on age. For example, at OJP, GPP in 2003 was reduced by 8% and R_e by 7% from 2002 cumulative values. However, in HJP94, GPP was reduced by 5% and R_e by 17% between years 2002 and 2003.

Environmental influences on LUE

The influences of diffuse versus direct radiation had clear but varied influences on LUE at jack pine stands of different ages. Other studies have found that diffuse radiation and the lack of within-canopy shadows significantly increased LUE (e.g., Roderick et al. 2001, Gu et al. 2002, Turner et al. 2003, Still et al. 2004, Schwalm et al. 2006, Jenkins et al. 2007, Pereira et al. 2007). Positive relationships between LUE and increased diffuse versus direct radiation have not been examined in different ages of the same species. Increased LUE occurs during cloudy conditions because more light is scattered and distributed in the canopy (Gu et al. 2002). Direct illumination of the canopy results in saturation of photosynthesis, whereas the remaining portion of the canopy (not saturated by sun flecks) is in shadow and is unable to photosynthesize efficiently (Gu et al. 2002). We have shown that the decrease in LUE between cloudy (diffuse) and partly sunny radiation conditions is greater than between partly sunny and sunny (direct) conditions at jack pine sites of different ages. This result agrees with that of Jenkins et al. (2007) who state that when the ratio of diffuse to total radiation is high, the efficiency of photosynthesis will also be great, and will increase linearly to the point where the sky is diffuse, but bright (before direct sunlight breaks through the clouds). However, as uniform cloud cover decreases and direct radiation increases, LUE will decrease and the photosynthetic rate will peak (Gu et al. 2002, Turner et al. 2003, Schwalm et al. 2006).

The increase in LUE from diffuse to direct light conditions tended to be great at OJP and HJP75, possibly because of slight shadowing in these open and low LAI canopies. The LUE at HJP94 was less influenced by the transition between direct and diffuse radiation than at OJP and HJP75, although light conditions had a significant influence on LUE. The canopy at HJP94 was not fully closed at many parts of the site and trees often had branches extending to the ground. Needles were located on the outer envelope of individual trees. Among sites, HJP02 tended to be most affected by the transition between diffuse and direct light, and had the greatest variability in LUE. In 2005, HJP02 consisted of small jack pine seedlings, alder (*Alnus crispa* Ait.) shrubs and a ground cover of herbs and grasses. Without any shadows, saturation of photosynthesis in combination with increased T_{air} and VPD occurred almost immediately with direct radiation. The linear increase in GPP with APAR was almost non existent (Figure 5d), possibly resulting in the large differences in LUE between cloudy and partly sunny conditions.

Meteorological driving mechanism influences on LUE varied between jack pine sites and ages. Vapor pressure deficit tended to have the greatest influence on LUE at most sites studied but was less important at HJP75. This may be due to increased leaf area, tree density and increased within-canopy shadowing, as well as decreased roughness. Gu et al. (2002) found that VPD and T_{air} tended to have varying influences on vegetation photosynthesis during different radiation conditions, possibly as a result of upper canopy as opposed to lower canopy leaf temperature. For example, during direct radiation, upper leaves may have higher temperatures and may experience greater VPD than lower leaves, which are in shadow. These results corroborate those of Turner et al. (2003) in several biomes, as well as data for a mixed conifer forest (Lagergren et al. 2005) and in several forest types (Gu et al. 2002). The VPD also co-varied with T_{air}, relative humidity and latent energy exchanges, which explained much of the variability in LUE at numerous sites studies by Schwalm et al. (2006). Jenkins et al. (2007) found a lack of correspondence between LUE and VPD and T_{air} at a northern hardwood stand. The influence of VPD or T_{air}, or both, on LUE may become more important in water-limited forests such as the boreal jack pine forests we studied. Mean daily θ had little influence on daily estimates of LUE (except at HJP94, where $r^2 = 0.20$). When averaged over the growing season at each site, θ tended to have a strong influence on the seasonal variability in LUE. Schwalm et al. (2006) found that soil water had a moderate influence on LUE at three mature deciduous sites and two regenerating forests, including HJP02, whereas Kljun et al. (2006) found an almost immediate response of CO_2 fluxes to θ at a mature aspen site.

Remote-sensing-based production efficiency models, would benefit from the inclusion of daily diffuse and direct LUE. Currently, MODIS GPP algorithms estimate 8-day cumulative GPP from mean fPAR multiplied by a maximum LUE term that is adjusted based on a high VPD and low T_{air}. Over our four-year study, 29% of days were cloudy, 50% were partly sunny and 21% were sunny, resulting in large differences in LUE during those days. The use of a mean biome-specific LUE may improve estimates of GPP by either increasing or decreasing LUE relative to the amount of cloud cover and diffuse radiation on a per day basis, and cumulated over the 8-day period.

In conclusion, we examined CO_2 fluxes and LUE over a unique period of drought, normal and wet conditions in a jack pine chronosequence in Saskatchewan, Canada, to determine meteorological and site-specific controls on LUE during years of severe drought and wet conditions. The efficiency with which vegetation uses light may change with increased air temperatures and drying, which may be one outcome of climatic change in the Canadian boreal forest (Kljun et al. 2006). We found that significant differences in LUE occurred at OJP, HJP75 and HJP94 during the drought of 2003, likely because of decreased mean θ. Light-use efficiency was not greatly affected by the transition between drought and wet conditions at HJP02, but NEP varied between years studied. Cumulative CO_2 fluxes (GPP, NEP and R_e) did not vary greatly at OJP between drought and wet years. Despite this, an early spring in 2003 resulted in early leaf flush and increased productivity until midsummer soil drying occurred. Similar variability in fluxes were found at HJP94, where GPP tended to be greater in 2003 during the early part of the growing season, but was reduced compared with other years toward the end of the growing season. Both GPP and R_e tended to be lower at all sites in 2004, perhaps in response to the previous-year drought, as well as lower growing season T_{air}. During 2004, leaf growth rates were significantly reduced at HJP94, and in 2005, leaf foliage cover was less than in 2004, despite typical rapid regeneration at this site. Mean daily VPD had the greatest influence on variability in LUE at all sites, whereas daily θ did not greatly affect LUE. Diffuse versus direct radiation had large but varying influences on LUE at different sites, depending on canopy structural characteristics. Differences between cloudy and partly sunny or sunny conditions were greatest at HJP02, possibly because of almost immediate saturation of GPP with increased PAR. OJP and HJP75 were also subject to large differences in LUE between cloudy and partly sunny conditions, likely because of within-canopy shading. These results suggest that the inclusion of radiation conditions (e.g., diffuse versus direct) in the calculation of LUE would improve remote-sensing estimates of GPP from MODIS.

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