Moisture sensitivity of ecosystem respiration: Comparison of 14 forest ecosystems in the Upper Great Lakes Region, USA

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ABSTRACT

Ecosystem respiration (ER) was measured with the eddy covariance technique in 14 forest ecosystems in the Upper Great Lakes Region during the growing seasons of 2002 and 2003. The response of ER to soil temperature and moisture was analyzed using empirical models. On average, ER was higher in the intermediate and young than in the mature stands, and higher in hardwood than in conifer stands. The seasonal mean temperature-normalized respiration rate (R_{10}) ranged from 1 to 3 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ and seasonal mean activation energy (E_a) from 40 to 110 kJ mol^{-1}. The variation in the residuals of temperature response function of ER was best explained by soil moisture content. ER showed higher temperature sensitivity (as indicated by lower E_a) in the young than in the mature stands of coniferous forests, but not in the hardwood forests. The inclusion of soil moisture as an explicit driver of R_{10} explained an additional 8% (range 0–21%) of variability in ER. Significant moisture sensitivity of ER was detected in only 5 out of 20 site-years and it was associated with bimodal soil moisture distribution. Moisture sensitivity could partially be predicted from statistical moments kurtosis and interquartile range. The data implied greater moisture sensitivity with increasing stand age, possibly due to faster depletion of soil water supplies from a greater evaporative surface in the older stands. Additional limiting factors to ER were implicated.

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1. Introduction

Ecosystem carbon balance is determined by the fluxes of assimilation (gross ecosystem productivity, GEP) and respiration (ecosystem respiration, ER). Recent efforts in Europe and the Americas have addressed the balance between these two fluxes (Janssens et al., 2001; Saleska et al., 2003; Valentini et al., 2000) and it is not completely clear which component is more important in determining the net balance. Some European studies (Pilegaard et al., 2001; Valentini et al., 2000) as well as our own work (Noormets et al., 2007) found that ER explained more of the site differences than did GEP, which was relatively constant across site latitudes. This conclusion has, however, been challenged by several studies conducted in North America, where the view of ''near-constant GEP'' did not hold (Arain et al., 2002; Barr et al., 2002; Griffis et al., 2003). In order to reliably quantify the sizes of terrestrial carbon pools and assess their changes, we must understand the mechanisms that govern GEP and ER that operate on those pools. This is particularly important in North America where forests have been implicated in playing a key role in the global carbon cycle (Ciais et al., 1995; Houghton et al., 2001).

Accurate assessment of ER remains difficult because it represents a sum of a number of sub-components, which can be classified by either organismal group (e.g. plants, fungi, bacteria, macrofauna; these are often grouped to auto- and heterotrophic classes, based on the carbon source) or metabolic function at the organismal level (Thornley and Cannell, 2000). Since soil respiration (SR) makes up at least 50% of ER in our study area (Bolstad et al., 2004; Noormets et al., 2007), one might expect that factors affecting SR also have significant influence on ER. It is well established for SR that soil temperature and moisture are confounding factors and their effects on SR are often impossible to separate conclusively (Chambers et al., 2004; Davidson et al., 1998). The component fluxes of both SR and ER have differing seasonal and diurnal variability, with stem and mineral soil respiration being relatively constant throughout the active growing period (Widen and Majdi, 2001), whereas leaf, root and litter respiration have more pronounced diurnal and seasonal patterns (Baldocchi et al., 1997; Griffin et al., 2002; Hanson et al., 1993; Lavigne et al., 1997).

In eddy covariance studies, ER is most often scaled as a temperature-dependent variable by fitting a universal model for the entire growing season (Goulden et al., 1997). Yet, studies of SR in seasonally dry ecosystems (Joffre et al., 2003; Reichstein et al., 2002a; Valentini et al., 1996) have shown that SR may be limited by either temperature or moisture availability, depending on the season and phenological stage. In comparison, little is known of the effect of moisture in temperate and boreal mesic ecosystems. Influenced by observations that temperature sensitivity of SR is lower at high than at low temperature (reviewed by Fang and Moncrieff (2001) and Lloyd and Taylor (1994)), models attributing the phenomenon to moisture availability have won wide support. A recent study by Reichstein et al. (2002b) presented a model with temperature sensitivity parameter, Q_{10}, explicitly defined as a linearly decreasing function of soil volumetric moisture content.

While the principles of environmental regulation of SR are applicable to ER, the additional component fluxes in the latter and the methodological difficulties of quantifying ER result in relatively noisy and patchy data. Because of the inherent variation in eddy covariance data, several recent studies on the environmental regulation of ER have used aggregated data, as daily sums (Ruimy et al., 1995) of fluxes and even multi-day running means (Reichstein et al., 2002a). This smoothing enhances ones ability to detect patterns in means, but does so on the account of additional information about the effects of air temperature, vapor pressure deficit (VPD) (Bowling et al., 2002), and diurnal patterns of carbohydrate transport (Geiger and Servaites, 1994; Kuehny and Topa, 1998) and nitrogen uptake (Gessler et al., 2002). While soil moisture varies little over the course of a day, soil temperature exhibits a diurnal cycle and may carry information about diurnal patterns of ER. In this study we analyze 30 min mean nighttime ER for its sensitivities to soil temperature and moisture availability, using data from 20 site-years of eddy covariance studies in the Northern Great Lakes Region in USA. The specific objectives were to: (i) compare the magnitude of ER at the different sites and during the 2 years of different precipitation regimes, (ii) quantify the role of soil moisture in affecting ER, and (iii) identify landscape-level patterns in the temperature and moisture response of ER as determined by forest functional type and stage of development.

2. Methods

2.1. Study area

The study sites are located in Northern Wisconsin and Northern Michigan, falling on the border of temperate and boreal forest types (Curtis, 1959). The measurements were conducted in a range of forest types and ages, including both naturally and anthropogenically regenerated stands, two fire-managed shrub-lands and a forested wetland, representing the predominant non-agricultural ecosystems in the region. Of the 14 sites (Table 1), measured over a 2-year period (2002–2003), five sites represent deciduous forests (MHWC, YHW, IHW, MHWW and MHWU) and four represent coniferous stands (MRPC, YRP, IRP and IJP). The classification of the remaining five stands is not as straightforward, as OGR represents a mixed old-growth forest, WET is a shrub wetland, PBA and PBB are shrubby fire-managed ecosystems and WLEF tall tower represents a regional integration across a variety of land cover types with its multiple levels of measurement (at 30, 122 and 396 m). The agricultural systems, mostly dairy farms and grain fields that are significant in the area, were not included in this study. Predominant species and key stand characteristics for the study sites are provided in Table 1. The sites are at similar latitude of 45.56°N–46.74°N and span longitudes from 84.7°W to 91.2°W. The relief in the area is low, undulating terrain, with glacial sandy loams and loamy tills the predominant soil type (Great Lakes Ecological Assessment, 2002, http://www.ncrs.fs.fed. us/gla/). The change in elevation from hilltop to valley is usually less than 20 m, but sufficient to allow the development of wetland areas at lower elevation with seasonally saturated soils. The region has been strongly affected by human activity, including farming and logging, with the latter being concentrated in the upland regions. Most

Table 1 – Study sites, some key characteristics and the reference of original publication

Site[a]	Dominant species	Age (year)	Latitude (°N), longitude (°W)	u^*-crit.	Wind screen (°)	Canopy cover (%)	LAI (m² m⁻²)	Basal area (m² ha⁻¹)	CWD (m³ ha⁻¹)	Canopy height (m)	Sensor height (m)	Fetch (m)	Reference of first mention
IHW	Populus grandidentata Populus tremuloides	17	46 00′ 35″ 91 13′ 22″	0.11	120–170		3.0			6	9	700	This study
IJP	Pinus banksiana	13–14	46 38′ 47″ 88 31′ 10″	0.3	–		0.93			3	6	700	Euskirchen et al. (2006)
IRP	Pinus resinosa	21	46 43′ 15″ 91 10′ 28″	0.11	120–170	60				6	9	600	This study
MHWC	Populus grandidentata Betula papyrifera Quercus rubra Acer rubrum Acer saccharum	65–66	46 38′ 05″ 91 05′ 56″	0.4 (2002) 0.34 (2003)	120–170	97	3.86	33.5	29.1	18–23	26	900	Noormets et al. (2007)
MHWU	Populus grandidentata P. tremuloides Acer rubra A. saccharum Quercus rubra Betula papyrifera Fagus grandifolia	90	45 33′ 35″ 84 42′ 50″	0.35	–		3.7			20	50		Schmid et al. (2003)
MHWW	Acer saccharum Tilia americana Fraxinus pennsylvanica	60–80	45 48′ 21″ 90 04′ 48″	0.3	90–180		5.3			24	30		Cook et al. (2004), Desai et al. (2005)
MRPC	Pinus resinosa Populus grandidentata	63–64	46 44′ 21″ 91 09′ 59″	0.32 (2002) 0.2 (2003)	120–170	73	2.5–2.8	26.9	13.5	17–19	23	1200	Noormets et al. (2007)
OGR	Tsuga canadensis Acer saccharum Betula papyrifera B. alleghaniensis Tilia americana Ostrya virginiana	200 (350)	46 37′ 31″ 89 20′ 21″	0.325	270–180, summer night, 30-90		4.06	33.1		20–27	35		Desai et al. (2005)
PBA	Andropogon scoparius Comptonia peregrina Vaccinium angustifolium Prunus serotina Salix humilis	12	46 37′ 9″ 91 16′ 44″	0.21	120–170	4	0.2	0.1	2.0	0.5–1	3	400	Noormets et al. (2007)
PBB	Andropogon scoparius Comptonia peregrina Vaccinium angustifolium	2	46 37′ 16″ 91 17′ 35″	0.12	120–170		0.05			0.5	3	300	This study

WET	*Alnus rugosa*	20	46 04′ 58″	0.05	–		4.9			2	10.2		This study
	Thuja occidentalis		89 58′ 45″				???						
	Larix lariciana												
	Picea mariana												
WLEF	*Populus grandidentata*	70	45 56′ 45″	0.3	–		3.7			20	30		Berger et al. (2001), Davis et al. (2003)
	Abies balsamifera		90 16′ 20″								122		
	Acer saccharum										396		
	A. rubrum												
	Tilia americana												
	Pinus resinosa												
	Betula papyrifera												
	B. alleghaniensis												
	Picea glauca												
YHW	*Acer rubrum*	3	46 43′ 18″	0.2	120–170	2	1.19–1.4	1.5	82.1	1–2	3	150	Noormets et al. (2007)
	Populus grandidentata		91 15′ 04″										
	Populus tremuloides												
YRP	*Pinus banksiana*	8	46 37′ 09″	0.18	120–170	17	0.52	4.7	4.3	3–4	6	300	Noormets et al. (2007)
	Pinus resinosa		91 04′ 54″										

[a] Site abbreviations: MHWC – mature northern hardwood at Chequamegon National Forest (CNF), MRPC – mature red pine at CNF, PBA – pine barrens with complete ground cover, PBB – recently burned and plowed pine barrens, YHW – young hardwood clearcut, IHW – intermediate hardwoods, YRP – young red/jack pine, IRP – intermediate red pine, IJP – intermediate jack pine, WET – Lost Creek shrub wetland, MHWW – mature hardwood at Willow Creek, WLEF – regionally averaging WLEF tall tower, MHWU –mature mixed hardwood at University of Michigan Biological Station, OGR – mixed old-growth stand at Sylvania Wilderness Area in Michigan.

of the region was clearcut at the beginning of 20th century and current naturally regenerated hardwood forests represent a transitional stage in succession.

2.2. Micrometerological parameters

The equipment used and recording interval for flux and micrometeorological measurements is given in Table 2. Soil temperature was measured at 10 or 5 cm depth (T_{S10}, °C; 5 cm at WLEF, OGR, MHWW, WET and MHWU, 10 cm at all other sites). Soil moisture was measured as volumetric water content (SWC_{10}, %; at the same depth with T_{S10}) at WLEF, OGR, MHWW, MHWU and IJP, as matric water potential (M_{10}, kPa; at the same depth with T_{S10}) at MHWC, MRPC, PBA, PBB, YHW, IHW, YRP, IRP and IJP or as water table depth (WT, cm) at WET. For comparability of scale (i.e. higher values reflecting higher soil moisture), the M_{10} data were converted to "pseudo-SWC" (pSWC) by taking the inverse and normalizing the data within each site in relation to maximum pSWC. It is important to note that the numerical values of SWC_{10} and pSWC are not comparable.

2.3. Flux calculation methods and data screening

Net ecosystem exchange of CO_2 (NEE) was measured with eddy covariance technique. Both open- and closed-path deployments were used (Table 1). All sites used 30 min averaging period for calculating fluxes, except at the MHWU and the tall WLEF tower where mean fluxes were calculated hourly and 30 min data were interpolated from those. Specific details of flux calculations can be found in original publications

(Table 1). These included despiking and detrending raw signals, coordinate rotation around two axes (Finnigan et al., 2003; McMillen, 1988), corrections for tube delays (Massman, 2000) and spectral correction for high-frequency loss (Berger et al., 2001; Massman and Lee, 2002) where closed-path infrared gas analyzer (IRGA) was used, Webb–Pearman–Leuning correction (Leuning and King, 1992; Massman and Lee, 2002; Webb et al., 1980) where open-path IRGA was used and corrections for CO_2 storage in canopy air column at sites with taller canopies (over 5 m) by measuring CO_2 concentration profile. Sites with AC or generator-power (WLEF, MHWU, OGR, MHWW) used a multiport sequential sampling from different levels in the canopy (for methodological details, see Cook et al. (2004) and Desai et al. (2005)). At solar-powered locations MHWC, MRPC, IHW, IRP air from four different canopy positions (at about 0.05, 0.2, 0.6 and 0.9 of canopy height) was mixed in a 5 L PVC chamber and the average change in CO_2 concentration from all different levels was used to estimate the storage flux (Noormets et al., 2007).

The focus of the current paper was on directly measured nighttime flux, restricted to periods of PAR < 4 μmol m^{-2} s^{-1}, verified against daily sunrise and sunset times, during the growing season (defined as periods when $T_{S10} > 2$ °C). The 30 min flux data were screened for periods of precipitation and dew (rain gauge and leaf wetness sensor or automatic gain control (AGC) in open-path IRGA), low turbulence (threshold u^* was determined individually for each site-year) and wind direction (when either an anomaly in observed fluxes was observed (Table 1) for predetermined wind directions or when wind was blowing through the tower and a change in the turbulent characteristics was suspected). All together, the

Table 2 – Sensors[a] and recording intervals used for micrometeorological and eddy covariance measurements at the study sites

Site[b]	IRGA	Anemometer	Net radiation	PAR	Ts	Moisture	Precip.	Ta, RH	Interval (min)
IHW	LI-7500	CSAT-3	Q7.1	LI-190SB	CS107	CS257	TE525	HMP45AC	30
IJP	LI-7500	CSAT-3	Q7.1	LI-190SB	CS107	CS257	TE525	HMP45AC	30
IRP	LI-7500	CSAT-3	Q7.1	LI-190SB	CS107	CS257	TE525	HMP45AC	30
MHWC	LI-7500	CSAT-3	Q7.1	LI-190SB	CS107	CS257	TE525	HMP45AC	30
MHWU	LI-6262	CSAT-3	Q7.1	LI-190SZ	E-type	type A	TE525	HMP45AC	60
MHWW	LI-6262	CSAT-3	CNR-1	LI-190SZ	T-type	CS615	TE525	CS500	30
MRPC	LI-7500	CSAT-3	Q7.1	LI-190SB	CS107	CS257	TE525	HMP45AC	30
OGR	LI-6262	CSAT-3	NR-LITE	PAR-LITE	T-type	CS616	TE525	HMP45AC	30
PBA	LI-7500	CSAT-3	Q7.1	LI-190SB	CS107	CS257	TE525	HMP45AC	30
PBB	LI-7500	CSAT-3	Q7.1	LI-190SB	CS107	CS257	TE525	HMP45AC	30
WET	LI-6262	CSAT-3	NR-LITE	PAR-LITE	T-type	PX242	TE525	CS500	30
WLEF	LI-6262	CSAT-3	Q7.1	LI-190SZ	CS107	CS616	TE525	HMP45AC	60
YHW	LI-7500	CSAT-3	Q7.1	LI-190SB	CS107	CS257	TE525	HMP45AC	30
YRP	LI-7500	CSAT-3	Q7.1	LI-190SB	CS107	CS257	TE525	HMP45AC	30

[a] Manufacturer information is as follows: LI-7500 (Li-Cor, Lincoln, Nebraska, USA), LI-6262 7500 (Li-Cor, Lincoln Nebraska, USA), CSAT-3 (Campbell Scientific Inc. (CSI), Logan, Utah, USA), Q7.1 (Radiation and Energy Balance Systems (REBS), Seattle, Washington, USA), LI-190SB 7500 (Li-Cor), LI-190SZ 7500 (Li-Cor), NR-LITE (Kipp and Zonen Inc., Bohemia, New York, USA), CNR-1 (Kipp & Zonen), PAR-LITE (Kipp & Zonen), CS107 (CSI), CS257 (CSI), T-type (copper-constantan thermocouples, 24 gauge, Omega Engineering, Stamford, Connecticut, USA), E-type (chrome-constantan thermocouples, 24 gauge, home-made), CS615 and CS616 (CSI), PX242 (PX242A-100G5V pressure transducer, Omega Engineering), type A (volumetric soil moisture probe, Vitel), TE525 (tipping bucket rain gauge, Texas Electronics, Dallas, TX).

[b] Site abbreviations: MHWC – mature northern hardwood at Chequamegon National Forest (CNF), MRPC – mature red pine at CNF, PBA – pine barrens with complete ground cover, PBB – recently burned and plowed pine barrens, YHW – young hardwood clearcut, IHW – intermediate hardwoods, YRP – young red/jack pine, IRP – intermediate red pine, IJP – intermediate jack pine, WET – Lost Creek shrub wetland, MHWW – mature hardwood at Willow Creek, WLEF – regionally averaging WLEF tall tower, MHWU –mature mixed hardwood at University of Michigan Biological Station, OGR – mixed old-growth stand at Sylvania Wilderness Area in Michigan.

screening criteria eliminated about 53% (range 22–76%) of available nighttime data. The remaining data were uniformly distributed throughout the summer, so the results of the analyses are not temporally biased (Fig. 1).

2.4. Modeling ecosystem respiration (ER)

Respiration generally increases with temperature, and a variety of empirical models have been used to describe this relationship (Fang and Moncrieff, 2001). The most often used are different modifications of first-order exponential model (Goulden et al., 1997), but for temporally integrated data the relationship becomes linear (Ruimy et al., 1995). In current study, the dependence of ER on soil temperature was analyzed on the basis of measured data (i.e. gaps in

data were not filled) using a modification (Law et al., 2002) of the temperature response function by Lloyd and Taylor (1994):

$$ER = R_{10}\, e^{(E_a/R(1/T_{ref} - 1/T_{S10}))} \tag{1}$$

where R_{10} is ER normalized to 10 °C, E_a is activation energy (kJ mol^{-1}), R is universal gas constant (8.3143 J mol^{-1} K^{-1}), T_{ref} is reference temperature (283.15 K) and T_{S10} is soil temperature (K). This model was chosen because the model residuals were unbiased with temperature (unlike those from Q_{10} and the original Lloyd–Taylor model). The analysis of the dependence of residuals on T_{S10}, SWC$_{10}$ (or pSWC) and VPD indicated that (i) there was no residual bias with soil temperature except in YHW, IHW, YRP and IRP (see Section 3.3), and (ii) the residual
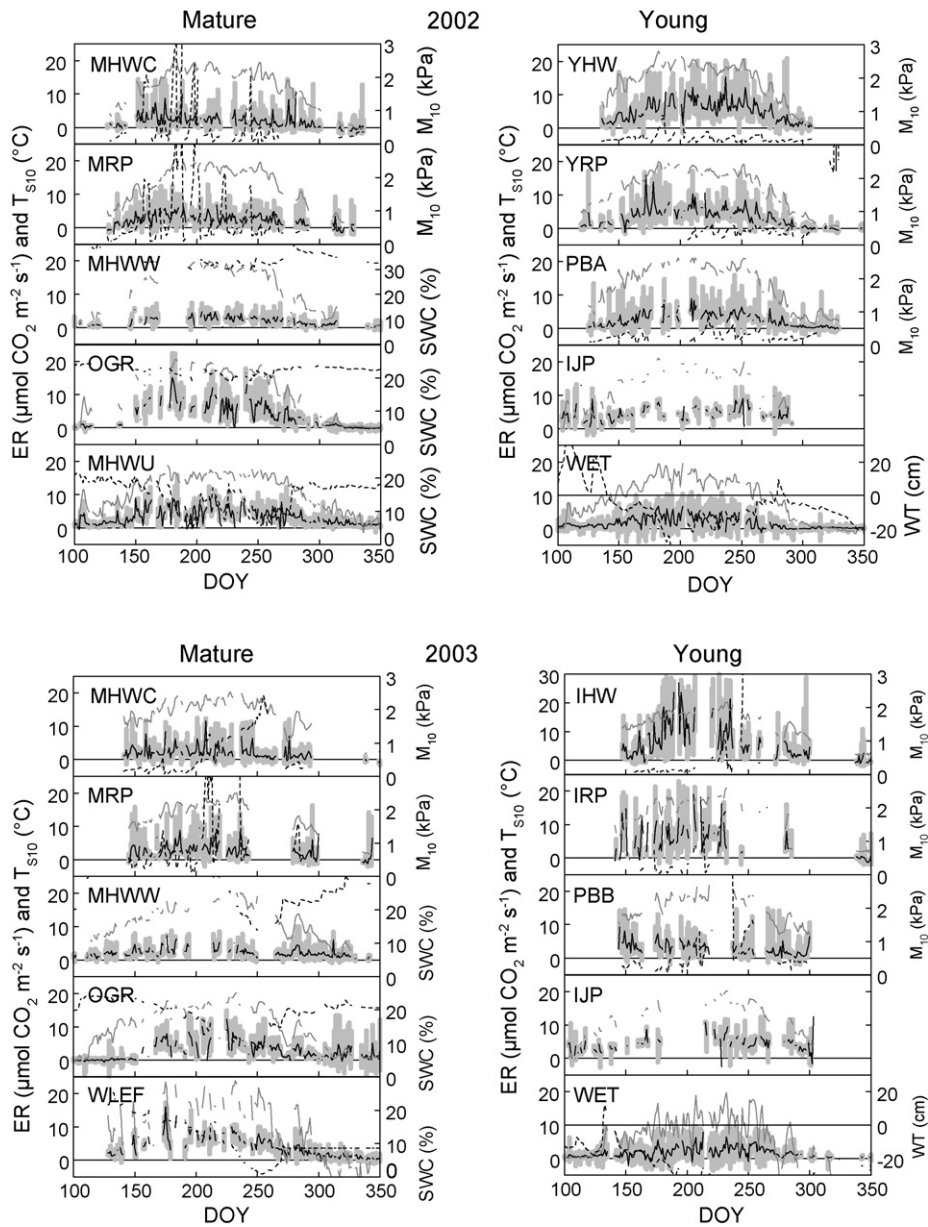

Fig. 1 – Seasonal profiles of ecosystem respiration (ER, nighttime mean shown with black line, nighttime range shown with grey shading), nighttime mean soil temperature (T_{S10}, thick grey line) and mean soil moisture (matric potential (M_{10}), volumetric water content (SWC) or water table depth (WT), all shown with dashed line).

variation was best explained by changes in soil moisture as measured with SWC_{10}, pSWC or WT.

The effect of soil moisture on ER from Eq. (1) was modeled first by classifying data to soil moisture bins, defined by the quartiles of the frequency distribution of soil moisture, based on SWC_{10} (%; MHWW, OGR, MHWU, WLEF), pSWC (1/kPa; MHWC, MRPC, PBA, PBB, YHW, IHW, YRP, IRP and IJP) or water table depth (WET) and fitting the Eq. (1) for each sub-set. Soil moisture classes each included 25% of the data and did not necessarily cover equal range. However, this division represents different moisture conditions by the frequency of their occurrence at each site. This analysis showed that (i) as expected, the range of E_a and R_{10} estimates increased significantly in comparison to the general seasonal model fits (ii) the differences between individual sites remained similar to what was observed with the general seasonal model fits and (iii) the response of model parameters E_a and R_{10} to moisture classes was non-linear. Therefore, R_{10} was defined a quadratic function of soil moisture (SWC_{10} or pSWC):

$$R_{10} = a_0 + a_1 \times SWC + a_2 \times SWC^2 \tag{2}$$

where a_0, a_1 and a_2 are empirical coefficients and SWC is either SWC_{10}, pSWC or WT.

Other models that were tested, included (i) a basic Q_{10} model, (ii) the original Lloyd and Taylor (1994) model with a specified minimum temperature, below which respiration ceases, (iii) one with Q_{10} defined as a linear function of soil moisture (e.g. Reichstein et al. (2002b)) and (iv) with E_a defined as a quadratic function of soil moisture (similar to Eq. (2)). The first two models yielded a residual bias with temperature and overall larger residuals than did Eq. (1), whereas the third and fourth models either failed to converge or yielded unstable parameter estimates. This apparent conflict with the findings of Reichstein et al. (2002b) could be related to the fact that they used 5-day running averages of spatially averaged daily mean SR, whereas the actual measured 30 min mean ER were used in current study. The additional variability in our data includes information about the effects of air temperature and VPD on aboveground respiration (Bowling et al., 2002; McDowell et al., 2004), growth respiration (Rambal et al., 2004), diurnal patterns related to carbohydrate transport (Geiger and Servaites, 1994; Kuehny and Topa, 1998) and nutrient uptake (Gessler et al., 2002), as well as greater random error.

The parameters of Eqs. (1) and (2) were estimated with nonlinear regression (PROC NLIN, SAS, SAS Institute Inc., Cary, NC, USA). The significance of the dependence of residuals on T_{S10}, SWC_{10} (or pSWC) and VPD was assessed by the P-value of the linear regression models fitted to the data. Comparison of mean ER, T_{S10} and SWC_{10} (or pSWC) between individual sites and forest types was performed with repeated measures analysis of variance using Tukey's honestly significant difference test (PROC MIXED, SAS). The statistical moments of soil moisture frequency distribution were calculated with PROC UNIVARIATE (SAS). The suitability of kurtosis (as a measure of the peakedness of the distribution), variance, range and interquartile range (as measures of the spread of the distribution) for predicting moisture sensitivity of ER was assessed based one their relationship with parameters a_1 and a_2 (Eq. (2)). The significance of mean stand age and LAI was determined with multiple forward stepwise regression (PROC REG, SAS).

3. Results and discussion

3.1. Environmental conditions

Total annual precipitation at the University of Wisconsin Agricultural Research Farm in Ashland (46.592N, -90.883W) was 844 and 675 mm in 2002 and 2003, respectively. Precipitation was higher in 2002 than in 2003 during all months, except in April and November. Across all sites the higher precipitation in 2002 was reflected in significantly ($P < 0.01$) higher soil moisture, but the difference was not significant at every site where measurements were conducted for both years. The higher precipitation in 2002 was reflected in significantly higher soil moisture during the months of June, July and August (the peak growing season) in MHWC, MHWW, OGR and WET, whereas no significant difference was seen in IJP even though the mean SWC_{10} was higher in 2002 than in 2003. MRPC, on the other hand, showed the opposite pattern, with higher pSWC (lower M_{10}) in 2003 than in 2002. The site-pairs that can be viewed together as a part of chronosequence (YHW-IHW, YRP-IRP and PBA-PBB) did not show significant differences between the 2 years. The lack of correlation between annual precipitation and growing season mean soil moisture in the coniferous stands is likely the result of the evergreen leaf habit (in contrast to deciduous), with higher transpiration in fall, winter and spring than in deciduous stands where the demand for ground water was likely smaller on an annual basis (Swank and Douglass, 1974) allowing the non-growing season precipitation to accumulate. For the months of June, July and August soil temperature was $1.35 \pm 0.64\,°C$ (mean ± S.E.) higher in 2002 than in 2003 across all sites where data were available for both years (i.e. MHWC, MRPC, IJP, WET, MHWW and OGR). The average temperature across all sites for the same period was 16.5 °C in 2002 and 15.2 °C in 2003 ($P < 0.0001$), which is likely to have lead to greater evaporative demand during the wetter year, 2002. The specific interactions of precipitation, temperature and evaporative demand are yet to be quantified and are outside the scope of this paper.

3.2. Differences between sites

On average, the coniferous stands were younger than the hardwood stands (30.5 and 54.6 years, respectively) and had lower LAI on average (1.5 and 3.8 $m^2\,m^{-2}$, respectively) as well as in comparison with similar-aged hardwood stands (Table 1; Fig. 2). These differences were reflected in the mean daily T_{S10} throughout the growing season during both years. The mean T_{S10} from June through August was 15.5 °C in hardwood stands and 16.6 °C in coniferous stands, with the biggest differences in July and August). Despite lower T_{S10} at the hardwood stands, the mean ER from June through August was not significantly different between the hardwood and coniferous stands (4.6 and 4.4 $\mu mol\ CO_2\,m^{-2}\,s^{-1}$, respectively), but during the transition periods in May and September the coniferous stands exhibited significantly higher ER than did the hard-
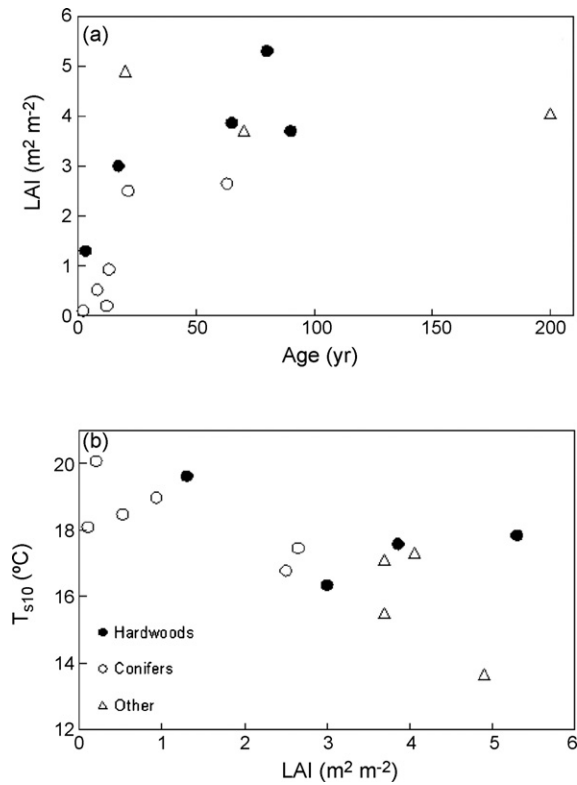
Fig. 2 – Leaf area index (LAI) in forests of different ages and composition (a). Soil temperature (T_{S10}) in forests of different LAI (b). Hardwoods included YHW, IHW, MHWC, MHWW and MHWU. Conifers included YRP, IRP, IJP and MRPC. "Other" category included PBA, PBB, WET, WLEF and OGR.

and IJP. The daily mean ER did not significantly differ between 2002 and 2003 at any of the sites, except in OGR, where the significantly higher T_{S10} and SWC_{10} lead to significantly higher ER in 2002 than in 2003 ($P < 0.01$). Soil moisture was significantly higher in 2002 than in 2003 in OGR, MHWW, IJP and WET ($P < 0.05$), and similar trends were observed in MHWC and YHW-IHW pair, as well. On the other hand MRPC, PBA-PBB pair and YRP-IRP pair showed slightly higher SWC in 2003 than in 2002, but none of them were statistically significant ($P > 0.1$).

3.3. Temperature response of ER

The estimated mean E_a (Eq. (1)) of ER throughout the growing season was about 40–110 kJ mol^{-1} and showed an increasing trend with stand age for coniferous ($P < 0.1$), but not for hardwood stands (Fig. 3). Temperature-normalized R_{10} was highest in OGR, in YHW and IHW, WLEF and MHWU, and in IJP, YRP and IRP. Among the coniferous stands, the intermediate age group showed significantly higher ($P < 0.01$) R_{10} than the mature or young stands, whereas in hardwoods the mature and the young and intermediate age groups is harder to define due to the wide variation in the mature age group ($P < 0.05$ for young and intermediate versus mature stand contrast). Across all stands, the trends of E_a and R_{10} were not significant with age. The models explained 10–80% of the variation in ER data, with large differences between individual sites (Fig. 3c).

Two sites, MHWC and OGR, and the YHW-IHW pair showed higher E_a in the drier 2003 growing season than in 2002, which could be anticipated given that water availability can limit metabolic activity (Bota et al., 2004; Yordanov et al., 2000). However, the PBA-PBB pair, WET and MHWW exhibited the opposite pattern, with higher E_a during the wetter 2002 growing season. However, we saw in Section 3.1 that MHWC, OGR, MHWW and WET showed higher SWC in 2002 than in 2003, but only MHWC and OGR responded with higher E_a in 2003 than in 2002, whereas for MHWW and WET the opposite was true. This implies that lower SWC in 2003 inhibited ER in MHWC and OGR, but not in the other stands.

The variation of the residuals of Eq. (1) was best explained with variation in SWC_{10} (Table 4), although in YHW, IHW, YRP

wood stands on average (ER in May was 2.3 and 1.7 ($P < 0.01$) and in September 3.9 and 3.4 ($P < 0.05$) μmol CO_2 m^{-2} s^{-1} in coniferous and hardwood stands, respectively). Mean growing season ER was significantly higher ($P < 0.05$) in young and intermediate than in mature stands (Table 3). The overall highest ER was observed in IHW, followed by OGR, WLEF, YHW

Table 3 – Mean ER in different age groups of different forest stands from June through August		
Age group	ER (μmol CO_2 m^{-2} s^{-1})	Site-year
Conifers		
Young	5.25 ± 0.29a	YRP02
Intermediate	5.95 ± 0.24a	IRP03, IJP02, IJP03
Mature	3.28 ± 0.20b	MRPC02, MRPC03
Hardwoods		
Young	6.50 ± 0.35b	YHW02
Intermediate	9.05 ± 0.40a	IHW03
Mature	3.28 ± 0.18c	MHWC02, MHWC03, MHWW02, MHWW03, MHWU02
Other		
Young	3.65 ± 0.30b	PBA02, PBB03
Intermediate	3.08 ± 0.14b	WET02, WET03
Mature	6.52 ± 0.18a	OGR02, OGR03, WLEF03

The significance of the difference was tested with Tukey's honestly significant difference test at $P < 0.05$ level and the results are indicated with letters following the means. Different letters mark statistically significant difference ($P < 0.05$) between age groups within given forest type.
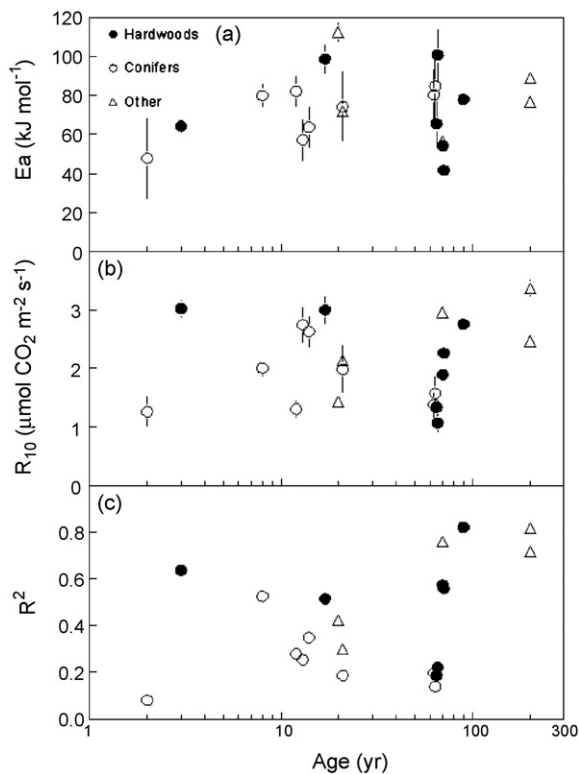
Fig. 3 – The parameters of the seasonal temperature response model of ER (Eq. (1)), activation energy (E_a, a), reference respiration (R_{10}, b) and coefficient of determination (R^2, c) as a function of stand age. Stands are grouped as in Fig. 2.

Table 4 – Significance of the slope of the linear regressions between the residuals of the temperature response model and T_{S10}, SWC and VPD

Site	T_{S10}	SWC_{10}	VPD
MHWC02	0.200	**0.032**	0.525
MHWC03	0.396	**0.008**	0.461
MRP02	0.224	0.960	**0.029**
MRP03	0.425	**0.021**	**0.064**
PBA02	0.251	**0.001**	0.584
PBB03	0.617	**0.083**	0.316
YHW02	**0.036**	**<0.001**	**<0.001**
IHW03	**0.055**	**0.019**	0.239
YRP02	**0.020**	**0.003**	**0.003**
IRP03	**0.036**	0.747	0.543
YJP02	0.230	0.915	**0.001**
YJP03	0.343	0.721	0.705
WET02	0.185	**0.020**	0.113
WET03	0.576	0.896	0.686
MHWW02	0.592	0.237	**0.060**
MHWW03	0.259	**0.015**	**0.072**
WLEF03	0.476	**0.008**	**<0.001**
MHWU02	0.407	n/a	0.522
OGR02	0.190	0.264	0.126
OGR03	0.273	**0.001**	**<0.001**

Significance levels $P < 0.1$ are highlighted in bold.

and IRP a significant ($P < 0.05$) bias remained with T_{S10}. That is, the model underestimated ER at higher temperatures at these sites, which is commonly seen with the majority of data sets and regression models (reviewed by Lloyd and Taylor (1994)) due to negative correlation between soil moisture and temperature. However, the residual variation showed a more significant relationship (lower P-value) with SWC_{10} than with T_{S10}.
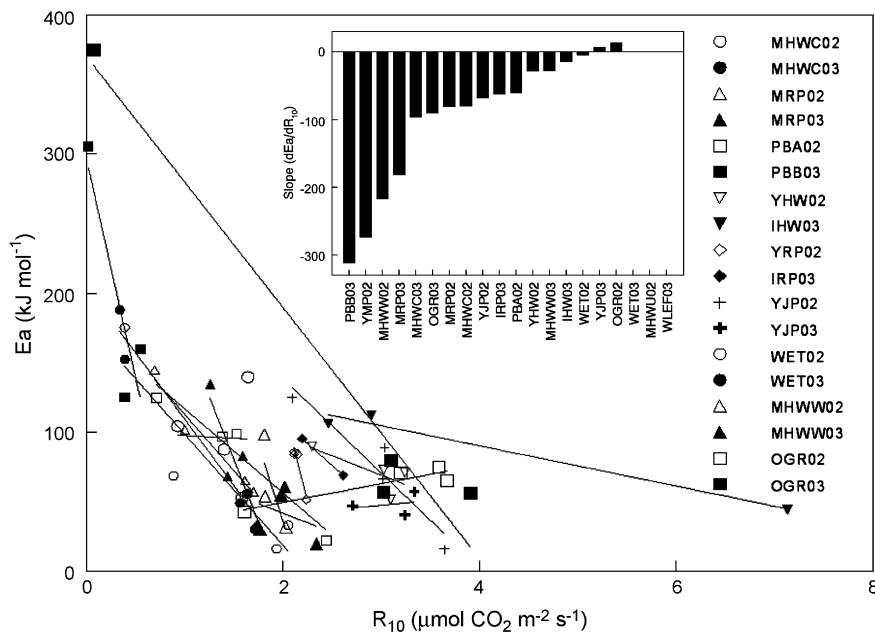

Fig. 4 – Negative relationship between activation energy (E_a) and reference respiration (R_{10}). Each site is characterized with the temperature-based estimates for individual soil moisture classes. The ranked slopes of these relationships are shown in inset.

The temperature response function applied to individual soil moisture classes (as defined by the quartiles of the soil moisture frequency distribution) showed (i) greater range of E_a and R_{10} estimates compared to the variance of global estimates (Eq. (1)), as was to be expected, and (ii) that the response of model parameters E_a and R_{10} to moisture classes was non-linear. Since the site differences remained similar to what was observed with the general seasonal model we shall not present the parameter values *per se*, but will look at the negative relationship of E_a and R_{10} (Fig. 4) in Section 3.5 in the context of potential mechanisms affecting the moisture sensitivity of ER.

3.4. Moisture sensitivity and improvement in model fit

Upon defining R_{10} as a quadratic function of SWC (Eq. (2)), as suggested by the non-linear changes in E_a and R_{10} in each of the soil moisture classes (Section 3.3), E_a was expected to decrease if soil moisture limited respiratory activity. This response was detected in only three out of 20 site-years (IHW03, MHWW02 and OGR03), whereas two sites actually responded with an increase in E_a (YHW02 and IJP02) and the other sites did not show a statistically significant change (Fig. 5).

The moisture sensitivity parameters a_0, a_1 and a_2 varied significantly between sites. Parameter a_0, which can be viewed as an equivalent of R_{10} in the absence of moisture limitation, did show a correlation with the latter ($R^2 = 0.69$). Parameters a_1 and a_2 define the moisture optimum for ER, a_1 describing increase in R_{10} up until optimal soil moisture conditions and a_2 describing the decrease in R_{10} beyond the optimum. These parameters were strongly correlated ($R^2 = 0.96$) indicating that in sites where ER increased with moisture, it also had a well-defined optimum, beyond which ER started to decrease. The magnitude of parameters a_1 and a_2 was also correlated with the change in E_a as the result of incorporating SWC in the regression model. The relationship was stronger when E_a
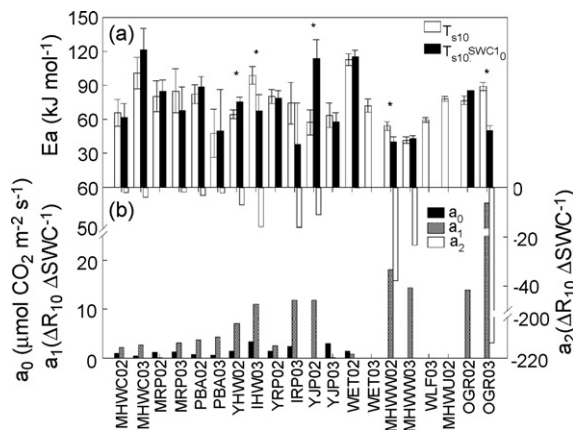

Fig. 6 – Moisture sensitivity parameters a_1 and a_2 in relation to change in activation energy (ΔE_a) as the result of letting R_{10} vary by soil moisture. Panel (b) is a sub-set of panel (a), excluding the OGR02, OGR03, MHWW02 and MHWW03, which were significant leverage points.

decreased, than when it increased (Fig. 6a). Upon excluding a few leverage data points from the analysis, however, the relationship became similar with both increasing and decreasing E_a (Fig. 6b). A threshold in change in E_a of about ± 25 kJ mol^{-1} could be identified, which was associated with a well defined moisture optimum, characterized by the absolute value of both a_1 and a_2 greater than 10 μmol CO$_2$ m^{-2} s^{-1} (% SWC)$^{-1}$. The phenomenon that moisture optimum can be equally well defined with either negative or positive change in E_a is attributable to the stochastic component in statistically estimating the model parameters. See, for example, Davidson et al. (1998) for a discussion on equally good model fit achievable with a number of different combinations of reference respiration and temperature sensitivity. They showed that equally good model fits were achieved on one hand by letting the temperature-based models pick unreasonably high Q_{10} value, in which case SWC contributed little to increasing model sum-of-squares (SS), or by forcing lower Q_{10} value and letting the T-and-SWC-based model fit the non-linear moisture dependence to account for poor fit with Q_{10} alone. Such confounding effects are more extreme when functionally different phenological phases are mixed in a single analysis (Curiel Yuste et al., 2004; Janssens and Pilegaard, 2003; Van Dijk and Dolman, 2004) and likely more pronounced for ER than for SR. This supports the hypothesis put forward by Davidson et al. (1998), Janssens et al. (2001), and Law et al. (1999) that abnormally high Q_{10} values reflect different biological processes operating at different temperature and moisture ranges. With the switching on and off being most pronounced between 0 and 5 °C, large changes in ER

Fig. 5 – Activation energy (E_a, a) and moisture sensitivity parameters (a_0, a_1 and a_2, b) of seasonal temperature and moisture response model of ER. Asterisks mark sites where E_a changed significantly upon including SWC in the model. White bars mark activation energy from a temperature-only model. Black bars mark activation energy when R_{10} was expressed as a function of soil moisture (Eq. (2)).
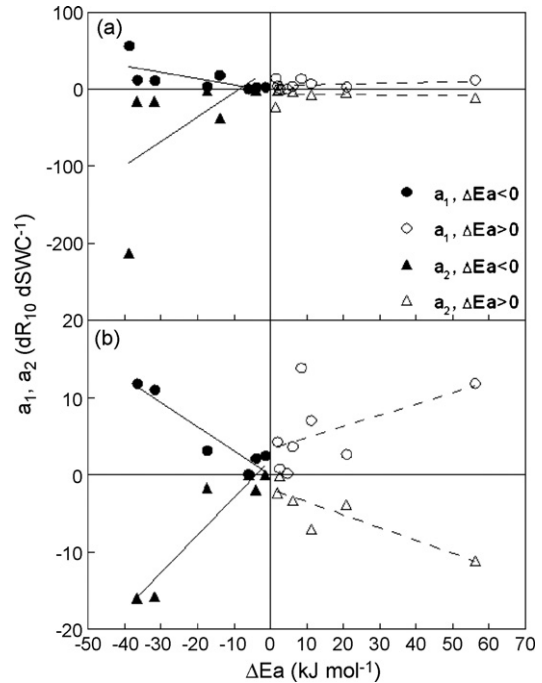
could result with only a small change in temperature. On the other hand, most heterotrophic processes in any given ecosystem are expected to be active and near temperature saturation above 20 °C, when moisture, nutrient and carbon availability (Bond-Lamberty et al., 2004) may become more significant in controlling the overall reaction rate.

The greatest increase in model fit, as assessed through the change in the coefficient of determination (R^2) upon expressing R_{10} as function of SWC was seen in the mature age group, but due to broad variation between different stands the trend was not significant ($P > 0.1$). Model fit increased by an average of 7.7% in 2002 and 4.4% in 2003 and ranged from 0 to 21%. Little difference was seen between hardwood and coniferous forests, with $\Delta R^2 = 7$ and 9%, respectively.

The three sites that had significantly lower E_a after the addition of SWC to the model than with the original temperature-based model (IHW03, MHWW02 and OGR03) all exhibited a distinctly bimodal soil moisture distribution. Since there is no universal statistical moment for identifying bimodal distributions, we tested the suitability of kurtosis, variance, range and interquartile range of soil moisture frequency distribution (see Methods for details) for predicting the moisture sensitivity of ER. The moisture sensitivity parameters a_1 and a_2 with greatest magnitude did exhibit kurtosis < 0 (Fig. 7) as would be expected from a bimodal distribution (i.e. the central peak of the distribution is defined weaker than that of a normal distribution). There were, however, three other stands that showed negative (IJP02) or low positive kurtosis (IRP03, MHWW03). These stands were also characterized by high moisture sensitivity (a_1, a_2), but showed higher E_a with SWC-dependent than with constant R_{10}, which we attribute to the stochasticity of statistical parameter estimates as mentioned above. Another parameter that partially resolved moisture-responsive stands was the interquartile range (IQR) of the soil moisture distribution. We expected wide interquartile range to correlate with bimodality of the distribution and thus the moisture sensitivity of ER. The three young stands with highest a_1 and a_2 (IHW03, IRP03 and IJP02), did conform to this pattern,

but the moisture-responsive mature and old-growth stands (MHWW02, MHWW03 and OGR03) showed some of the lowest IQR values. It is unclear why the young and mature stands line up at different ends of the interquartile range spectrum, because the mature stands did not have a significantly lower SWC. It is important to note that only a combination of different methods could uniquely identify sites with moisture-sensitive ER. With refined thresholds, we believe that properties of soil moisture conditions could be used in conjunction with other criteria to automatically identify sites responsive to moisture.

3.5. Mechanisms of moisture sensitivity of ER

Sensitivity to moisture can be attributed to either R_{10} or E_a (Eq. (1)). It is more common to find the temperature sensitivity parameter (E_a or Q_{10}) described as a function of soil moisture (e.g. Reichstein et al., 2003b) and fewer works attribute the sensitivity to reference or base respiration (Irvine and Law, 2002). In either case, usually no justification is given as to why one or other option had been chosen. The use of the inverse of temperature in the exponent term in the Arrhenius-type equation effectively reduces the temperature sensitivity with increasing temperature—a property which makes this model more suitable over wider range of temperatures than a standard Q_{10} model. A similar effect was achieved by Reichstein et al. (2002b) when allowing Q_{10} to vary with SWC (positive relationship). These two approaches accomplish the same because higher soil temperature is often correlated with lower SWC. Often, however, moisture sensitivity is attributed to Q_{10} without exploring the possibility of moisture-sensitive R_{10} (Reichstein et al., 2003b, 2002b; Xu and Baldocchi, 2004).

The moisture sensitivity of temperature sensitivity (Q_{10} or E_a) would agree with the notion that with different biological processes switching on and off at different temperature and/or moisture thresholds (Davidson et al., 1998; Janssens et al., 2001; Law et al., 1999), which would explain large changes in the apparent Q_{10}. If, however, moisture sensitivity operates through R_{10}, it would imply changes in the intensity of various processes, without changes to the balance between the component fluxes. Given the pronounced seasonal changes in temperature in our study area, and the non-synchronous seasonal cycles of different processes, E_a-mediated moisture sensitivity of ER is more intuitive when the annual changes in ER are considered. On the other hand, when temperature is more stable, like during the growing period, moisture effect on E_a is likely to decrease and its' effect on R_{10} to increase.

Both E_a and R_{10} varied with soil moisture class and were generally negatively related to each other (Fig. 4). Although the degree of this interdependence varied from site to site, all but two of the sites showed negative relationship within site (Fig. 4 inset) and the cross-site relationship was highly significant ($P < 0.0001$). Thus, the common practice of treating reference respiration (R_{10}) and temperature sensitivity (E_a or Q_{10}) as independent and equally informative parameters in analyzing environmental regulation of ER is not justified. Theoretically, decreasing moisture limitation on ER can result in either lower E_a or higher R_{10} or both. Our data showed that (i) both E_a and R_{10} changed with changing soil moisture conditions and (ii) model parameters were more stable with R_{10} expressed as a function of SWC than when E_a varied by soil moisture.
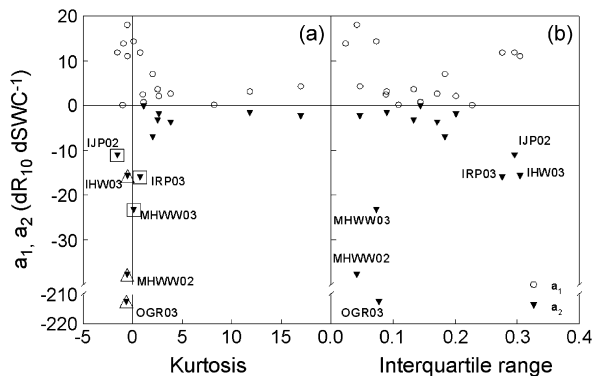

Fig. 7 – Moisture sensitivity parameters a_1 and a_2 in relation to the kurtosis (a) and interquartile range (b) of soil moisture frequency distribution. a_2 values of sites showing expected decrease in E_a in response to including soil moisture as an explicit driver of R_{10} are marked with large triangles (Δ). Sites with increasing E_a and significant moisture sensitivity of R_{10} are marked with large squares (□).

The interdependence of R_{10} and E_a and the problem of unstable parameter estimates might be reduced if R_{10} was not allowed to vary freely but was constrained to optimal soil moisture conditions. In our empirical model fits, it was not guaranteed that other conditions were optimal and R_{10} represented solely temperature-limited rate. On the other hand, had we defined R_{10} as moisture-optimized ER, we could not have estimated this parameter for individual SWC-classes, as it would be a condition not represented by data in three out of four classes. Furthermore, because of the interdependence of soil temperature and moisture, isolating a representative sub-set from field data for R_{10} estimation would not be a straightforward task. Among published studies Reichstein et al. (2003a) realized the importance of defining R_{10} strictly at optimal moisture conditions, but their model did not, in fact, ensure the independence of R_{10} from soil moisture. Thus, further consolidation of physiological and empirical models is needed to characterize the sources of variation for ER.

3.6. Additional limitations

The relationship of ER and T_{S10} exhibited a seasonal pattern, where ER in early and in late season differed by over 2-fold despite similar soil temperatures. Of the 20 site-years, eight exhibited higher ER in early than in late season, five showed the opposite pattern and seven did not exhibit pronounced seasonality (Table 5). The residuals of Eq. (1), however, did not exhibit any detectable seasonality at any of the sites (not shown).

The seasonal changes in ER reflect the combined effects of temperature, moisture, substrate availability and phenologi-cal phase, all of which co-vary with one another at different temporal and spatial scales. Given the pattern of seasonal changes, the role of moisture contribution could be evaluated by first comparing the mean soil moisture during the early and late season when the difference in ER at equal temperature was generally the largest. The analysis of variance showed that in most sites SWC_{10} did differ between the months of May and September (Table 5), yet it lends only partial support to the hypothesis that the seasonality was driven by soil moisture availability. If moisture was limiting ER, peak ER and SWC should co-occur in the same season. This pattern was observed in PBA02, MHWW02, MHWW03, WLEF03, OGR02, OGR03 and IHW03, whereas in MHWC03, MRPC02 and PBB03 the peak ER co-occurred with low SWC (Table 5) even though they did not represent wet habitats where such a response would be expected. The remaining sites did not clearly support either scenario either because of limited seasonality in ER or limited SWC data.

While current data does not allow quantifying other limiting factors to ER, and it is possible that the lack of detectable SWC effect in some sites was due to non-representative spatial sampling, the seasonal patterns of ER and SWC with tempera-ture (not shown) highlight the need for further studies into the role of carbohydrate (Schimel and Weintraub, 2003) and nitrogen limitation of ER (Schimel and Bennett, 2004). This hypothesis rests on three main observations. First, the seasonal temperature-dependent cycle of ER at some sites went against that of SWC, suggesting the existence of a third limiting factor. Second, the transition in the seasonal cycle of ER from the early season type of temperature dependence to the late season type occurred in July in 2002 and in August in 2003, and was

Table 5 – Mean soil moisture content (SWC_{10} or fractional pSWC) and mean daily ecosystem respiration (ER) in May and September at different study sites					
Site	Measure (unit)	SWC		ER	
		May	September	May	September
MHWC02	Relative pSWC	0.088a	0.105a	0.76a	1.36a
MHWC03	Relative pSWC	0.079b	0.729a	2.39a	1.34b
MRPC02	Relative pSWC	0.072b	0.136a	1.07b	2.53a
MRPC03	Relative pSWC	0.064	–	2.50	–
PBA02	Relative pSWC	0.142b	0.220a	1.19b	3.85a
PBB03	Relative pSWC	0.058b	0.334a	5.26a	1.76b
YHW02	Relative pSWC	0.151a	0.196a	2.42b	6.29a
IHW03	Relative pSWC	–	–	3.49a	4.08a
YRP02	Relative pSWC	–	0.43	1.46b	4.43a
IRP03	Relative pSWC	–	–	5.12a	8.07a
IJP02	Relative pSWC	0.782a	0.613b	2.94b	5.80a
IJP03	Relative pSWC	0.749	–	2.81b	4.63a
WET02	WT (cm)	5.32a	−8.425b	1.16b	1.54a
WET03	WT (cm)	−10.1a	−67.53b	1.13b	2.77a
MHWW02	SWC_{10} (%)	35.44a	32.48b	1.93a	2.47a
MHWW03	SWC_{10} (%)	38.83a	17.65b	2.02a	1.57a
WLEF03	SWC_{10} (%)	22.08a	3.19b	2.75b	4.55a
MHWU02	SWC_{10} (%)	–	–	2.27b	4.10a
OGR02	SWC_{10} (%)	23.42a	21.44b	2.27b	5.09a
OGR03	SWC_{10} (%)	23.84a	13.0b	0.14b	3.51a

The significance of the difference was tested with Tukey's "honestly significant difference" test at $P < 0.05$ level and the results are indicated with letters following the means. Different letters mark statistically significant difference ($P < 0.05$) between May and September for a given site-year.

independent of changes in soil moisture. The timing and nature of the change suggest that it could be related to increased root growth (Burke et al., 1992) and concomitant increase in bioavailability of carbon for heterotrophic respiration either from root turnover and exudates or new leaf fall (Bond-Lamberty et al., 2004; Zak et al., 1994). The significance of fresh litter input for ER is becoming increasingly clear (Högberg et al., 2001; Lötscher et al., 2004). And third, the different seasonal changes of ER in young and mature stands suggest a different mechanism of environmental regulation, potentially bioavailable carbohydrates in one case and bioavailable nitrogen in the other. The nature and magnitude of these (or other) limiting factors at forests of different age and composition remains to be determined.

4.   Summary

1. Ecosystem respiration was higher in the intermediate and young than mature stands. High ER was also seen in OGR and in the regionally averaging WLEF site.

2. The site differences in respiration were reflected in temperature-normalized respiration rates (R_{10}), but higher soil temperature in the younger stands also contributed to this effect.

3. Hardwood stands had higher measured ER and R_{10} than conifer stands of similar age.

4. ER showed higher temperature sensitivity (as indicated by lower activation energy, E_a) in the young than in the mature stands of coniferous forests, but not in the hardwood forests.

5. Soil moisture explained an additional 8% (range 0–21%) of variability in ER.

6. Significant moisture sensitivity of ER was detected in only 5 out of 20 site-years and it was associated with bimodal soil moisture distribution. Moisture sensitivity could partially be predicted from statistical moments kurtosis and inter-quartile range.

Acknowledgements

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