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Abstract

Winter CO₂ fluxes represent an important component of the annual carbon budget in northern ecosystems. Understanding winter respiration processes and their responses to climate change is also central to our ability to assess terrestrial carbon cycle and climate feedbacks in the future. The factors influencing the spatial and temporal pattern of winter respiration (RECO) of northern ecosystems are poorly understood. For this reason, we analyzed eddy covariance flux data sets from 57 ecosystem sites ranging from ~35° N to ~70° N. Deciduous forests carry the highest winter RECO ratios (9.7–10.5 g C m⁻² d⁻¹), when winter is defined as the period during which air temperature remained below 0°C. By contrast, wetland ecosystems had the lowest winter RECO (2.1–2.3 g C m⁻² d⁻¹). Evergreen needle-leaved forests, grasslands and croplands were characterized by intermediate winter RECO values of 7.4–7.9 g C m⁻² d⁻¹, 5.8–6.0 g C m⁻² d⁻¹, and 5.2–5.3 g C m⁻² d⁻¹, respectively. Cross site analysis showed that winter air or soil temperature, and the seasonal amplitude of the leaf area index inferred from satellite observation, which is a proxy for the amount of litter available for RECO in the subsequent winter, are the two main factors determining spatial pattern of daily mean winter RECO. Together, these two factors can explain 71% (T_{air} , ΔLAI) or 69% (T_{soil} , ΔLAI) of the spatial variance of winter RECO across the 57 sites. The spatial temperature sensitivity of daily winter RECO was determined empirically by fitting an Arrhenius relationship to the data. The activation energy parameter of this relationship was found to decrease at increasing soil temperature at a rate of 83.1 KJ °C⁻¹ ($r = -0.32$, $p < 0.05$), which implies a possible dampening of the increase in winter RECO due to global warming. The interannual variability of winter RECO is better explained by soil temperature than by air temperature, likely due to the insulating effects of snow cover. The increase in winter RECO with a 1°C warming based calculated from the spatial analysis was almost that double that calculated from the temporal analysis. Thus, models that calculate the effects of warming on RECO based only on spatial analyses could be over-estimating the impact.

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1 Introduction

The processes controlling the winter carbon cycle of northern ecosystems, mainly ecosystem respiration, have received much less attention than processes active during the growing season. The long-time standing view of marginal wintertime biological activity (e.g. Coyne and Kelley, 1971; Steudler et al., 1989) suggests that winter respiration is very small compared to growing season respiration. Recent field studies refuted this view by unravelling significant wintertime respiration rates in Arctic tundra, bog, and mountain ecosystems (e.g. Oechel et al., 1997; Fahnestock et al., 1998; Grogan and Chapin, 1999; Panikov and Dedysh, 2000; Aurela et al., 2002; Monson et al., 2006; Bergeron et al., 2007). These studies suggested that winter ecosystem respiration should not be ignored when attempting to quantify and understand the annual carbon balance of ecosystems (Hobbie et al., 2000; Grogan and Jonasson, 2005; Johansson et al., 2006). However, due to large variations in carbon storage and functioning across northern ecosystems and the limited spatial representativeness of individual studies, winter ecosystem respiration remains incompletely understood.

In general, mid and high-latitude ecosystems in general contain large amounts of soil carbon (Post et al., 1982). Part of this soil organic carbon (SOC) mass could be decomposed more actively than fresh input (e.g. litterfall) in response to future warming. The increased high-latitude warming projected by climate models includes winter warming (Serreze et al., 2000; Giorgi et al., 2001) and has already been observed over the past 30 years (IPCC, 2007). The response of SOC balance to warming differs widely among coupled climate-carbon models (Friedlingstein et al., 2006). This is because the net balance in these models depends on two fluxes of opposite directions, i.e., the litter input that may increase under warming if vegetation net primary productivity increases, and the soil carbon microbial decomposition rate that also responds positively to warming (e.g. Jones et al., 2005). Therefore, it is important to disentangle from available observations how temperature and vegetation productivity separately control winter respiration.

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Many studies suggested that major drivers of temporal and spatial variations of winter carbon respiration are temperature (Clein and Schimel, 1995; Hobbie, 1996; Mikan et al., 2002), substrate quality (Grogan et al., 2001; Grogan and Jonasson, 2005) and snow depth (Monson et al., 2006; Nobrega and Grogan, 2007). For example, Grogan and Jonasson (2005) found that both the amount of substrate available for respiration and soil temperature determine landscape level variation of winter ecosystem respiration of birch forest and heath tundra. Monson et al. (2006) observed that interannual variations of a montane forest winter carbon balance were strongly coupled with soil temperature and variability in snow depth changes. These studies are very valuable for understanding site-specific processes, but their results cannot be readily extrapolated across sites and climate gradients to infer regional sensitivities.

Eddy covariance measurements of CO₂ fluxes collected continuously together with climate variables are available across temperate, boreal, and arctic ecosystems (Baldocchi et al., 2001, 2008). These data represent a valuable source of information for the analyses of winter RECO spatial and temporal variability. In this study, we focus on northern hemisphere sites from 36° N to 70° N, covering a climate gradient of 24 °C of mean annual temperature. In the first part, we investigate the importance of winter respiration, winter RECO and its contribution to annual RECO for different ecosystem types. The results are based on two different definition of the winter season. In the second part, we analyzed the temperature dependency of daily winter RECO site by site using an Arrhenius type model. We also considered a total of 252 site-years that have been aggregated to quantify the sensitivity of anomalies of winter RECO to temperature on inter-annual time scale. In the final part, which tries to open the path for spatial analysis of winter RECO, we examine the relationships between winter RECO and climate variables and productivity-related variables across sites.

2 Materials and methods

2.1 Data sources

2.1.1 Eddy covariance flux data

The eddy covariance data used in this study are extracted from La Thuile FLUXNET synthesis database which contains 965 site years processed according to standardized protocols (Papale et al., 2006) (<http://www.fluxdata.org>). Air temperature, upper soil temperature (between 2 and 10 cm depth) and precipitation measured both on a half-hourly and daily bases at each site were used. The net ecosystem exchange (NEE, in $\text{g C m}^{-2} \text{ day}^{-1}$) was measured at a 30 min time step, and flux toward the surface was considered to be negative in sign. The NEE time series can be separated into the gross fluxes GPP (gross primary productivity) and RECO (ecosystem respiration) where, by definition $\text{NEE} = -\text{GPP} + \text{RECO}$ (Reichstein et al., 2005). This flux-partitioning algorithm adopted short-term temperature sensitivity to extrapolate night-time respiration to daytime, and this approach avoids significantly biased estimates of RECO which can be obtained using long-term temperature sensitivity affected by confounding factors such as growth dynamics (Reichstein et al., 2005). This partitioning yields information about the ecosystem-scale processes controlling spatiotemporal variation in the measured NEE. Nighttime NEE on half-hourly time step is used for the derivation of winter RECO temperature sensitivity at each site, and other analyses are based on daily RECO. Ancillary observations of maximum LAI from site measurements were used in this study.

Out of the 255 sites located north of 36°N , a subset of 57 was identified which accomplished the following requirements: having at least two years of air and upper soil temperature, precipitation and RECO measurements and the missing gap is below 30% of the data for each site year. A total of 57 sites containing 256 site years of data were selected, covering evergreen needleleaf forest (100 site \times years), deciduous

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broadleaf forest (65), mixed forest (19), wetland (13), cropland (24) and grassland (34) (Table 1).

2.1.2 LAI dataset

Leaf Area Index data were retrieved for each investigated site from MODIS-Aqua downloaded from the ORNL-DAAC MODIS – Collection-5 LAI ASCII data (MYD15A2) (https://daac.ornl.gov). These LAI data have a spatial resolution of 1 km and a temporal resolution of 8-days. They also include quality control (QC) information about cloud and data processing conditions. Coarser resolution LAI data from a 1 km × 1 km area around each site were also collected during the observation period. Only LAI data without significant cloud contamination described in the LAI user's guide (http://landweb.nascom.nasa.gov/cgi-bin/QA_WWW/) within an area of 1 km × 1 km centered on each site were retained for each 8-day period to obtain the maximum and minimum LAI values for each site year. The seasonal amplitude (Δ LAI) is defined as the difference between maximum and minimum of LAI and can be considered as a proxy for recent carbon inputs to soil, i.e. substrate available for sustaining winter respiration.

2.2 Arrhenius equation to describe the temperature dependency of RECO

The temperature dependency of daily winter RECO at each site was analyzed using the Arrhenius type equation (Lloyd and Taylor, 1994):

$$R = R_{\text{ref}} \cdot \text{EXP} \left(\frac{E_0}{R_e} \cdot \left(\frac{1}{T_{\text{ref}}} - \frac{1}{T} \right) \right) \quad (1)$$

where, $T_{\text{ref}} = 273.16$ K (0°C), R_{ref} ($\text{g C m}^{-2} \text{d}^{-1}$) is a reference respiration rate at the reference temperature (T_{ref} , K) related both to the amount of substrate available for decomposers, and its quality (Lloyd and Taylor, 1994). E_0 (KJ mol^{-1}) is the activation

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energy parameter and represents the ecosystem respiration sensitivity to temperature, and R_e the universal gas constant. Across sites, this model was reformulated by adding the dependency of reference respiration on the site characteristics. The model accuracy was then assessed by a cross-validation technique: one site at a time was excluded using the remaining subset as the training set and the excluded one as the validation set, and the model was fitted against the training set and then applied to calculate the modeled value for the validation set.

2.3 Winter season definition

Two winter season definitions were tested to estimate the effect of an arbitrary choice to define the winter season in analyzing winter RECO drivers. The first one (D1) defines winter as the period during which the 10-day smoothed air temperature remained below 0°C for at least five consecutive days. It should be noted that the calculation of winter length according to D1 is based on mean air temperature of all available years for each site. The second definition (D2) defines winter as the 90-day period from 1 December to 28 February.

3 Winter RECO and its ratio to annual RECO among ecosystem types

Figure 1 shows the histogram of cumulative winter RECO based on total winter season – (a) and (b) – and the histogram of p -ratios – (c) and (d) – according to both definitions. The p -ratio is defined as the ratio of cumulative winter RECO to annual total RECO. These histograms contain data from all site-years. The total winter RECO for both winter definitions ranges from 5.1 to 192.9 g C m^{-2} (median = 66.9, 25th percentile = 45.7 and 75th percentile = 88.5) and from 0.6 to 240.5 g C m^{-2} (median = 57.5, 25th percentile = 27.9, and 75th percentile = 95.1), respectively. The p -ratio (%) varies from 1.0 to 37.8 (median = 7.4, 25th percentile = 5.1, and 75th percentile = 7.8) and from 0.2

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to 29.0 (median = 6.1, 25th percentile = 4.0, and 75th percentile = 8.7) for D1 and D2, respectively.

Table 2 provides the statistics of winter RECO rates and cumulative winter RECO for different ecosystem types. Deciduous broadleaf forests have the highest winter RECO (rates: 0.97–1.05 g C m⁻² d⁻¹; cumulative: 86.9–96.2 g C m⁻²), whereas wetlands have the lowest (rates: 0.21–0.23 g C m⁻² d⁻¹; cumulative: 19.2–31.5 g C m⁻²) with numbers in parenthesis showing the range between winter definitions D1 and D2. The winter RECO rates (cumulative winter RECO) range for evergreen needleleaf forest, mixed forest, grassland and cropland are 0.74–0.79 g C m⁻² d⁻¹ (66.2–67.0 g C m⁻²), 0.80–0.86 g C m⁻² d⁻¹ (72.4–75.4 g C m⁻²), 0.58–0.60 g C m⁻² d⁻¹ (54.4–52.2 g C m⁻²) and 0.52–0.53 g C m⁻² d⁻¹ (43.2–47.2 g C m⁻²), respectively. Using the definition D2, wetlands that are essentially wet tundra sites in the Arctic, have a smaller winter RECO, compared to definition D1 for which winter lasts 156 days. This can be expected due to microbial activity decreases rapidly as soil temperature descend towards –5 °C (Clein and Schimel, 1995) and wetland has the lowest soil temperature (–3.6 °C). Showing generic values for winter RECO among different ecosystem types is as important as improving the estimates of primary production often derived from remote-sensing indices (e.g. Bunn et al., 2007; Goetz et al., 2005, 2007) when trying to address the evolution of the total carbon balance, as pinpointed by Piao et al. (2008) focusing on autumn warming.

The *p*-ratio varies among ecosystem types (Table 2). Using definition D1, the highest *p*-ratio values (%) are found in the Arctic wetlands (10.3 ± 3.2, *N* = 13), intermediate values in evergreen needleleaf forest (8.3 ± 4.2, *N* = 100), deciduous broadleaf forest (9.0 ± 2.9, *N* = 65) and mixed forest (8.3 ± 2.0, *N* = 19), and the lowest values in grassland (6.8 ± 6.1, *N* = 34) and cropland (4.7 ± 2.3, *N* = 24). In contrast, when using definition D2 with a much shorter winter duration in the high latitudes, wetland (5.3 ± 1.7, *N* = 13) have the lower *p*-ratio. Another type of *p*'-ratio is also presented in Table 2, which is defined as the ratio of winter RECO rates to annual mean RECO. Compared to *p*-ratio, *p*'-ratio (%) is much less varied among different ecosystem types, and it

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ranges from 21.3 to 34.5 using D1 and from 21.2 to 31.2 using D2. Similar to p -ratio, the high productive cropland carries the lowest p' -ratio values (D1: 21.3 ± 9.9 ; D2: 21.2 ± 9.6), which might be related to agricultural management practices that removed crop residuals for winter respiration. With winter definition D1, p -ratio increase with latitude ($r = 0.20$, $p = 0.05$, data not shown) since higher-latitude sites often have longer winter length ($r = 0.51$, $p < 0.01$, data not shown). This implies that winter RECO in colder regions carries a higher relative contribution to total annual RECO than at warmer sites using D1 and thus further stresses the importance of winter RECO in the carbon balance of arctic and boreal ecosystems, as already pointed out by other studies (e.g. Oechel et al., 1997; Fahnestock et al., 1998; Bergeron et al., 2007). Due to sparse data for cold regions in global FLUXNET, the p -ratio (4.7–10.3%) is on average lower in this study than in previous work (15–50%) by Zimov et al. (1996) and Fahnestock et al. (1998), focused on arctic ecosystems. More in-situ winter RECO measurements in cold regions such as permafrost regions (e.g. Kononov et al., 2004) should be thus involved in the future for robust analysis of winter ecosystem respiration in high latitudes.

It should be noted that the use of the open-path gas analyzers for eddy covariance estimates of small fluxes relying on the WPL correction (Webb et al., 1998) can introduce the errors (e.g. Kondo and Tsukamoto, 2007), and CO_2 releases can be systematic underestimated during off-season periods especially in cold-climate ecosystems due to instrumental surface heating effects that are associated with open-path gas analyzers (e.g. Licor 7200) (Burba et al., 2008). For example, Burba et al. (2008) found that flux measurements made with open-path LI-7500 can underestimate CO_2 release by 33% during the winter season compared to closed-path instrument.

4 Temperature and productivity controls on winter RECO

4.1 Temperature sensitivity of winter RECO

Since daytime RECO is separated from NEE based on the temperature sensitivity of nighttime NEE in La Thuile dataset (Reichstein et al., 2005), for each site and using winter season definition D1, nighttime NEE on a half-hourly time step was regressed against the corresponding (soil or air) nighttime temperature during the whole winter season based on the Arrhenius function (Eq. 1) thus providing site-specific couples of parameters (R_{ref} , E_0).

Values of reference respiration rate R_{ref} range from 0.18 to 1.75 ($\text{g C m}^{-2} \text{d}^{-1}$) when air temperature is used as the predictor, and from 0.16 to 1.22 ($\text{g C m}^{-2} \text{d}^{-1}$) when soil temperature is used. Across all the sites, R_{ref} significantly increases with ΔLAI (Fig. 2a). This indicates that substrate availability and quality exerts a significant control on the spatial variation of R_{ref} across sites, and thus supports the conclusions of Grogan and Jonasson (2005) who found that R_{ref} was significantly reduced after removing plant and litter in a birch and heath tundra.

The activation energy E_0 increases with decreasing soil temperature across the sites (excluding the Arctic wetland site US-Atq) (Fig. 2b). The value of the correlation coefficient is very small, but significant. It has been assumed that microorganisms at temperatures around -10°C in Siberia are in a state of anabiosis (Vorobyova et al., 1997), and thus low E_0 (23.4 kJ mol^{-1}) might be expected due to microbial metabolic activity constrained by very cold winter soil temperature (around -11°C in US-Atq). R_{ref} positively correlate also with soil temperature ($r = 0.27$, $p < 0.01$, data not shown). Since R_{ref} can be interpreted as a proxy for substrate quality (Lloyd and Taylor, 1994; Mikan et al., 2002), it can be argued that the colder sites may contain a higher fraction of recalcitrant soil carbon, which decreases R_{ref} . Therefore, the inferred increase in E_0 at colder soil temperatures might be related to the presence of more recalcitrant soil organic compounds, with higher activation energy than labile compounds, according to

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kinetic theory (Bosatta and Agren, 1999; Davidson and Janssens, 2006). If US-Atq is not considered, a decreasing rate of $83.1 \text{ KJ mol}^{-1} \text{ K}^{-1}$ for E_0 has been estimated. The effects of such a decreased sensitivity of winter RECO to soil temperature at warmer sites could be tested in terrestrial ecosystem models. Extrapolating the relationship in Fig. 2 from space to time would imply that the future warming trends reduce the activation energy of winter soil C decomposition, hence dampening the potential increase of RECO with temperature.

4.2 Temperature sensitivity of winter RECO on inter-annual time scale

Owing to the short length of RECO and temperature records, temporal correlations between winter RECO and predictor climate variables are not applicable to study the inter annual sensitivity of RECO to climate in details at each site. Instead, we calculate annual winter RECO and winter temperature anomalies at each site, by removing the long-term mean RECO value from yearly values, and perform a least squares regression between all site-years anomalies of winter RECO and winter temperature to quantify the response of winter RECO to interannual variations in temperature. Results from this analysis show that winter RECO anomalies positively correlate with winter (D1 and D2) soil temperature anomalies (Fig. 3), which explained more (D1: $R^2 = 0.18$, $p < 0.01$, Fig. 3a; D2: $R^2 = 0.14$, $p < 0.01$, Fig. 3b) than air temperature (D1: $R^2 = 0.09$, $p < 0.01$; D2: $R^2 = 0.05$, $p < 0.01$, data not shown). The soil temperature was a better driver of winter RECO likely because of the influence of snow cover which acts as a thermal insulator controlling soil microbial activity (Zhang et al., 2005). This is consistent with the results of a six-year record of eddy covariance measurements at the Niwot Ridge Ameriflux site in the Rocky Mountains, Monson et al. (2006) showed that interannual variability of net carbon exchange is not controlled by air temperature anomalies, but rather by soil temperature anomalies which were controlled by snow depth. To check this observation with our dataset, daily snow water equivalent from AMSR-E/Aqua (Kelly et al., 2004) was used but we did not find significant relationship between anomalies of snow water equivalent and winter RECO (data not shown). This

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can be expected since the snow characteristics at site level can not be truly reflected by a remote sensing product at a spatial resolution of $25 \times 25 \text{ km}^2$. In addition, we found no significant relationship between winter RECO and precipitation anomalies (winter definition D1: $r = 0.00$, $p = 0.49$; D2: $r = 0.00$, $p = 0.71$) and no correlation with ΔLAI anomalies (D1: $r = 0.00$, $p = 0.44$; D2: $r = 0.00$, $p = 0.818$).

The winter RECO sensitivity to soil temperature defined by the linear regression slope q_1 ($\text{g C m}^{-2} \text{ d}^{-1} \text{ }^\circ\text{C}^{-1}$) calculated from the spatial relationship across sites (D1: $y = 0.14x + 0.71$, $R^2 = 0.55$, $p < 0.01$, $q_1 = 0.14$; D2: $y = 0.12x + 0.72$, $R^2 = 0.49$, $p < 0.01$, $q_1 = 0.12$ data not shown) is higher than the RECO temporal (inter-annual) sensitivity to soil temperature (D1: $y = 0.09x - 6E - 18$, $R^2 = 0.18$, $p < 0.01$, $q_1 = 0.09$; D2: $y = 0.07x + 1E - 17$, $R^2 = 0.14$, $p < 0.01$, $q_1 = 0.07$, Fig. 3a and b). This result might suggest that a 1°C warming increases winter ecosystem CO_2 loss by $0.12\text{--}0.14 \text{ g C m}^2 \text{ d}^{-1}$ based on the spatial relationship (range corresponding to D1 or D2 winter definitions) against only by $0.07\text{--}0.09 \text{ g C m}^2 \text{ d}^{-1}$ based on the temporal relationship. The difference between these two winter RECO temperature sensitivities is due to the fact that inter-annual variation in winter RECO temperature sensitivity is mainly driven by direct climate effects, but the spatial variability accounts both for transient climate effects on respiration and long-term climate-induced biological variation in space (e.g. aboveground biomass, soil organic carbon and litter) that support the respiration (Hibbard et al., 2005). For this reason the application of the two sensitivities in models for the future projections of winter RECO may be more complex than thought. Temperature sensitivity as observed in time may be appropriate for simulating short term responses and space sensitivity for representing the long term (equilibrium) responses. Thus, simply projecting winter RECO in response to future warming based on spatial relationships incorporated in models can overestimate CO_2 losses by ecosystems.

4.3 Environmental and biotic controls on winter RECO across sites

Under the winter definition D1, winter RECO is found to increase exponentially with increasing air temperature ($R^2 = 0.66$, $p < 0.01$; Fig. 4a) and soil temperature ($R^2 = 0.65$,

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validation of the regression models in Eqs. (2) and (3) performed using cross-validation approach (Fig. 5) shows that 67% and 62% of winter RECO variance can be explained by Eqs. (2) and (3). Given that temperature is the dominant controlling factor of winter RECO across sites and co-varies with some of the other potential drivers, we regressed the fit residuals of Eqs. (2) and (3) against winter duration and winter precipitation to determine if these two alternative drivers could explain additional variance. There was no significant correlation between the fit residuals and either winter precipitation (Eq. 2: $r = 0.00$, $p = 0.756$; Eq. 3: $r = 0.01$, $p = 0.889$, data not shown) or winter length (Eq. 2: $r = 0.00$, $p = 0.864$; Eq. 3: $r = 0.06$, $p = 0.179$, data not shown). Both Eqs. (2) and (3) describe empirically the winter RECO spatial variability and thus have predictive power to extrapolate winter RECO on the continental scale.

5 Conclusions

Availability of climate and eddy covariance flux data across different ecosystems opens a new opportunity to quantify winter RECO and its empirical spatial and temporal controls across North Hemisphere ecosystems. Given a winter definition based upon temperature below the freezing point, we found an increase in the ratio of winter to annual respiration towards higher latitude. This shows that the relative importance of winter processes in controlling respiration is higher than that of summer processes. More research is therefore needed to include winter RECO in order to assess annual carbon budgets, especially at high latitudes where biogeochemical models often assume zero decomposition in cold winter.

Our empirical characterization of temperature controls on winter RECO has two major implications. First, winter RECO temperature sensitivity obtained on space and temporal scales should be treated differently, since the RECO sensitivity to warming obtained from spatial gradients will definitely be exaggerated when extrapolated to future warming. Second, soil temperature has a larger predictive power than air temperature in explaining interannual variations of winter RECO, likely through snow depth

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thermal isolation effects already indicated by individual studies. However, this should be further explored in future studies with an access to more in-situ snow data. This indicates that winter carbon exchanges in a future warmer northern hemisphere can not simply be deduced from air temperature changes, but need to account for interactions between soil carbon, soil temperature, moisture, and snow cover effects (start and end of snow accumulation, snow density and structure) on soil thermal regime.

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Table 1. Sites characteristic in this study.

Site	Type ¹	Latitude	Longitude	Index	Annual Precip. (mm)	Annual Temp. (°C)	WLEN (D1) (d)	Δ LAI (SD) ($m^2 m^{-2}$)	WRECO rates (D1) (SD) ($g C m^{-2} d^{-1}$)	WRECO rates (D2) (SD) ($g C m^{-2} d^{-1}$)	Available years
AT-Neu*	GRA	47.1	11.3	1	1040	6.3	90	5.8 (0.35)	1.18 (0.24)	1.1 (0.25)	2002–2005
BE-Vie	MF	50.3	6	2	1065	7.4	72	5.4 (0.18)	1.18 (0.18)	1.13 (0.17)	1996–2005
CA-Ca1	ENF	49.9	-125.3	3	1369	9.9	37	5.6 (0.63)	1.41 (0.15)	1.51 (0.21)	1998–2004
CA-Ca2*	ENF	49.9	-125.3	4	1474	9.9	47	4.4 (0.71)	1.26 (0.30)	1.27 (0.23)	2000–2004
CA-Let	GRA	49.7	-112.9	5	398	5.4	103	1.1 (0.48)	0.19 (0.07)	0.18 (0.06)	1998–2004
CA-Mer	WET	45.4	-75.5	6	891	6.1	120	5.5 (0.30)	0.33 (0.04)	0.3 (0.04)	1998–2004
CA-Oas	DBF	53.6	-106.2	7	429	0.3	161	6 (0.18)	0.51 (0.08)	0.34 (0.08)	1997–2004
CA-Obs	ENF	54	-105.1	8	406	0.8	167	3.9 (0.22)	0.45 (0.06)	0.28 (0.04)	1999–2004
CA-Ojp	ENF	53.9	-104.7	9	431	0.1	165	3 (0.44)	0.23 (0.04)	0.12 (0.03)	1999–2004
CA-Qcu*	ENF	49.3	-74	10	950	0.1	170	2.2 (0.21)	0.24 (0.06)	0.14 (0.01)	2001–2005
CA-Qfo	ENF	49.7	-74.3	11	962	-0.4	161	4 (0.15)	0.45 (0.08)	0.31 (0.05)	2004–2005
CA-SJ1*	ENF	53.9	-104.7	12	430	0.1	176	2.3 (0.16)	0.14 (0.07)	0.08 (0.04)	2001–2004
CA-SJ2	ENF	53.9	-104.6	13	430	0.1	167	1.3 (0.49)	0.06 (0.01)	0.02 (0.01)	2003–2004
CA-TP4*	ENF	42.7	-80.4	14	936	8.7	107	5.8 (0.14)	0.72 (0.02)	0.69 (0.03)	2003–2004
CA-WP1*	MF	55	-112.5	15	461	1.1	145	3.9 (0.28)	0.2 (0.01)	0.12 (0.01)	2003–2004
CH-Oe1*	GRA	47.3	7.7	16	945	9.1	81	2.4 (0.39)	0.91 (0.26)	0.9 (0.24)	2002–2005
CN-HaM*	GRA	37.4	101.2	17	577	-0.8	173	4.7 (0.28)	0.16 (0.07)	0.02 (0.02)	2002–2003
CZ-BK1	ENF	49.5	18.5	18	1026	4.7	105	5.8 (0.60)	0.58 (0.01)	0.59 (0.02)	2004–2005
DE-Bay	ENF	50.1	11.9	19	1159	5.2	92		1.28 (0.12)	1.23 (0.14)	1997–1998
DE-Geb*	CRO	51.1	10.9	20	444	8.7	84	5.7 (0.61)	0.62 (0.30)	0.61 (0.30)	2004–2005
DE-Hai	DBF	51.1	10.5	21	780	7.2	76	6.2 (0.27)	1.08 (0.15)	1.08 (0.13)	2001–2004
DE-Meh	GRA	51.3	10.7	22	695	7.8	83	5.1 (0.73)	0.58 (0.09)	0.59 (0.09)	2003–2005
DE-Tha	ENF	51	13.6	23	643	8.1	68	5.7 (0.49)	1.02 (0.12)	1.03 (0.11)	1996–2005
DK-Sor	DBF	55.5	11.6	24	573	8	70	5.8 (0.24)	1.75 (0.27)	1.66 (0.23)	1996–2005
FI-Hyy	ENF	61.8	24.3	25	620	2.2	135	5.9 (0.57)	0.55 (0.14)	0.49 (0.13)	1996–1998, 2000–2002, 2004
FI-Kaa	WET	69.1	27.3	26	454	-1.4	174	1.5 (0.12)	0.17 (0.06)	0.16 (0.06)	2000, 2003–2005
FI-Sod	ENF	67.4	26.6	27	525	-1.1	161	2.2 (0.23)	0.4 (0.11)	0.34 (0.18)	2000–2001, 2003–2005
FR-Hes	DBF	48.7	7.1	28	793	9.2	74	5.8 (0.5)	1.33 (0.27)	1.21 (0.25)	1997–1998, 2000–2005
HU-Bug*	GRA	46.7	19.6	29	555	10.5	85	1.5 (0.12)	0.44 (0.14)	0.48 (0.16)	2002–2005
IT-Amp*	GRA	41.9	13.6	30	945	10.6	69	2 (0.17)	0.97 (0.22)	1.01 (0.24)	2002–2004
IT-Col	DBF	41.8	13.6	31	971	7.3	100	6.3 (0.35)	0.8 (0.13)	0.77 (0.15)	1996, 2000, 2004
IT-MBo*	GRA	46	11	32	1185	5.4	111	5.8 (0.36)	0.86 (0.23)	0.87 (0.20)	2003–2005
IT-Ren	ENF	46.6	11.4	33	965	6.2	130	5.4 (0.24)	0.43 (0.12)	0.38 (0.22)	2001–2005
JP-Tak	DBF	36.1	137.4	34	1024	6.5	114	6.2 (0.12)	0.57 (0.16)	0.54 (0.17)	2000–2003
JP-Tom*	MF	42.7	141.5	35	1156	6.7	105	6 (0.32)	0.52 (0.05)	0.47 (0.05)	2001–2002
NL-Loo	ENF	52.2	5.7	36	786	9.4	33	5.7 (0.46)	2.1 (0.55)	2.08 (0.42)	1996–1999, 2002–2005

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Table 1. Continued.

Site	Type ¹	Latitude	Longitude	Index	Annual Precip. (mm)	Annual Temp. (°C)	WLEN (D1) (d)	Δ LAI (SD) ($m^2 m^{-2}$)	WRECO rates (D1) (SD) ($g C m^{-2} d^{-1}$)	WRECO rates (D2) (SD) ($g C m^{-2} d^{-1}$)	Available years
RU-Fyo	ENF	56.5	32.9	37	671	4.4	123	5.9 (0.35)	0.86 (0.21)	0.8 (0.27)	1998–2005
US-Atq*	WET	70.5	−157.4	38	93	−12.3	253	0.9 (0.1)	0.02 (0.01)	0 (0.00)	2003–2005
US-Bkg*	GRA	44.3	−96.8	39	586	6	126	1.8 (0.06)	0.19 (0.10)	0.14 (0.10)	2004–2005
US-Bo1*	CRO	40	−88.3	40	991	11	77	4.5 (0.41)	0.42 (0.32)	0.41 (0.27)	1996–1998, 2001–2006
US-Bo2*	CRO	40	−88.3	41	991	11	90	4.5 (0.41)	0.56 (0.47)	0.55 (0.50)	2004–2005
US-Ha1	DBF	42.5	−72.2	42	1071	6.6	101		1.37 (0.30)	1.34 (0.31)	1991–1992, 1994–1998
US-Ho1	ENF	45.2	−68.7	43	1070	5.3	115	5.5 (0.22)	0.59 (0.14)	0.53 (0.13)	1996–2003
US-IB2*	GRA	41.8	−88.2	44	930	9	105	1.7 (0.29)	0.49 (0.09)	0.42 (0.09)	2004–2005
US-Ivo	WET	68.5	−155.8	45	304	−8.3	241	2 (0.06)	0.06 (0.06)	0.03 (0.02)	2003–2004
US-LPH	DBF	42.5	−72.2	46	1071	6.7	120	6.1 (0.22)	0.89 (0.19)	0.79 (0.27)	2002–2004
US-MMS*	DBF	39.3	−86.4	47	1032	10.9	73	5.9 (0.11)	0.98 (0.19)	0.94 (0.19)	2000–2004
US-MOz*	DBF	38.7	−92.2	48	878	13.5	70	6.4 (0.21)	0.87 (0.36)	0.92 (0.20)	2004–2005
US-NR1	ENF	40	−105.5	49	595	0.4	177	4.3 (0.22)	0.82 (0.30)	0.66 (0.28)	1999, 2002
US-Ne1	CRO	41.2	−96.5	50	790	10.1	81	2.3 (0.29)	0.63 (0.04)	0.64 (0.02)	2001–2004
US-Ne2	CRO	41.2	−96.5	51	789	10.1	82	2.1 (0.24)	0.6 (0.11)	0.6 (0.12)	2002–2004
US-Ne3	CRO	41.2	−96.4	52	784	10.1	82	2.2 (0.38)	0.57 (0.06)	0.57 (0.06)	2001–2004
US-PFa	MF	45.9	−90.3	53	823	4.3	129		0.55 (0.09)	0.53 (0.12)	1996–1998
US-Syv	MF	46.2	−89.3	54	826	3.8	141	6.3 (0.19)	0.50 (0.01)	0.4 (0.35)	2002, 2004–2005
US-UMB	DBF	45.6	−84.7	55	803	5.8	124	6.4 (0.2)	0.85 (0.04)	0.79 (0.04)	1999–2002
US-WCr	DBF	45.8	−90.1	56	787	4	132	6 (0.15)	0.65 (0.18)	0.48 (0.17)	1999–2002, 2004–2005
US-Wrc	ENF	45.8	−122	57	2452	9.5	51	5.7 (0.38)	1.65 (0.14)	1.26 (0.01)	2000–2001

Type: DBF: deciduous broadleaf forests; ENF: evergreen needleleaf forests; GRA: grasslands; CRO: croplands; WET: wetlands; MF (mixed forests).

* denotes the sites that use open-path gas analyzer.

Annual precip. and Annual temp. represent annual total precipitation and mean annual temperature, respectively.

WLEN is the winter length (unit: day).

Δ LAI: the average difference between maximum and minimum of MODIS LAI ($m^2 m^{-2}$) from corresponding available years and the MODIS LAI data is only available after year 2000.

WRECO are average winter ecosystem respiration rates ($g C m^{-2} d^{-1}$) for D1 (air temperature $< 0^\circ C$) and D2 (December–February) over available years, respectively.

SD is standard deviation.

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Table 2. Summary statistics of winter ecosystem respiration (RECO) rates ($\text{g C m}^{-2} \text{d}^{-1}$), cumulative winter RECO (g C m^{-2}), p -ratio values (%) and p' -ratio values (%) with different winter definitions across ecosystem types.

Vegetation type	Winter (air temperature < 0 °C)					Winter (December–February)					
	Num	Winter Length (SD) d	Cumulative Winter RECO (SD) (g C m^{-2})	p -ratio (SD) (%)	Winter RECO rates (SD) ($\text{g C m}^{-2} \text{d}^{-1}$) × 0.1	p' -ratio (SD) (%)	Num	Cumulative Winter RECO (SD) (g C m^{-2})	p -ratio (SD) (%)	Winter RECO rates (SD) ($\text{g C m}^{-2} \text{d}^{-1}$) × 0.1	p' -ratio (SD) (%)
DBF	65	102 (32) ^a	96.2 (28.9) ^d	9.0 (2.9) ^b	10.5 (4.6) ^c	34.5 (12.1) ^a	65	86.9 (42.3) ^b	7.8 (3.2) ^a	9.7 (4.8) ^b	31.2 (13.0) ^a
ENF	100	113 (50) ^a	66.2 (27.8) ^{b,c}	8.3 (4.2) ^{a,b}	7.9 (5.7) ^{b,c}	30.1 (14.7) ^a	100	67.0 (53.9) ^b	6.6 (4.3) ^a	7.4 (6.0) ^b	26.9 (17.3) ^a
MF	19	99 (31) ^a	75.4 (23.1) ^{c,d}	8.3 (2.0) ^{a,b}	8.6 (3.9) ^{b,c}	33.1 (12.0) ^a	19	72.4 (35.6) ^b	7.6 (3.3) ^a	8.0 (4.0) ^b	30.7 (13.4) ^a
GRA	34	99 (24) ^a	54.4 (33.4) ^{a,b,c}	6.8 (6.1) ^{a,b}	6.0 (3.9) ^{a,b}	26.3 (22.2) ^a	34	52.2 (35.8) ^{a,b}	6.1 (5.2) ^a	5.8 (3.9) ^{a,b}	24.9 (21.1) ^a
CRO	24	81 (4) ^a	43.2 (20.0) ^{a,b}	4.7 (2.3) ^a	5.3 (2.4) ^{a,b}	21.3 (9.9) ^a	24	47.2 (20.5) ^{a,b}	5.2 (2.4) ^a	5.2 (2.2) ^{a,b}	21.2 (9.6) ^a
WET	13	156 (47) ^b	31.5 (12.9) ^a	10.3 (3.2) ^b	2.3 (1.2) ^a	24.6 (5.9) ^a	13	19.2 (10.4) ^a	5.3 (1.7) ^a	2.1 (1.1) ^a	21.5 (7.1) ^a

ENF, DBF, MF, GRA, CRO and WET represent evergreen needle leaf forest, deciduous broadleaf forest, mixed forest, grassland, cropland and wetland respectively.

p -ratio and p' -ratio is the ratio of cumulative winter RECO to annual total RECO and the ratio of winter RECO rates to annual mean RECO rates, respectively. SD is the standard deviation, and (SD) within a column followed by different letters (^a, ^b and ^c) were significantly different ($p < 0.05$).

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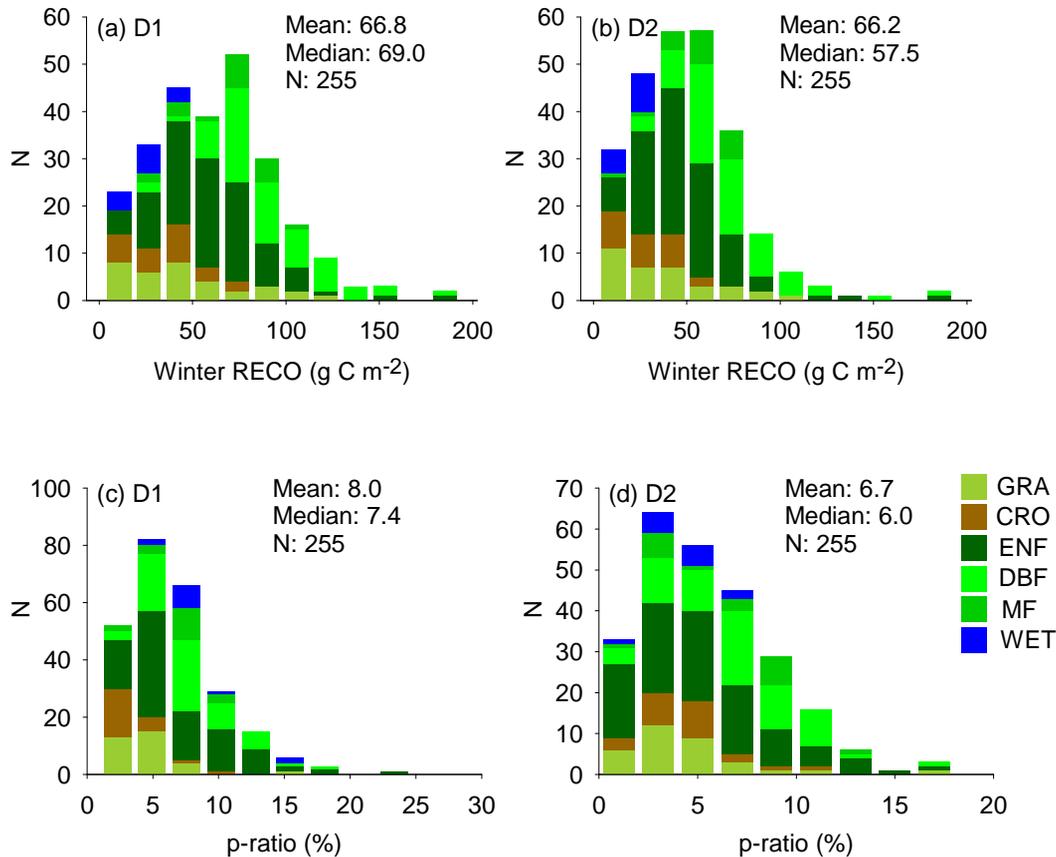


Fig. 1. Frequency histograms of total winter ecosystem respiration (RECO) and the ratio of cumulative winter RECO to annual total RECO (p -ratio) (%) according to both winter definitions across all of the site-years.

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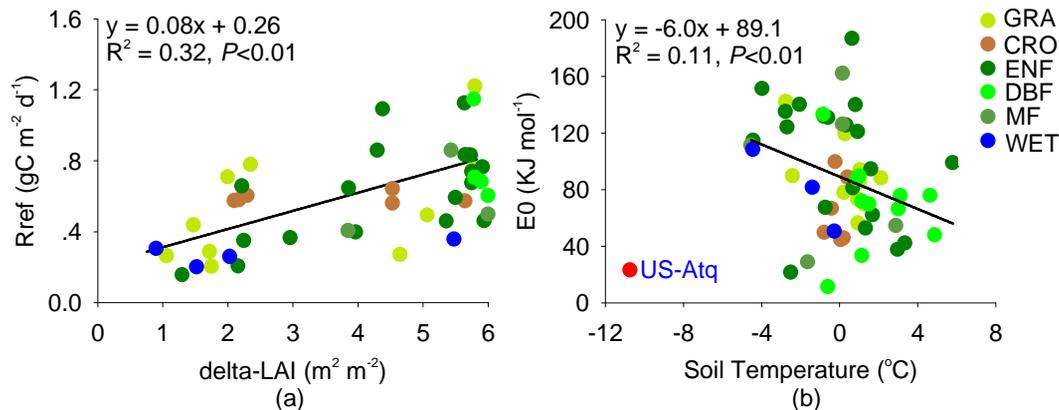


Fig. 2. Reference winter respiration (R_{ref}) dependence on Δ LAI (the difference between seasonal maximum and minimum leaf area index) (a) and activation energy (E_0) dependence on soil temperature (b). All values are calculated according to winter definition D1 (air temperature $< 0^{\circ}\text{C}$).

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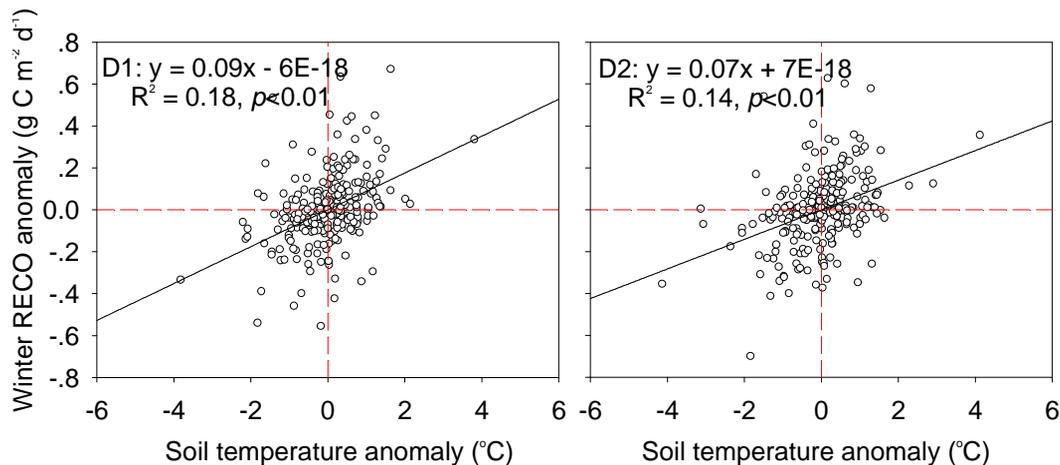


Fig. 3. Winter ecosystem respiration (RECO) anomalies dependence on soil temperature anomalies according to winter definition D1 (air temperature < 0 °C) **(a)** and D2 (December–February) **(b)**.

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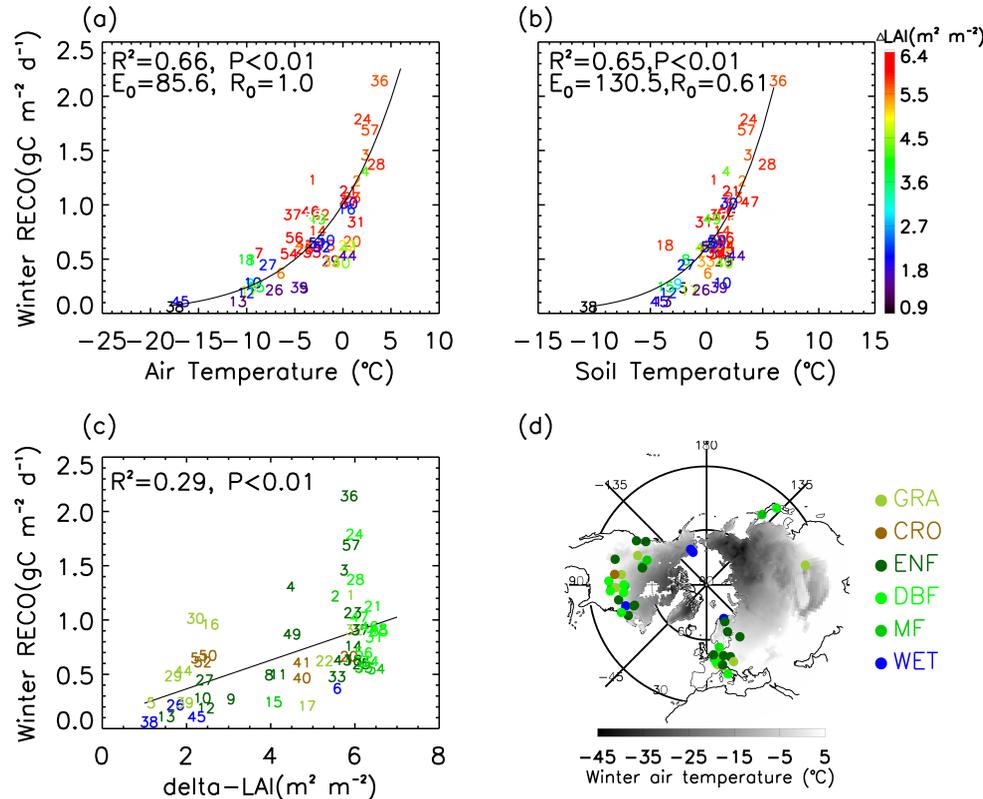


Fig. 4. Relationships between winter ecosystem respiration (RECO) and air temperature **(a)**, soil temperature **(b)** and ΔLAI (the difference between seasonal maximum and minimum leaf area index) **(c)** across sites with winter definition D1 (air temperature $< 0^{\circ}\text{C}$). Spatial distribution of eddy covariance sites are displayed in **(d)**. Winter air temperature from 1 December to 28 February is used as the background in **(d)**. Model parameters (Activation energy E_0 and reference winter RECO R_{ref}) values are also reported. And ΔLAI is on the color scale. The data points in **(c)** and **(d)** are colored by ecosystems.

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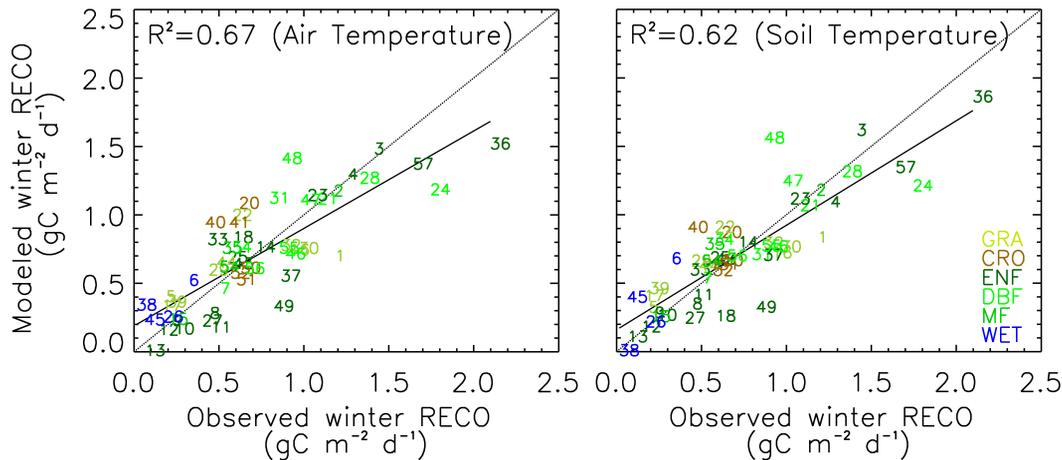


Fig. 5. Modeled versus observed winter ecosystem respiration (RECO) values based on winter D1 (air temperature < 0°C). Modeled values are calculated according to Eq. (2) (a) and Eq. (3) (b). Shown are the root mean square and the linear regression between observed and modeled values. The regression line (solid) is compared to the 1:1 line (broken).

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