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Convergence of potential net ecosystem production among contrasting C₃ grasslands

Matthias Peichl^{1,2,*}, Oliver Sonnentag³, Georg Wohlfahrt⁴, Lawrence B. Flanagan⁵, Dennis D. Baldocchi⁶, Gerard Kiely², Marta Galvagno⁷, Damiano Gianelle⁸, Barbara Marcolla⁸, Casimiro Pio⁹, Mirco Migliavacca¹⁰, Michael B. Jones¹¹, and Matthew Saunders¹²

¹Swedish University of Agricultural Sciences, Department of Forest Ecology & Management, Umeå, Sweden ²University College Cork, Center for Hydrology, Micrometeorology & Climate Change, Department of Civil and Environmental Engineering, Cork, Rep. of Ireland. ³Université de Montréal, Département de Géographie, Montréal, QC, Canada ⁴Universität Innsbruck, Institut für Ökologie, Innsbruck, Austria ⁵University of Lethbridge, Department of Biological Sciences, Lethbridge, AB, Canada ⁶University of California at Berkeley, Department of Environmental Science, Policy and Management, Ecosystem Sciences Division, Berkeley, CA, USA ⁷Environmental Protection Agency of Aosta Valley, ARPA Valle d'Aosta, Climate Change Unit, Aosta, Italy ⁸Fondazione Edmund Mach, IASMA Research and Innovation Centre, Sustainable Agro-ecosystems and Bioresources Department, San Michele all'Adige, (TN), Italy ⁹University of Aveiro, CESAM & Department of Environment, Aveiro, Portugal ¹⁰European Commission, DG-JRC, Institute for Environment and Sustainability, Climate Change and Risk Management Unit, Ispra, VA, Italy ¹¹University of Dublin, Botany Department, Trinity College, Dublin, Ireland ¹²University College Dublin, School of Biology & Environmental Science, Dublin, Ireland

Abstract

Metabolic theory and body size dependent constraints on biomass production and decomposition suggest that differences in the intrinsic potential net ecosystem production (NEP_{POT}) should be small among contrasting C₃ grasslands and therefore unable to explain the wide range in the annual apparent net ecosystem production (NEP_{APP}) reported by previous studies. We estimated NEP_{POT} for nine C₃ grasslands under contrasting climate and management regimes using multi-year eddy covariance data. NEP_{POT} converged within a narrow range suggesting little difference in the net carbon dioxide uptake capacity across C₃ grasslands. Our results indicate a unique feature of C₃ grasslands compared to other terrestrial ecosystems and suggest a state of stability in NEP_{POT} due to tightly coupled production and respiration processes. Consequently, the annual NEP_{APP} of C₃ grasslands is primarily a function of seasonal and short-term environmental and management constraints, and therefore especially susceptible to changes in future climate patterns and associated adaptation of management practices.

*Corresponding author; current address: Swedish University of Agricultural Sciences, Department of Forest Ecology & Management, 901 83 Umeå, Sweden, Phone: +46 90 786 8463; Matthias.Peichl@slu.se.

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MP conceived the study, analyzed the data, wrote the paper

OS conceived the study, assisted with paper writing, provided substantial intellectual input

GW conceived the study, provided data, provided substantial intellectual input

LBF conceived the study, provided data, provided substantial intellectual input

DDB, GK, MG, DG, BM, CP provided data and substantial intellectual input

MBJ provided data

MM and MS provided substantial intellectual input

Keywords

climate; ecosystem traits; eddy covariance; inter-comparison; grassland ecosystem functioning; management practices; metabolic theory

INTRODUCTION

Grasslands cover approximately 40% of the Earth's surface and are located across contrasting climatic and management gradients, which results in considerable variation in ecosystem structure, environmental conditions and disturbance regimes (White et al. 2000; Gilmanov et al. 2010). A decade of eddy covariance measurements made over C₃ grasslands across the globe has revealed considerable differences in their annual apparent net ecosystem production (NEP_{APP}), ranging approximately from -300 to 500 g C m² y⁻¹ APP (following the ecological sign convention, the positive sign indicates net uptake of carbon dioxide (CO₂)) (Novick et al. 2004; Ma et al. 2007; Wohlfahrt et al. 2008a, 2008b; Gilmanov et al. 2010). A number of studies have shown that environmental conditions and management practices commonly account for a large proportion of the variability in the annual apparent NEP (NEP_{APP}) (Wohlfahrt et al. 2008a, 2008b; Gilmanov et al. 2010; Schmitt et al. 2010; Zeeman et al. 2010). However, little is known about the extent to which contrasting C₃ grassland ecosystems exhibit different potentials for NEP (NEP_{POT}; i.e., the maximum net CO₂ uptake reached during optimum conditions) due to differences in ecosystems traits, environmental conditions and management practices. However, such understanding is necessary since variations in NEP_{POT} might regulate the maximum 'baseline' capacity for the annual net CO₂ uptake, and thus, provide some additional explanatory power (supplementary to the seasonal and short-term effects from environmental and management constraints) for the observed range in annual NEP_{APP} among global C₃ grasslands.

Although NEP is a flux that can be measured by the eddy covariance technique, it is important to realize that NEP itself is not a process *per se* but rather the net result of the imbalance between the two ecosystem processes of gross ecosystem production (GEP; i.e. the micrometeorological term equivalent to gross primary production, GPP, assuming that reabsorption of respired CO₂ within the canopy is negligible) and ecosystem respiration (ER) (i.e., NEP = GEP - ER) (Chapin III et al. 2006). Furthermore, ER is composed of both autotrophic (R_a) and heterotrophic (R_h) respiration. After accounting for the carbon loss via R_a, which is commonly considered to be a conservative fraction of GEP (Gifford 1994), NEP is essentially the difference between the net primary production (NPP; NPP = GEP - R_a) and R_h (i.e., NEP = NPP - R_h). Remarkably, recent studies have indicated that R_h is strongly controlled by the abundance and properties of the dominant plant functional type resident in an ecosystem (Chapin III 2003; Bardgett 2011). Specifically, slow-growing vegetation is known to produce low-quality litter which decomposes more slowly compared with fast-growing vegetation types. The more labile and easily decomposable litter produced by fast-growing vegetation may also stimulate soil microbial activity through the enhanced release of labile carbon forms contained in root exudates (Hobbie 1992; De Deyn et al. 2008). In return, changes in the mineralization rate affect nutrient availability and uptake and thus plant productivity, which suggests a strong correlation and feedback between NPP and R_h (Hobbie 1992; De Deyn et al. 2008; Bardgett 2011). Moreover, metabolic theory suggests that body size constraints on metabolic rates of biomass production and decomposition may further condition the relationship between NPP and R_h (Brown et al. 2004; Allen et al. 2005). This is because any change in body size and/or NPP rates would be counterbalanced by a subsequent adjustment of decomposer communities and/or rates of R_h and *vice versa* driven by a supply (i.e., amount and quality) - demand mechanism. Given a

10 000-fold increase in carbon turnover rates moving from tree- to phytoplankton-dominated ecosystems (Allen et al. 2005), such adjustment is likely to occur on relatively short time scales in grassland ecosystems, which are characterised by a short canopy (i.e. relatively small body size). Consequently, one might expect that ecosystems dominated by a given plant functional type might converge to a very similar NEP_{POT} under optimum conditions (i.e., conditions during which the imbalance between NPP and R_h is maximized by stimulation of NPP and/or suppression of R_h). This is also in line with the metabolic theory that predicts that after adjusting metabolic rates for body size and temperature, organisms should have similar rates of production (Brown et al. 2004). In contrast to similar NEP_{POT} under optimum conditions, NEP_{APP} as measured by the eddy covariance method in observational studies, should vary for a given ecosystem type in contrasting regions of the world due to the different region- and site-specific constraints on NPP and R_h .

The three main controls on NPP and R_h that subsequently determine NEP_{POT} include the stationary long-term effects from i) environmental conditions (e.g., adaptation to annual mean air temperature, radiation, total precipitation, etc.), ii) management practices (e.g., adaptation to fertilizer input, grazing, cutting) and iii) ecosystem traits (Figure 1). In this context, ecosystem traits are understood to encompass any plant- or soil-related ecosystem property such as species composition, maximum leaf area index (LAI), maximum leaf photosynthetic capacity, litter quality and soil nutrients. Each of these three controls may affect ecosystem production and respiration processes through modifications of the carbon assimilation, allocation and turnover mechanisms and thus may alter the intrinsic potential for net CO_2 uptake.

Given such a baseline for potential net CO_2 uptake, NEP_{APP} then deviates from NEP_{POT} as a function (f) of seasonal and short-term constraints from environmental conditions (e) and management (m) events, each bound between zero and unity, which reduce the imbalance between NPP and R_h and thus determine NEP_{APP} on a daily (superscript d) and ultimately annually (superscript a) basis (Eq.1, Figure 1):

$$NEP_{APP}^a = \sum_{d=1}^{365} NEP_{APP}^d = NEP_{POT} \sum_{d=1}^{365} f(e^d) f(m^d) \quad (\text{Eq.1})$$

Constraints from environmental conditions, i.e., $f(e)$ in Eq. (1), are understood to comprise effects resulting from i) seasonal variation in environmental conditions which determine the length and timing of the growing season period typical for a given climate region (e.g., the occurrence of summer drought in Mediterranean climates or the existence of a winter snow cover at high latitudes/altitudes) as well as from ii) short-term weather and inter-annual deviations from the long-term mean seasonal climate (e.g., a summer drought in a temperate climate).

Previous studies have quantified and compared maxima of daily or annual GEP_{APP} and NEP_{APP} for individual years (Falge et al. 2002a, 2002b; Gilmanov et al. 2010). However, daily maxima may be subject to spurious artefacts and data spikes due to unusual events (e.g., short-term effects from weather, disturbance, management, atmospheric phenomena, etc.) and the inherent random variability of eddy covariance flux measurements (Moncrieff et al. 1996; Massman & Lee 2002; Jolly et al. 2005; Stoy et al. 2009). Meanwhile annual estimates are likely constrained by environmental conditions and/or management (Wohlfahrt et al. 2008a; Stoy et al. 2009). Thus, neither daily nor annual maxima might serve as a suitable indicator for NEP_{POT} . Here, we derive a robust estimate of NEP_{POT} over a time frame of 30 days, which approximately spans the duration of the peak net production period as evident from the slope of the cumulative NEP_{APP} . The main underlying assumption is that NEP_{POT} is not necessarily reached in every year and therefore the true NEP_{POT} is best

approximated from the maximum 30-day NEP_{APP} observed over multiple years. To our knowledge, NEP_{POT} by such definition has not yet been explicitly investigated for grasslands or any other terrestrial ecosystem type. In this paper we use the outlined approach to explore multi-year eddy covariance data for the existence of a convergence of NEP_{POT} for nine different C_3 grassland ecosystems from three contrasting climate regions to test the hypothesis that differences in NEP_{POT} are small among contrasting C_3 grasslands.

METHODS

Site selection

The primary criteria for site selection were (i) the availability of four or more complete years of data (with two exceptions, see below) and (ii) their location in one of three generalized and contrasting climate regions:

- i. cold-temperate: region with continuous winter snow cover and/or freezing temperatures,
- ii. Mediterranean: region with dry, hot summers and cool, wet winters,
- iii. maritime: region with ample water availability and without snow cover and/or freezing temperatures.

The cold-temperate sites included three alpine sites at different elevations as well as one continental prairie site. We also added two sites with less than four years of continuous data (i.e., the cold-temperate alpine site Torgnon and the maritime site Carlow) to determine whether NEP_{POT} could also be confidently estimated for smaller data sets. Another reason to include the Torgnon site was to obtain an elevation gradient among the cold-temperate alpine sites. The final selected grasslands were the cold-temperate alpine sites Neustift (N), Monte Bondone (MB), Torgnon (TN) and the cold-temperate prairie site Lethbridge (L), the Mediterranean sites Vaira (V) and Tojal (T), and the maritime sites Dripsey (D), Wexford (W) and Carlow (CW). In addition, the site selection contained a gradient of management intensity encompassing natural (abandoned or unmanaged) (L, TN), extensively (V, T, MB) and intensively (N, D, W, CW) managed grasslands. The site-specific details and references are summarized in Table 1.

Data

We used gap-filled flux and meteorological (precipitation, soil temperature, photosynthetically-active photon flux density, and volumetric soil water content) data supplied by either the principal investigators (PI) at the sites D, W, N, MB, TN, L or retrieved as Level 4 data (quality checked and gap-filled) data from the CarboEurope (T, CW) and Ameriflux (V) databases, both regional networks within FLUXNET (<http://fluxnet.ornl.gov/>). The procedures for gap-filling and partitioning into the component fluxes GEP and ER followed the methods described by Reichstein et al. (2005) (all but L, D, W) and Barr et al. (2004) (L, D, W). Previous studies have shown consistent estimates of NEP, GEP and ER obtained by the different methods (Moffat et al. 2007; Lasslop et al. 2010). Positive NEP values indicate net CO_2 uptake (i.e., $GEP > ER$). Although the eddy covariance technique provides estimates of the biosphere-atmosphere net ecosystem exchange of CO_2 (NEE), we instead use the term NEP (with opposite sign convention to NEE) with the purpose of maintaining an ecological perspective. It is however important to note that due to the underlying measurement methodology, the term NEP as used here does not include (commonly small) lateral losses of respiration-derived dissolved carbon (Chapin III et al. 2006). Additional supporting environmental data including information on LAI and soil properties were either obtained from the site PIs or retrieved from the respective FLUXNET databases.

Potential NEP, GEP and ER

To obtain an estimate of NEP_{POT} we first determined the mean NEP_{APP} over 30 consecutive days (i.e., the mean of 30 daily totals of NEP_{APP}) at each site using a moving window (with 1-day increments starting from January 1) over all available site-years. In a second step, the maximum of all 30-day averages observed across all years at each site was defined as the site-specific NEP_{POT} . Thus, we assume that the maximum *apparent* rate occurring under optimum conditions (i.e., conditions resulting in highest productivity with concurrent lowest respiration) within a multi-year time series should approach or ideally equal the *potential* rate. Clearly, the probability of finding the true NEP_{POT} increases with the number of years available at a given site. It is therefore possible that NEP_{POT} was underestimated at the CW and TN sites where only two years of data were available. Furthermore, optimum conditions may have never occurred even within a multi-year data set at a given site. In this case however, the continued constraint on ecosystem functioning is a site characteristic and the period with the least severe constraints was, therefore, considered 'optimum' instead. Furthermore, we estimated 30-day means of apparent GEP and ER (GEP_{APP} and ER_{APP}) with the same approach used to determine 30-day mean NEP_{APP} , and denoted GEP_{APP} and ER_{APP} at the time of NEP_{POT} as GEP_{POT} and ER_{POT} , respectively.

The averaging period (i.e., window size) of 30 days to determine the apparent mean and potential NEP, GEP and ER was chosen because: i) the cumulative NEP curves for the grasslands commonly showed maximum slopes lasting for about one month during the peak growth period in spring/summer, and ii) this reduced the impact of spurious artefacts and data spikes occurring on shorter time scales (daily to weekly) due to unusual weather (e.g., rain pulses) and management (e.g., soil disturbance from the use of heavy machinery, fertilizer application) events or short-term violation of any of the underlying assumptions in the eddy covariance theory (e.g., occurrence of advection processes, gravity waves, etc.) (Massman & Lee 2002; Jolly et al. 2005; Stoy et al. 2009). Meanwhile, a window size >30 days was not considered in order to avoid interference from periodically re-occurring management practices at longer time scales. Repeating our analysis using 10 and 20-day averaging periods altered the absolute values of NEP_{POT} which increased with decreasing length of the averaging period, but did not change our overall findings (see Appendix S in Supporting Information, Figure S1). It is noteworthy that given the relationship between absolute potential values and the length of the averaging period, the focus in this approach is on the relative comparison of potential rates for a given averaging period whereas the absolute values are of secondary importance.

Statistical analysis

Significant differences in the potential rates across sites were tested by assessing their respective underlying non-normally distributed (Shapiro-Wilk test, $p < 0.05$) data points ($n = 30$ values of daily totals) using the non-parametric Kruskal-Wallis One-Way Analysis-of-Variance (ANOVA) on ranks followed by a Bonferroni type multiple comparison. Using the comparably less and more conservative Tukey-Kramer and Scheffé multiple comparison tests, respectively, did not alter the results. With the same approach, the mean environmental conditions during the period in which NEP_{POT} occurred were also determined and compared. According to the partial auto-correlation function (PACF) plots, daily NEP replicate samples were independent over the investigated 30-day period at all sites except for one (W). Thus, in addition, we conducted a sign test (which makes very few assumptions about the nature of the underlying distribution) for differences in the medians using a piecewise linear non-parametric empirical cumulative distribution function (ECDF) (Samuels & Witmer 2002). In this approach, NEP_{POT} values originate from the distribution of the annual maximum 30-day mean NEP_{APP} over all site years. As an additional advantage, this approach also adjusts for the unequal numbers of data-years among sites and

its effect on the probability of NEP_{POT} occurring (i.e., being reached) at a given site within the site-specific available number of data-years.

RESULTS

Environmental conditions

Multi-year averages ($n = 2$ to 9) of daily environmental variables (as described by $f(e)$ in Eq. 1) showed distinct and characteristic patterns for the three climate regions (Figure 2). Daily precipitation was highest and evenly distributed throughout the year at the maritime sites, and lowest at the cold-temperate-prairie site. In contrast to the summer peak in precipitation at the other sites, the two Mediterranean sites experienced a prolonged period with reduced precipitation during the summer. The peak and amplitude of daily soil temperature were greatest at the Mediterranean sites and smallest at the maritime sites. Soil temperature remained above freezing temperatures at all times at both the Mediterranean and the maritime sites. Among the cold-temperate-alpine sites, a clear elevation gradient was noted for the onset of soil thawing and summer soil temperature maxima. The multi-year average of maximum daily photosynthetically-active photon flux density was lowest at the maritime sites and highest at the Mediterranean sites. Sufficient soil water availability all year round at the maritime sites was in contrast to summer water deficits occurring at the Mediterranean sites. Overall, the maritime sites experienced lower environmental constraints on net CO_2 uptake compared to the cold-temperate (extended snow cover) and Mediterranean (pronounced summer water stress) regions.

Maximum LAI estimates ranged from 1.2 to 5.5 $m^2 m^{-2}$ (Table 1). Furthermore, the seasonal patterns of LAI development varied among the different grasslands, with maximum LAI occurring in spring at the Mediterranean sites, whereas LAI at the other sites peaked in summer and was occasionally characterized by periodic reduction caused by management practices (i.e., cutting/grazing) (Figure 2).

Cumulative apparent NEP

Cumulative NEP_{APP} showed characteristic temporal patterns for each climate region (e.g., steady net CO_2 loss during the dry summer and winter periods at the Mediterranean and cold-temperate sites, respectively) and management regimes (e.g., temporary net CO_2 loss following grazing and harvest events) (Figure 3). Annual sums of NEP_{APP} ranged widely from a net source of $-108 g C m^{-2} y^{-1}$ to a net sink of $404 g C m^{-2} y^{-1}$ across all sites and years. Averaged for each climate region, mean (\pm standard deviation, SD) annual NEP_{APP} of $222 \pm 104 g C m^{-2} y^{-1}$ was higher in the maritime region than in the Mediterranean ($64 \pm 70 g C m^{-2} y^{-1}$) and cold-temperate regions ($60 \pm 98 g C m^{-2} y^{-1}$).

Potential NEP, GEP, and ER

Averaged over 30 days, values for NEP_{POT} were within a narrow range of 4.6 to 6.0 $g C m^{-2} d^{-1}$ and not significantly different ($p > 0.05$ based on results from both the various multiple comparison tests and the sign test) for six out of nine sites (Figure 4). The remaining three sites (TN, T, and CW) were those at which NEP_{POT} was estimated from four or fewer site years, with the lowest rate of 3.3 $g C m^{-2} d^{-1}$ occurring at T and CW. The mean (\pm SD) NEP_{POT} across the six converging sites was $5.3 \pm 0.5 g C m^{-2} d^{-1}$.

The timing (defined as the day-of-year, DOY, representing the center point of the NEP_{POT} period) at which NEP_{POT} occurred spanned from DOY 97 at the Mediterranean site V to DOY 198 at the cold-temperate prairie site L and correlated with the length of the snow cover (and/or freezing temperatures) period (Figure 4a, see also Table 1 and Figure 2).

NEP_{POT} occurred at the time when the 30-day mean GEP_{APP} was equal (i.e., at MB, TN, L, V, T and D) or close to (i.e., at N, W and CW) its maximum (Figure 5a). NEP_{POT} occurred close to or lagged (by 17 ± 13 days) the maximum of the 30-day mean ER_{APP} at the unmanaged sites and extensive pastures (i.e., TN, V, T and L). In contrast, at the meadows and intensively managed pastures (i.e., N, MB, D, W and CW) the timing of NEP_{POT} preceded the peak of 30-day mean ER_{APP} by 57 ± 39 days. GEP_{POT} and ER_{POT} ranged from 6.4 to 12.6 g C m⁻² d⁻¹ and from 3.1 to 6.7 g C m⁻² d⁻¹, respectively (Appendix S, Table S1), and showed a strong linear relationship among sites (Figure 5b).

No convergence or any consistent pattern was observed among the various environmental parameters within the period in which NEP_{POT} occurred (Appendix S, Figure S2). At the maritime sites, NEP_{POT} occurred during periods that were cooler and wetter and received less radiation compared to the other regions.

DISCUSSION

Convergence of potential NEP

While previous synthesis studies of grassland and other ecosystem types commonly compared *apparent* rates in CO₂ exchange (e.g., Falge et al. 2002a, 2002b; Lindroth et al. 2008; Gilmanov et al. 2010; Lund et al. 2010; Moors et al. 2010), we are unaware of any study investigating the *potential* NEP based on multi-year eddy covariance datasets. Such an analysis has been hampered by the limited number of sites that could provide five or more years of continuous data, which, as suggested by our study, are necessary to estimate NEP_{POT}. The convergence of NEP_{POT} observed among the six sites with 5 site-years of data available suggests that contrasting C₃ grasslands generally hold a similar potential for net CO₂ uptake despite vast differences in ecosystem traits, environmental conditions and management practices.

The considerable differences in magnitude and patterns of the environmental variables among the investigated sites indicate that the convergence of NEP_{POT} was not related to a convergence of the underlying environmental conditions among climate regions (Figure 2, Figure S2). The apparent lack of universal optimum environmental conditions for NEP_{POT} suggests that the maximum imbalance (i.e., NEP_{POT}) between production and decomposition rates in C₃ grasslands is determined by site-specific optimum combinations of site, climate and management characteristics.

Furthermore, it is noteworthy that NEP_{POT} was identified to occur at different times among the sites spanning from spring at the Mediterranean sites to late summer at the cold-temperate sites. The different timing of NEP_{POT} and its temporal relationships with maximum GEP_{APP} and ER_{APP} reflect the impact of the site-specific seasonal and short-term constraints from environmental conditions and management events on production and decomposition processes. Specifically, the lag of maximum ER_{APP} compared to NEP_{POT} (and GEP_{POT}) in the managed systems was likely a disturbance effect from the harvest events, demonstrating a functional difference to the extensive systems where maximum ER_{APP} and GEP_{APP} more or less coincided with NEP_{POT}. The wide range and climate region-specific timing of the optimum CO₂ uptake among the three climate regions entail further implications regarding the impact of future changes in climate and management on the carbon sink strength of C₃ grasslands because non-optimum conditions (i.e., droughts, heat waves, cold spells, grazing and harvest events) during these peak productivity periods may considerably reduce the annual NEP_{APP} (see also Craine et al. 2012).

One possible explanation for the convergence in NEP_{POT} might be the fast and tightly coupled metabolic rates of the carbon cycle in C₃ grassland ecosystems due to the relatively

small body size of grasses (Brown et al. 2004; Allen et al. 2005). A close connection among grassland GEP, R_a and R_h through the amount of biomass and litter production has been previously highlighted in other studies (Bahn et al. 2008; Gilmanov et al. 2010; Schmitt et al. 2010; Migliavacca et al. 2011b; Peichl et al. 2011). Moreover, in our study we observed that those sites with higher GEP also showed higher ER rates (with regards to both apparent maxima and at the time when NEP_{POT} was reached), which demonstrates the tight coupling of these two processes. However, R_a is commonly a conservative fraction of GEP (Gifford 1994) and therefore unlikely to be the process responsible for major differences in the carbon budget among sites. In contrast, R_h is affected by various factors including soil microbial abundance and activity, the supply of decomposable material as well as soil environmental conditions (Chapin 2003; Davidson et al. 2006), and is therefore more likely to vary independently of GEP among different ecosystems. This supports the argument that any differences in NEP_{POT} would essentially result from a change in the imbalance between NPP and R_h . However, given the strong correlation between NPP and R_h highlighted in previous studies (Hobbie 1992; De Deyn et al. 2008; Bardgett 2011), NEP_{POT} may remain insensitive to a concurrent increase (or decrease) in NPP and R_h , which, consequently, may explain the convergence of NEP_{POT} among different sites as a result of a self-regulating supply (i.e. amount and quality) - demand mechanism. Nevertheless, given the current lack of suitable data (i.e., high-resolution time series of NPP and R_h) to further examine underlying mechanisms, additional evidence is required to corroborate this hypothesis in future work.

Another possible explanation that might support the convergence of NEP_{POT} in C_3 grasslands is that, in comparison to other terrestrial ecosystem types, the differences in ecosystem traits are relatively small among contrasting C_3 grasslands. The range in vegetation (i.e., living plants) properties such as canopy height, LAI, rooting depth and biomass pool is limited and additional non-vegetation controls (such as woody debris pools affecting R_h in forests or water table position and micro-topography controlling production and decomposition in peatlands) are basically absent. In addition, grasses die back annually because of their life form and provide easily degradable organic matter that, in combination with shorter canopy and rooting systems, allow for fast belowground transport and re-mineralisation of assimilated carbon. Moreover, grasslands are characterized by relatively small differences in body size and associated constraints on production and decomposition (Allen et al. 2005). In contrast, forested ecosystems exhibit a greater span in vegetation properties in relation to stand age and produce tall woody plants with prolonged life times. Furthermore, forested ecosystems build up large amounts of biomass and dead organic material over time which results in a temporal lag and decoupling of production and respiratory processes on longer (seasonal to multi-annual) time scales at both plant and ecosystem levels. Similar scenarios regarding the build up and delay in turnover of dead organic material apply to peatlands (Limpens et al. 2008). For example, maximum monthly NEP_{APP} data over five years from four temperate pine chronosequence sites (spanning stand ages from 3 to 69 years) (Peichl et al. 2010a) indicated a wide range of 1.6 to $8.3 \text{ g C m}^{-2} \text{ d}^{-1}$ as approximation for NEP_{POT} . Given the same climate and management regimes, this range is solely related to different ecosystem traits (e.g., forest age, LAI, biomass and woody debris pools) among the four forest stands. Thus, ecosystem traits that are critical determinants of NEP_{POT} vary much less widely in C_3 grasslands compared to other biomes, which may facilitate the convergence of NEP_{POT} . However, while variations in the three controls (i.e., ecosystem traits, environmental conditions, management) did not cause any apparent difference in NEP_{POT} among the grassland sites in our study, the extent of compensating effects among these three controls and their individual impact on NEP_{POT} remains unclear.

Implications for the annual CO₂ sink-source strength of contrasting global C₃ grasslands

The convergence of NEP_{POT} implies that there are relatively small differences in the net CO₂ uptake capacity predetermining the annual CO₂ sink-source strength of C₃ grasslands and that the range of the latter should be small among global C₃ grasslands under optimum conditions. In reality, however, seasonal and short-term constraints from environmental conditions specific to each climate region (e.g., the presence and duration of snow cover, extreme temperatures, summer water deficits, and the length of the growing season, Figure 2) and from management practices (e.g., harvest, grazing, re-seeding) reduce NEP_{POT} to climate region-specific and site-specific NEP_{APP} . Thus, given the lack of differences in NEP_{POT} , it follows that these seasonal and short-term environmental and management constraints may be considered as the major controls of the variations in the annual net CO₂ uptake among global C₃ grasslands. Moreover, given the interactive effects between weather/climate and associated adaptation in management (i.e., shifts in frequency and timing of management events) (Wohlfahrt et al. 2008a, 2008b), the CO₂ exchange of C₃ grasslands might be especially sensitive to future climatic changes which modify the occurrence patterns of these seasonal and short-term environmental and management constraints. This finding has also implications with regards to improving process-based models. With a few exceptions (e.g., Hidy et al. 2012), the focus has been on implementing complex processes that describe ecosystem functioning. However, given the convergence of NEP_{POT} , it follows that i) C₃ grasslands may be treated as one functional type and ii) that adequately simulating the impacts from the seasonal and short-term environmental and management constraints (i.e., $f(e)$ and $f(m)$ in Eq.1) should be the primary concern of future model improvement (Groenendijk et al. 2011).

The limited impact of NEP_{POT} on annual NEP_{APP} suggests that ecosystem traits, being one of the three main controls on NEP_{POT} , are also not likely the key determinants of the annual NEP_{APP} in C₃ grasslands. This lack of impact from ecosystem traits on the annual grassland NEP_{APP} is in contrast to other terrestrial ecosystem types. In forests, for instance, considerable differences in forest stand characteristics (e.g., stand age, plant functional type, biomass pools, LAI) were reported as primary controls on annual NEP_{APP} over climatic controls (Luyssaert et al. 2007; Lindroth et al. 2008; Peichl et al. 2010a, 2010b; Drake et al. 2011). Similarly, ecosystem traits (i.e., water table depth, species composition, LAI, micro-topography, nutrient status) were noted as important controls on growing season and annual NEP_{APP} in peatland ecosystems (Humphreys et al. 2006; Lund et al. 2010; Sonnentag et al. 2010). However, Limpens et al. (2008) previously argued that the NEP_{APP} of undisturbed peatlands (that are similar to grasslands in that they are characterized by a limited range of biomass and LAI) should be less variable than forests, and instead should be primarily controlled by environmental conditions. Species and location were suggested as the primary controls on differences in growing season NEP_{APP} among croplands (Moors et al. 2010). Thus, the limited effect of ecosystem traits on the cumulative seasonal and annual NEP_{APP} might be a unique feature of C₃ grasslands.

Based on this first work to quantify and compare NEP_{POT} using multi-year eddy covariance data, we conclude that NEP_{POT} converges within a narrow range among contrasting C₃ grasslands given long-term observations. This finding indicates a general state of stability in grassland NEP_{POT} during optimum conditions most likely due to body size and supply-demand related metabolic constraints on production and decomposition processes. Given the wide range in annual NEP_{APP} compared with the narrow range of NEP_{POT} reported in this study, we conclude that the control of NEP_{POT} on the annual NEP_{APP} is limited. This implies that the variation of the annual sink-source strength for atmospheric CO₂ among global C₃ grasslands is primarily a function of seasonal and short-term constraints from environmental conditions and site-specific management practices, i.e., the time dependent

functions $f(e)$ and $f(m)$ in Eq. (1). Compared to other ecosystems, the CO₂ exchange of C₃ grasslands might therefore be especially susceptible to the direct and indirect effects from expected future changes in climate and associated (adaptive) changes in management.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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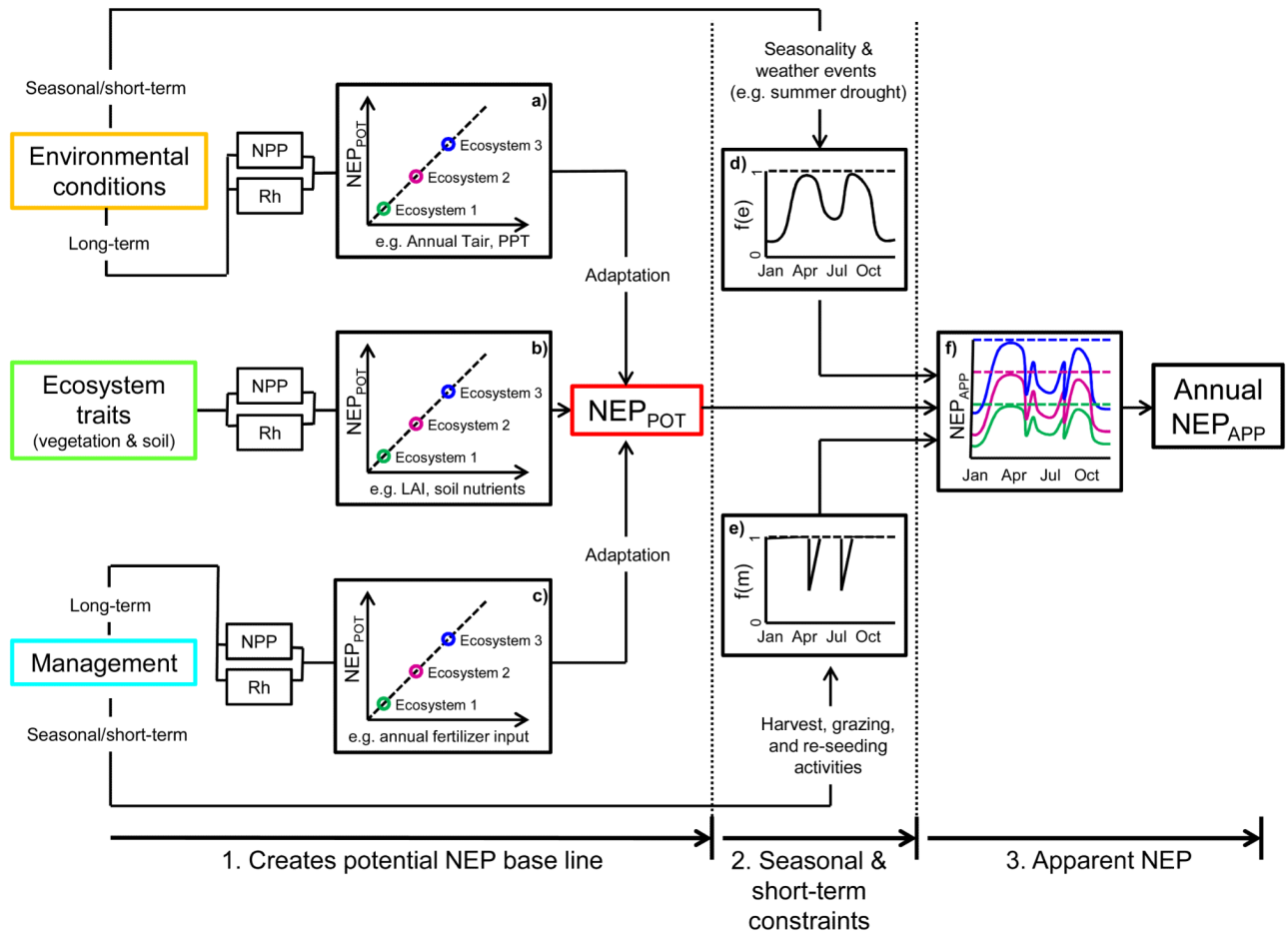


Figure 1. Conceptual diagram outlining the interactions between ecosystems traits, environmental conditions, management, net primary production (NPP), heterotrophic respiration (R_h), potential net ecosystem production (NEP_{POT}) and apparent NEP (NEP_{APP}). It describes NEP_{APP} as the product of NEP_{POT} ($= NPP - R_h$) and functions of seasonal and short-term environmental $f(e)$ and management $f(m)$ constraints. Dotted lines in f) indicate $NEP_{APP} = NEP_{POT}$.

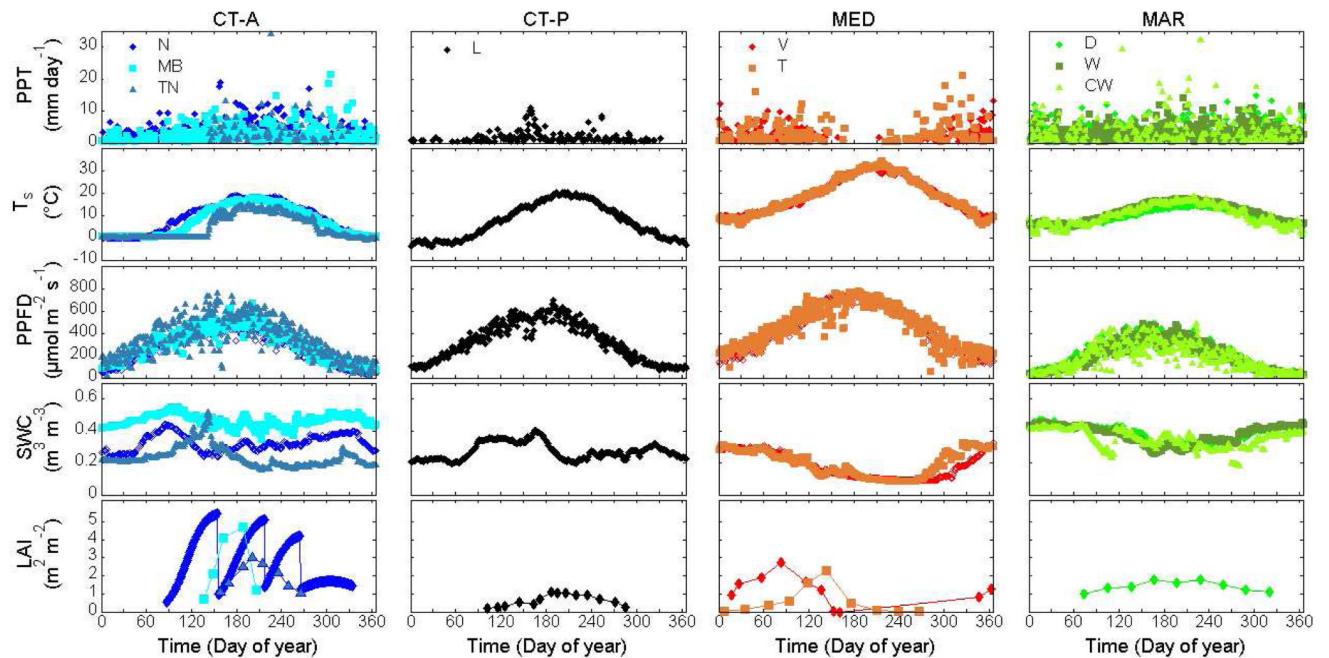


Figure 2. Multi-year averages of daily precipitation (PPT), soil temperature (T_s), photosynthetically active photon flux density (PPFD), volumetric soil water content (SWC) and leaf area index (LAI; for selected years and sites according to data availability) at the nine grassland sites Neustift (N), Monte Bondone (MB), Torgnon (TN), Lethbridge (L), Vaira (V), Tojal (T), Dripsey (D), Wexford (W) and Carlow (CW) in the three climate regions: cold-temperate (CT; alpine, A, and prairie, P), Mediterranean (MED) and maritime (MAR).

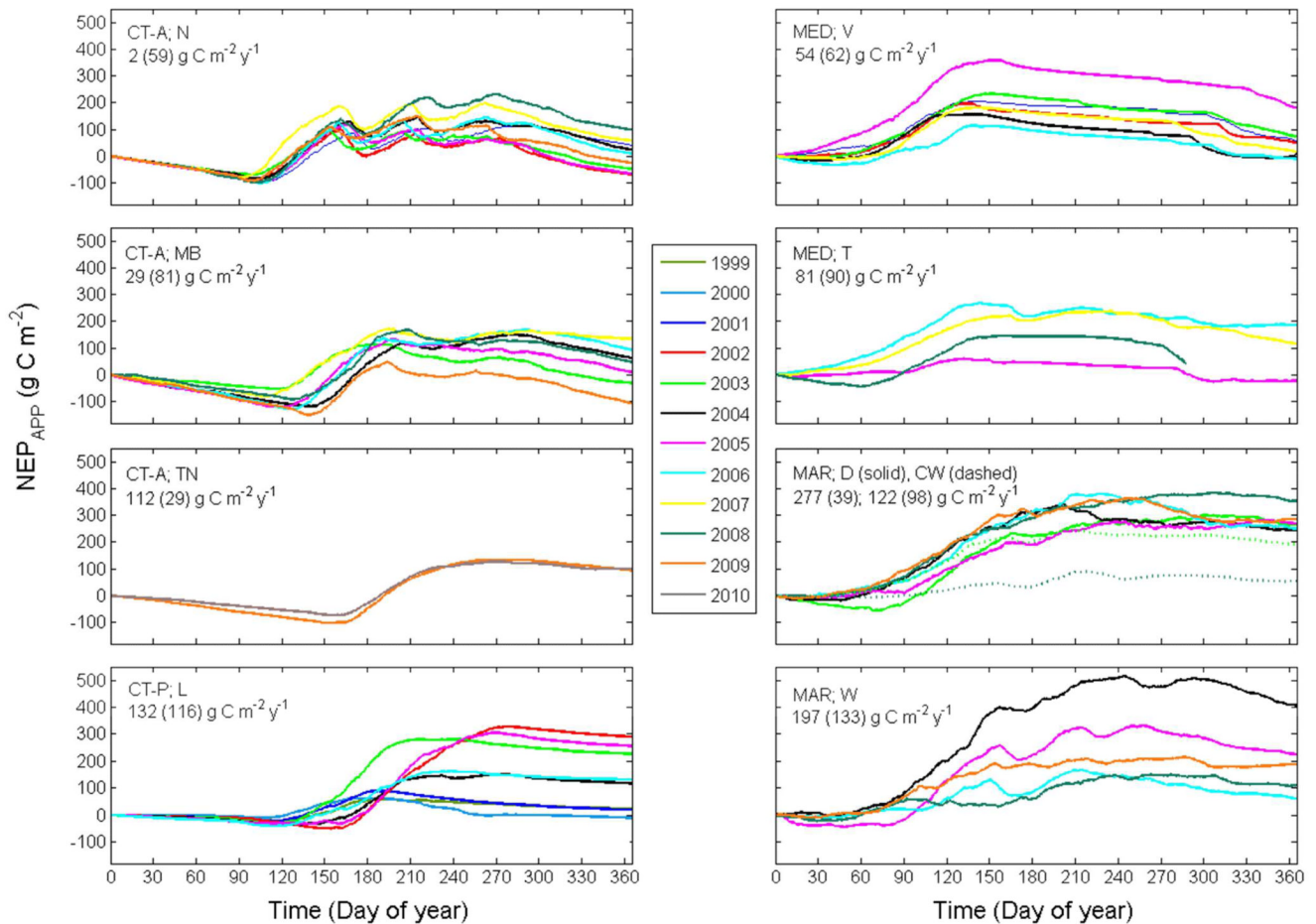


Figure 3. Cumulative annual apparent net ecosystem production (NEP_{APP}) for available site-years at the nine grassland sites Neustift (N), Monte Bondone (MB), Torgnon (TN), Lethbridge (L), Vaira (V), Tojal (T), Dripsey (D), Wexford (W) and Carlow (CW) in the cold temperate (CT; alpine, A, and prairie, P), Mediterranean (MED) and maritime (MAR) climate regions. Values in upper left corner represent site-specific multi-year average NEP (values in parentheses indicate standard deviation)

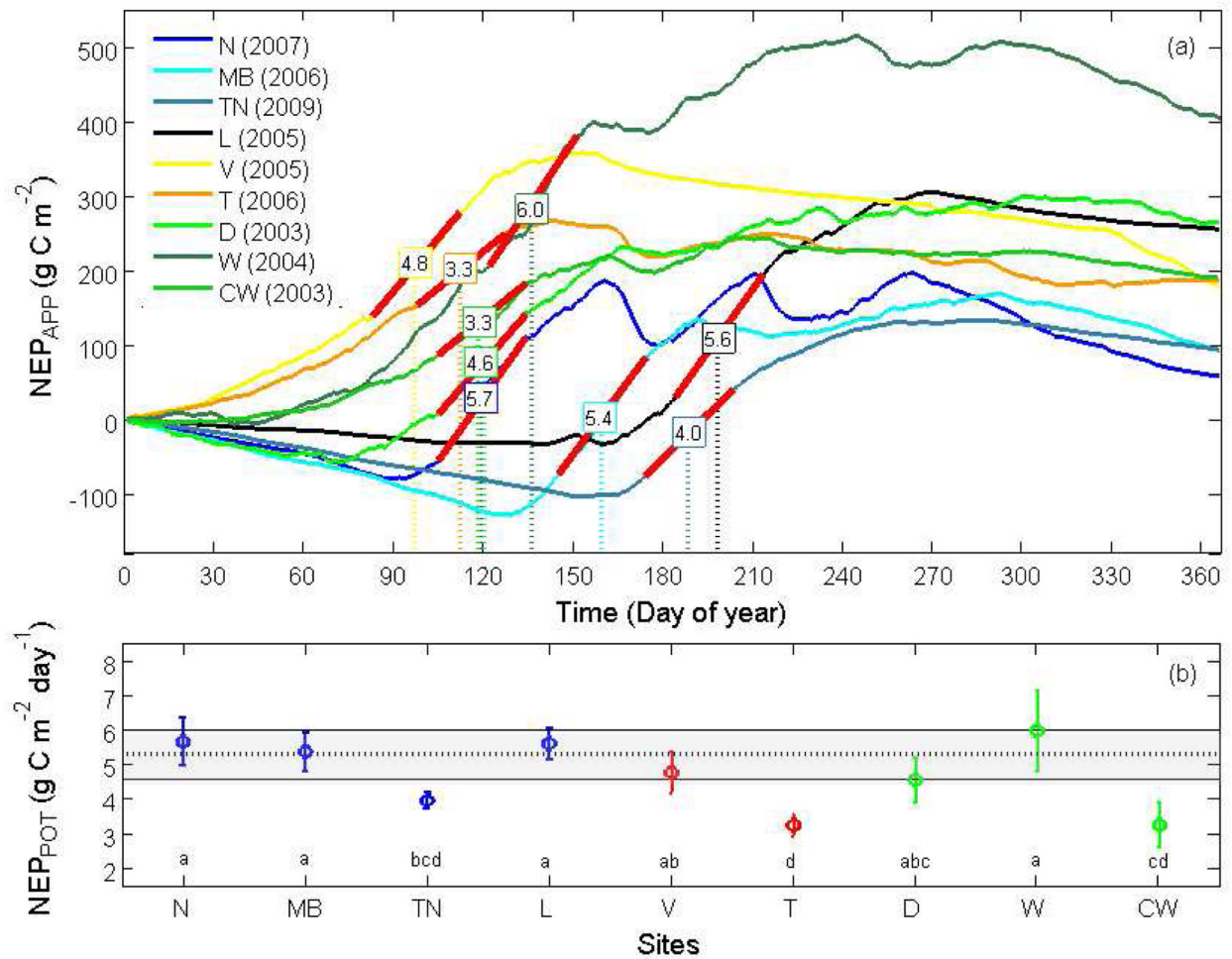


Figure 4. (a) Cumulative apparent net ecosystem production (NEP_{APP}) for years when potential [=maximum 30-day mean NEP_{APP}] NEP (NEP_{POT}) occurred at the grasslands sites Neustift (N), Monte Bondone (MB), Torgnon (TN), Lethbridge (L), Vaira (V), Tojal (T), Dripsey (D), Wexford (W) and Carlow (CW). Red slopes visualize NEP_{POT} sustained over 30 days; numbers in rectangles show associated slope values; dotted vertical lines visualize the timing of NEP_{POT} (b) NEP_{POT} for grasslands in the cold-temperate (blue), Mediterranean (red), and maritime (green) regions; grey band indicates the convergence zone for NEP_{POT} (dotted horizontal line shows mean NEP_{POT}); same letters indicate no significant difference; error bars indicate ± 2 standard error of site-specific NEP_{POT} ($n = 30$)

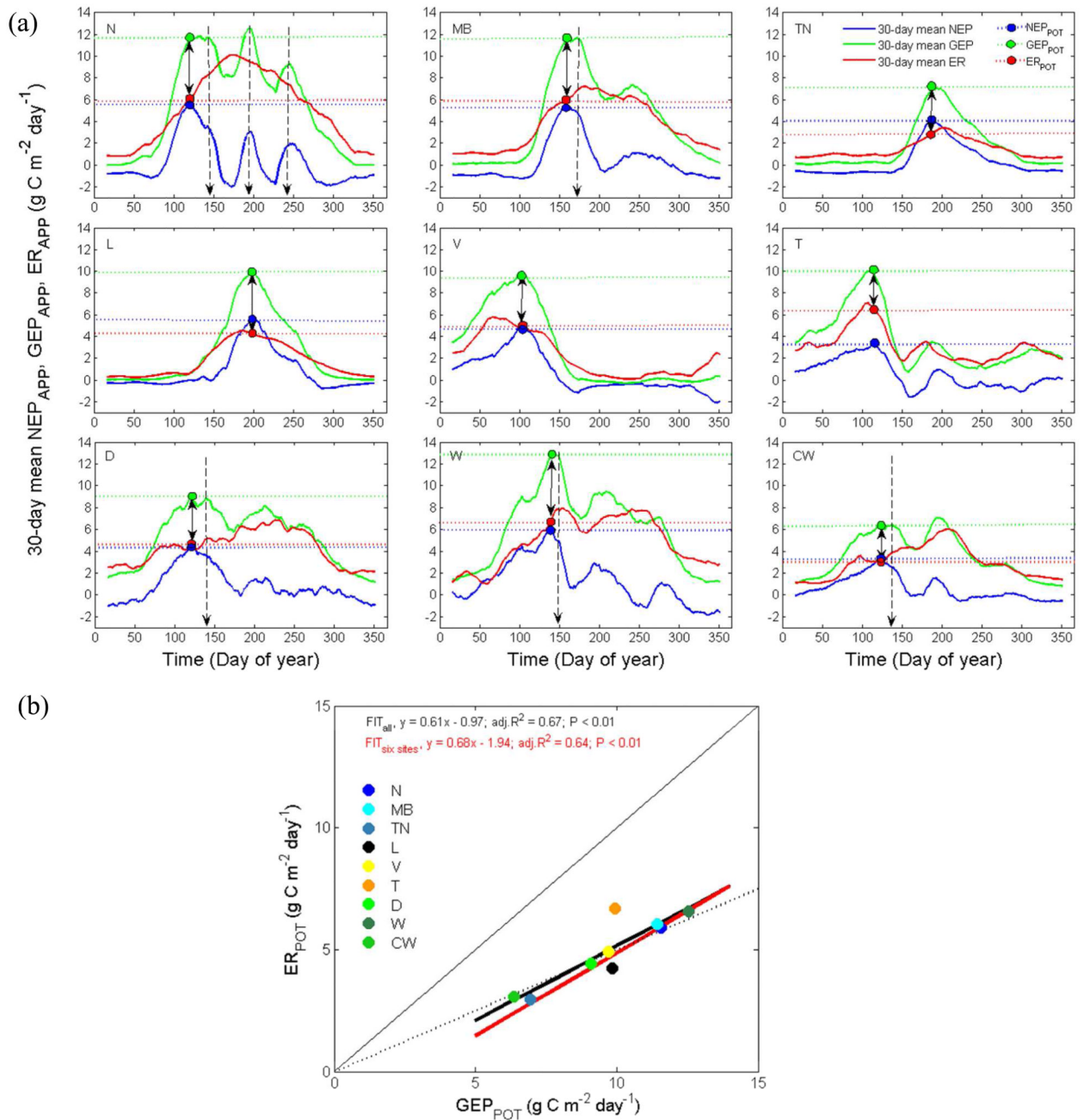


Figure 5. (a) 30-day mean apparent net ecosystem production (NEP_{App}), gross ecosystem production (GEP_{App}) and ecosystem respiration (ER_{App}) at the nine sites (denoted as in Figures 2-4) during the year in which potential NEP (NEP_{POT}) occurred. Blue, green and red dots and horizontal dotted lines indicate timing and magnitude of NEP_{POT} and of GEP_{App} and ER_{App} at the time of NEP_{POT} (GEP_{POT} and ER_{POT}, respectively). Double arrows visualize the difference between GEP_{POT} and ER_{POT}. Vertical dotted arrows indicate harvest events. **(b)** regression between GEP_{POT} and ER_{POT}; thick lines indicate linear fits for all sites (black line) and the six conserving sites (red line); thin solid and dashed lines show 1:1 and 2:1 fits, respectively; GEP and ER are shown in absolute values.

Table 1

Site characteristics of the nine investigated grassland sites (Neustift, N; Monte Bondone, MB; Torgnon, TN; Lethbridge, L; Vaira, V; Tojal, T; Dripsey, D; Wexford, W; Carlow, CW)

Site	N	MB	TN	L	V	T	D	W	CW
Country	Austria	Italy	Italy	Canada (AB)	USA (CA)	Portugal	Ireland	Ireland	Ireland
Coordinates	47°07' N 11°19' E	46° 01' N 11° 2' E	45° 50' N 7° 34' E	49° 43' N 112° 56' W	38° 41' N 120° 05' W	38°28' N 8°01' W	51°59' N 8°45' W	52°30' N 6°40' W	52°57' N 6°54' W
Elevation (m a.s.l.)	970	1550	2160	951	129	190	195	57	56
Climate region	Cold-Temperate	Cold-Temperate	Cold-Temperate	Cold-Temperate	Mediterranean	Mediterranean	Maritime	Maritime	Maritime
Mean T_a (°C)	6.5	5.5	3.1	5.4	16.5	15.5	9.4	10.1	9.4
Mean PPT (mm)	852	1189	920	402	562	669	1207	877	824
Snow cover and/or $T < 0^\circ\text{C}$	Nov - Apr	Nov - Apr	Nov - May	Oct - Apr	none	none	none	none	none
Management	intensive meadow	extensive meadow	abandoned pasture	unmanaged prairie	extensive pasture	extensive pasture	intensive meadow/ pasture	intensive meadow/ pasture	intensive meadow/ pasture
Nitrogen fertilizer application (kg N ha ⁻¹ y ⁻¹)	manure	low	none	none	none	none	~150-250 (inorganic, manure, slurry)	~200-300 (inorganic, manure, slurry)	~200 (inorganic, manure, slurry)
Soil type	Fluvisol	Typic Hapludalfs	Cambisol	Orthic dark- brown chernozem	Lithic haploxerepts	Luvisol	Gleysol	(Gleyic) Cambisol	Calcic Luvisol
Soil texture	(sandy) loam	loam	loamy sand	clay loam	silt loam	sandy (clay) loam	loam	loam	sandy loam
Soil C (kg C m ⁻²)	8.1 (0-30cm)	8.7 (0-20cm)	2.8 (0-20cm)	3.7 (0-10cm)	6.0 (0-30cm)	3.3 (0-30cm)	9.0 (0-30cm)	3.9 (0-10cm)	4.2 (0-10cm)
Soil N (kg N m ⁻²)	n.a.	0.76 (0-20cm)	0.22 (0-20cm)	n.a.	0.60 (0-30cm)	n.a.	0.76 (0-30cm)	0.34 (0-10cm)	0.42 (0-10cm)
Max. LAI (m ² m ⁻²)	5.5	4.7	2.8	1.2	2.7	2.3	2.5	na	5.1
Dominant species	<i>Dactylis glomerata</i> , <i>Festuca pratensis</i> , <i>Phleum pratensis</i> , <i>Ranunculus acris</i> , <i>Trifolium</i>	<i>Festuca rubra</i> , <i>Nardus stricta</i> , <i>Trifolium</i>	<i>Nardus stricta</i> , <i>Arnica montana</i> , <i>Trifolium alpinum</i> , <i>Carex</i>	<i>Agropyron dasystachyum</i> , <i>Agropyron smithii</i> , <i>Vicia americana</i> , <i>Artemisia frigid</i> , <i>Koeleria</i>	<i>Brachypodium distachyon</i> , <i>Hypochaeris glabra</i> , <i>Trifolium spp.</i> , <i>Dichelostema volubile</i>	<i>Avena barbata</i> , <i>Luzitana spp.</i> , <i>Vulpia spp.</i> , <i>Medicago spp.</i> , <i>Trifolium spp.</i> , <i>Cynodon</i>	<i>Lolium perenne</i> , <i>Alopecurus pratensis</i> , <i>Holcus</i>	<i>Lolium perenne</i>	<i>Lolium perenne</i> , <i>Trifolium</i>

Site	N	MB	TN	L	V	T	D	W	CW
Data coverage	<i>spp.</i> 2001 - 2009	<i>alpinum</i> 2003 - 2009	<i>sempervirens</i> 2009 - 2010	<i>viridula</i> 1999 - 2006	<i>Erodium botrys</i> 2001 - 2007	<i>dactylon</i> 2005 - 2008	<i>lanatus</i> 2003 - 2006, 2008, 2009	2004 - 2006, 2008, 2009	<i>repens</i> 2003, 2008
References	Wohlfahrt et al. (2008b)	Marcolta et al. (2011)	Migliavacca et al. (2011a)	Flanagan and Adkinson (2011)	Ma et al. (2007)	Aires et al. (2008)	Peichl et al. (2011)	Peichl et al. (2012)	Flechar et al. (2007)