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ECOSYSTEMS

Biotic, Abiotic, and Management Controls on the Net Ecosystem CO_2 Exchange of European Mountain Grassland Ecosystems

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ABSTRACT

The net ecosystem carbon dioxide (CO_2) exchange (NEE) of nine European mountain grassland ecosystems was measured during 2002–2004 using the eddy covariance method. Overall, the availability of photosynthetically active radiation (PPFD) was the single most important abiotic influence factor for NEE. Its role changed markedly during the course of the season, PPFD being a better predictor for NEE during periods favorable for CO_2 uptake, which was spring and autumn for the sites characterized by summer droughts (southern sites) and (peak) summer for the Alpine and northern study sites. This general pattern was interrupted by grassland management practices, that is, mowing and grazing, when the variability in NEE explained by PPFD decreased in concert with the amount of aboveground biomass (BM_{ag}). Temperature was the abiotic influence factor that explained most of the variability in ecosystem respiration at the Alpine and northern study sites, but not at the southern sites characterized by a pronounced

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summer drought, where soil water availability and the amount of aboveground biomass were more or equally important. The amount of assimilating plant area was the single most important biotic variable determining the maximum ecosystem carbon uptake potential, that is, the NEE at saturating PPFD. Good correspondence, in terms of the magnitude of NEE, was observed with many (semi-) natural grasslands around the world, but not with grasslands sown on fertile soils in lowland locations, which exhibited higher maximum carbon gains at lower respiratory costs. It is concluded that, through triggering rapid changes in the amount and area of the aboveground plant matter, the timing and frequency of land management practices is crucial for the short-term sensitivity of the NEE of the investigated mountain grassland ecosystems to climatic drivers.

Key words: biomass; Carbomont; ecosystem respiration; eddy covariance; green area index; grazing; light response; mowing.

INTRODUCTION

Deemed responsible for more than half of the observed global warming (IPCC 2001), carbon dioxide (CO_2) and changes in the global carbon cycle have received much public attention during recent years. One of the major challenges ecologists face in this context is to quantify the rates at which ecosystems exchange CO_2 with the atmosphere and to analyze how these rates are controlled by biotic, abiotic, and management factors (Steffen and others 1998; Running and others 1999; Baldocchi and others 2001). The latter is not only required to understand current CO_2 exchange rates, but also for projecting the effects of future scenarios of climate and land use, which is a prerequisite for the development and implementation of appropriate abatement strategies (IPCC 2001).

The net exchange of CO_2 between an ecosystem and the atmosphere (NEE) is the residual of assimilatory uptake and respiratory release of CO_2 by the ecosystem and is thus governed by both sets of factors that control assimilation and respiration of CO_2. The assimilation of CO_2 depends on the amount and photosynthetic potential of the aboveground plant matter, as well as the environmental drivers that affect photosynthesis. At the leaf level, the availability of photosynthetically active radiation (PPFD, 400–700 nm) is the major environmental driver of photosynthesis, providing the energy for the carboxylation of CO_2 (Larcher 2001). At the canopy level, the response of assimilation to photosynthetic active radiation (PPFD) also depends on the distribution of PPFD within the canopy and thus the directionality and quality of the incoming radiation (Gu and others 2002), the amount, optical properties, and spatial organization of foliage elements (Cescatti and Niinemets 2004), as well as their adaptation to the average within-canopy light conditions (De Pury and Farquhar 1997). In the absence of other limitations (for example, water stress), the availability of PFFD very often explains well in excess of 50% of the variation in canopy-scale assimilation (Ruimy and others 1995). Through its effect on enzyme kinetics, temperature is another abiotic factor influencing the assimilation of CO_2 (Medlyn and others 2002), in particular for high-latitude and high-elevation ecosystems (Huxman and others 2003; Suni and others 2003; Monson and others 2005). Low soil water availability and air humidity, which reduce stomatal conductance and thus the diffusion of CO_2 into leaves (Buckley and others 2003), are additional abiotic factors affecting assimilation, not only in arid or semi-arid (Hastings and others 2005), but as well in temperate ecosystems (Baldocchi 1997; Novick and others 2004).

Ecosystem respiration consists of both autotrophic (above and belowground plant respiration) and heterotrophic components, the latter reflecting (mostly belowground) microbial (and to a lesser degree animal) respiratory activity. Both respiration components depend on the respective substrate availability (photosynthate, litter and soil organic matter), providing a direct link between respiration and productivity (Högberg and others 2001; Wan and Luo 2003; Whitehead and others 2003). The most important abiotic influence factors on ecosystem respiration are temperature (for example, Wohlfahrt and others 2005a), again through its effect on enzyme kinetics, and in the case of soil respiration, also soil water availability (Davidson and others 1998; Reichstein and others 2003; Griffis and others 2004; Bahn and others 2008).

Land management activities, such as harvesting, mowing, and grazing, affect assimilation and ecosystem respiration in several, mutually coupled ways: Canopy CO_2 assimilation is directly influenced by management through changes in the amount of assimilating plant matter (Barcza and others 2003; Marcolla and Cescatti 2005; Nieven and others 2005; Novick and others 2004; Rogiers and others 2005; Wohlfahrt 2004; Wohlfahrt and others 2008), which in turn governs the availability of respiratory substrate (assimilates and litter) and thus also feeds back on ecosystem respiration (Wan and Luo 2003). In addition, the removal of aboveground plant matter indirectly modifies the soil climate (temperature and humidity), which may lead to changes in soil respiration (Bahn and others 2006; Wan and Luo 2003). Another indirect affect of land management is through mineral and organic fertilization, which affects the nutrient availability and thus leaf photosynthetic activity (Evans 1989) and the components of ecosystem respiration (Verburg and others 2004).

Globally, grasslands cover around 40% of the ice-free terrestrial surface (White and others 2000), but until the recent synthesis by Gilmanov and others (2007) and Soussana and others (2007) their role in the carbon cycle was poorly understood due to lack of data, by comparison to the wide availability of flux measurements over forest ecosystems (Baldocchi and others 2001). For mountain grassland ecosystems, however, hardly any long-term measurements of NEE have been published (but see Kato and others 2004a, b; Rogiers and others 2005; Wohlfahrt and others 2005a, b, 2008). This may reflect the methodological challenges associated with conducting defensible flux measurements in complex mountain terrain, although Hammerle and others (2007) showed that with short grassland canopies and measurement heights this seems to be much less of a problem as compared to tall (forest) ecosystems (Feigenwinter and others 2008).

The mountain regions of Europe are currently experiencing relatively rapid changes in both land use (Bätzing 1996) and climate (Grabher and others 1994). In southern and central European mountain areas, changes in land management, as opposed to climate change (Theurillat and Guisan 2001), are currently considered the major drivers for changes in ecosystem structure and functioning (Garcia-Ruiz and others 1996; Cernusca and others 1999). With ongoing changes in EU agricultural financing, these land-use changes are predicted to become even more prominent in the near future (Bayfield and others 2008). In contrast, with the highest warming rates anticipated for northern latitudes (IPCC 2001), climate change may be regarded as the major influence factor for carbon cycling in the sub-arctic mountain grasslands of Europe.

Motivated by these changes in land management and climate, as well as the scarcity of long-term data on the carbon cycling in mountain grassland ecosystem, the EU project CarboMont aimed at quantifying the carbon pools and fluxes of European mountain grasslands. The overarching objective of the present article, which is part of the CarboMont special feature (Cernusca and others 2008), is to synthesize the NEE flux measurements made within the CarboMont project and to provide a first characterization of the NEE of mountain grasslands. Given the ongoing changes in climate and land use in European mountain regions, particular emphasis is given to the analysis of biotic, abiotic, and management factors controlling the NEE of the investigated mountain grasslands. To this end we analyze the NEE measured at nine CarboMont sites during 2002–2004 in terms of functional relationships to the major environmental and biologic drivers. Management controls are identified by analyzing the perturbation of these relationships in response to management practices, such as mowing and grazing.

MATERIAL AND METHODS

Site Description

Within the CarboMont project, grassland study sites were selected to represent the major mountain regions of Europe. Accordingly the study sites encompass a latitudinal range of 42–68° (compare Figure 1 of Cernusca and others 2008), and an elevation range of 270–1770 m a.s.l. (Table 1). The present article covers the following nine study sites (Table 1).

Amplero and Alinya

Situated in the Mediterranean mountain regions of Italy and Spain, these two sites are characterized by a distinct summer drought. Amplero is managed as a hay meadow and is cut once a year with some subsequent grazing, whereas Alinya is grazed during the summer months.

Monte Bondone, Seebodenalp, Neustift

These three sites are situated in the Italian, Swiss and Austrian Alps at elevations between 1000 and 1500 m a.s.l. and experience typical Alpine climatic conditions with precipitation peaking in summer. All three sites are managed as hay meadows, being cut between 1 and 3 times per year with occasional grazing in late autumn.

Matra

This site is situated in the Hungarian part of the Carpathians and is characterized by a continental climate with low precipitation during the summer months. The site is cut once per year, and additional grazing varies from year to year.

Auchencorth Moss

Situated in the southern uplands of Scotland, this site, due to the oceanic influence, experiences an almost year-round vegetation period with moderate temperatures and abundant precipitation. The site is subject to extremely low grazing by horses and sheep at approximately one livestock unit per 10 hectares.

Varriö, Stordalen

Situated in the sub-arctic regions of Finland and Sweden, these two sites are characterized by low temperatures and a short vegetation period. These sites are subject to very low grazing by wild animals only.

Net Ecosystem CO$_2$ Exchange

The NEE was measured using the eddy covariance method (Aubinet and others 2000; Baldocchi 2003). The three wind components and the speed of sound were measured using three-dimensional ultra-sonic anemometers, and CO$_2$ mole fractions using both open- (OP) and closed-path (CP) infrared gas analyzers (IRGA), as detailed in Table 1. The sensor separation between the sonic anemometer and either the OP IRGA or the intake of the CP IRGA ranged from 0.2 to 0.3 and 0.05–0.1 m, and the height aboveground at which the sensors were mounted ranged from 2.2 to 4.0 m (Table 1). Raw data were acquired at 20–21 Hz, from which 30 min averages were calculated in post-processing. Means and turbulent fluctuations of the vertical wind speed and the CO$_2$ mixing ratio were calculated by Reynolds (block) averaging, except for three sites in which a linear trend removal or a recursive digital filter were applied (Table 1). Any time lag of the CO$_2$ signal was determined by maximizing the cross correlation with the vertical wind velocity and assumed constant at the set values for CP and OP systems, respectively. The vector basis of the co-ordinate system was aligned with the mean wind streamlines (Wilczak and others 2001) using three-axis (6 sites), two-axis (2 sites) and planar fit (1 site) co-ordinate rotations (Table 1). Frequency response corrections were applied to raw eddy fluxes accounting for low-pass (sensor separation, dynamic frequency sensor response, scalar and vector path averaging, frequency response mismatch) and high-pass filtering following Moore (1986) and

Table 1. Characterization of Study Sites and Experimental Setup

	Amplero (I)	Alinya (E)	Monte Bondone (I)	Seebodenalp (CH)	Neustift (A)	Matra (H)	Auchencorth Moss (UK)	Varriö (FI)	Stordalen (S)
Latitude/Longitude (decimal)	41.90/13.22	42.15/1.45	46.02/11.07	47.08/8.77	47.12/11.32	47.84/19.72	55.79/3.24	67.72/29.60	68.22/19.03
Elevation (m a.s.l.)	900	1770	1550	1025	970	300	270	480	360
Land use	Cut (1×)	Grazing	Cut (1×)	Cut (3×)	Cut (3×)	Cut (1×)	Grazing[1]	Grazing[1]	Grazing[1]
Fertilization	–	–	–	–	Manure	–	–	–	–
Eddy covariance:									
Data coverage	2002–2004	2002–2004	2002–2003	2002–2004	2002–2004	2003–2004	2002–2004	2002–2004	2002–2004
Measurement system	OP-1	OP-1	OP-1	OP-2	CP-1	OP-3	CP-2	OP-4	OP-1
Detrending algorithm	LD	BA	BA	BA	BA	LD	BA	LD	RM (200 s)
Coordinate rotation	3D	2D	2D	3D	3D	3D	PF	3D	3D
Sensor separation (m)	0.2	0.3	0.3	0.3	0.1	0.3	0.05	0.1	0.1
Day/Night u_* threshold (m s^{-1})	–/0.15	0.10/0.10	–/–	–/–	–/0.10	–/–	–/–	–/0.25	0.05/0.05
Air/soil reference height (m)	4.0/–0.05	2.2/–0.1	3.0/–0.1	2.4/–0.05	3.0/–0.05	3.0/–0.05	3.6/–0.05	1.8/–0.05	2.7/–0.05

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[1] *Sites subject to extremely low grazing; OP-1—Li-7500 (LI-COR, Lincoln, NE, USA) and R3 (Gill, Lymington, UK), OP-2—Li-7500 and HS (Gill, Lymington, UK), OP-3—Li-7500 and CSAT3 (CSI, Logan, USA), OP-4—Li-7500 and USA-1 (Metek, Elmshorn, D), CP-1—Li-6262 (LI-COR, Lincoln, NE, USA) and R3, CP-2—Li-7000 (LI-COR, Lincoln, NE, USA) and R2 (Gill, Lymington, UK), 3D—three-axis coordinate rotation, 2D—two-axis coordinate rotation, PF—planar fit rotation, LD—linear detrending, BA—block averaging, RM—running mean (time constant).*

Aubinet and others (2000). In addition, CO_2 flux densities measured by OP systems were corrected for the effect of air density fluctuations following Webb and others (1980), whereas CO_2 flux densities measured by CP systems were corrected for the attenuation of concentration fluctuations down the sampling tube (Aubinet and others 2000). In the latter case tube flow rates ranged between 5 and 9 l min^{-1}; tube lengths ranged from 3 to 23 m (0.004 m inner diameter). NEE was finally calculated as the sum of the corrected vertical eddy covariance term and the storage flux, the latter being estimated from the time-rate-of-change of the CO_2 mixing ratio at the reference height. Negative flux densities denote a net flux into the ecosystems and vice versa.

Quality control of the half-hourly NEE data was exercised in a two-step procedure. First, periods were identified when the eddy covariance system would not work properly due to adverse environmental conditions (rain, snow), instrument malfunction, and so on. These data were excluded from any further analysis. In a second step, data were subjected to several quality control tests following Foken and Wichura (1996) and Aubinet and others (2000). As the eddy covariance method is often found to underestimate the true NEE during periods of low turbulent mixing (Gu and others 2005), data were also excluded below certain thresholds of friction velocity (u_*), where such an underestimation was evident from the data (Table 1).

There are concerns about the ability of the eddy covariance method to close the CO_2 mass balance in complex (mountainous) terrain due to the presence of advection (Aubinet and others 2005; Feigenwinter and others 2008). Yet, as shown by Wohlfahrt and others (2005a) and Hammerle and others (2007) for Neustift and a grassland on a steep mountain slope, respectively, there is a favorable correspondence with CO_2 flux measurements made contemporarily with closed-dynamic ecosystem chambers. In addition, there is no difference with regard to the ability to close the energy balance between sites in complex mountainous and flat terrain (Hammerle and others 2007; Wohlfahrt and others 2007). Appropriate quality control of data provided (see above), we thus do not expect a systematic bias in the reported eddy covariance CO_2 flux measurements.

Supporting environmental measurements included photosynthetically active radiation (quantum sensors), air temperature (PT100, thermistor and thermoelement sensors), and humidity (capacitance sensors) at some reference height aboveground, and soil temperature (PT100, thermistor and thermoelement sensors) and water content (dielectric and time-domain reflectometry sensors) in the main rooting horizon (Table 1). Measurements of water content were normalized with the respective saturation water content to obtain the relative soil water content (RSWC).

Green Area Index and Biomass

Green area index (GAI) and biomass (BM_{ag}) were determined periodically throughout the vegetation period from both destructive samples and by optical methods, as described in detail by Wohlfahrt and others (2001).

Statistical Analysis

To relate NEE to PPFD we followed Ruimy and others (1995) and fitted (using the SPSS statistics software package) the data from each site (pooled over the vegetation period or separately for weekly blocks of data) to the following rectangular hyperbolic model:

$$F_{\mathrm{NEE}} = \frac{-\alpha Q F_{\mathrm{GPP,sat}}}{\alpha Q + F_{\mathrm{GPP,sat}}} + R_{\mathrm{eco}} \qquad (1)$$

Here F_{NEE} represents NEE (μmol m^{-2} s^{-1}), α the apparent quantum yield (mol CO_2 mol photons^{-1}), Q the PPFD (μmol m^{-2} s^{-1}), $F_{\mathrm{GPP,sat}}$ the asymptotic value of the gross primary production (GPP) at high irradiance (μmol m^{-2} s^{-1}), and R_{eco} the ecosystem respiration (μmol m^{-2} s^{-1}). As $F_{\mathrm{GPP,sat}}$ often tends to be reached at light intensities outside the natural range (Ruimy and others 1995) and is moreover auto-correlated with R_{eco}, we used Eq. (1) to calculate $F_{\mathrm{NEE,1500}}$, the NEE at a light intensity of 1500 μmol m^{-2} s^{-1}, which is applied in the following to represent the net ecosystem CO_2 assimilation capacity. The rectangular hyperbolic model was given preference over the non-rectangular hyperbolic model favored by Gilmanov and others (2003, 2007) as it generally provided an equally good fit to the data at lesser degrees of freedom and converged considerably better than the latter (data not shown).

RESULTS

With half-hourly NEE's reaching −30 μmol m^{-2} s^{-1} (Figure 1), the most negative average $F_{\mathrm{NEE,1500}}$ among all sites, −13.5 ± 0.2 μmol m^{-2} s^{-1} (Table 2), was observed for Neustift. On the other end, the lowest minimum NEE's (−2 μmol m^{-2} s^{-1}), which are hardly visibly in Figure 1, were observed for Varriö, which also exhibited the least negative

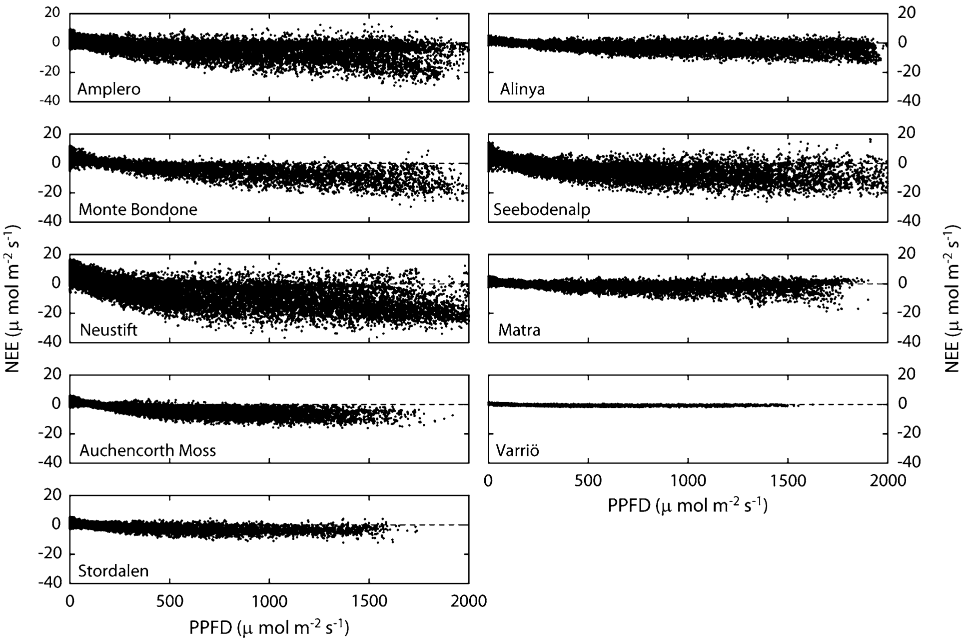

Figure 1. Net ecosystem CO$_2$ exchange (NEE) as a function of photosynthetically active radiation (PPFD) for the nine investigated sites (data pooled over vegetation periods).

Table 2. Regression Statistics and Parameters of Eq. (1)

	n	r^2	α	R_{eco}	$-F_{NEE,1500}$
Amplero	18798	0.48	0.028 ± 0.0009	2.61 ± 0.05	7.10 ± 0.10
Alinya	13006	0.48	0.017 ± 0.0007	1.83 ± 0.04	3.81 ± 0.06
Monte Bondone	9617	0.68	0.019 ± 0.0005	3.29 ± 0.05	9.95 ± 0.28
Seebodenalp	13895	0.58	0.045 ± 0.0013	4.38 ± 0.06	8.49 ± 0.10
Neustift	15264	0.55	0.045 ± 0.0013	5.53 ± 0.11	13.46 ± 0.17
Matra	12311	0.32	0.015 ± 0.0008	1.29 ± 0.03	2.38 ± 0.05
Auchencorth Moss	23917	0.74	0.022 ± 0.0003	2.00 ± 0.02	7.67 ± 0.08
Varriö	7507	0.55	0.022 ± 0.0008	1.45 ± 0.04	4.14 ± 0.06
Stordalen	4347	0.70	0.015 ± 0.0006	0.68 ± 0.01	0.80 ± 0.01

Parameters are given as means with standard errors derived from a bootstrapping analysis.
Data have been pooled over the vegetation period. Abbreviations: n—number of half-hourly measurements, r^2—correlation coefficient, α—apparent quantum yield (mol mol^{-1}), R_{eco}—ecosystem respiration (μmol m^{-2} s^{-1}), $F_{NEE,1500}$—net ecosystem CO$_2$ exchange at a photosynthetic photon flux density of 1500 μmol m^{-2} s^{-1} (μmol m^{-2} s^{-1}).

average $F_{NEE,1500}$ (-0.8 ± 0.01 μmol m^{-2} s^{-1}; Table 2). The remaining sites exhibited $F_{NEE,1500}$ values roughly between -4 and -10 μmol m^{-2} s^{-1} (Table 2). $F_{NEE,1500}$ scaled with R_{eco} across all sites, the average ratio of $-F_{NEE,1500}$ to R_{eco} being 2.5 ($r^2 = 0.85$, $P < 0.01$), as depicted in Figure 2. Values for the apparent quantum yield, α (Table 2), ranged from 0.015 to 0.028 mol CO$_2$ mol photons^{-1}, except for Neustift and Seebodenalp, whose apparent quantum yield was about twice as high (0.045 mol CO$_2$ mol photons^{-1}). All study years pooled, PPFD explained between 48 and 74% of the variability in vegetation period NEE (Table 2), except for Matra, where PPFD explained only 32% of the variability. The fraction of variability in NEE explained by PPFD varied markedly during the season, as shown in the uppermost panels of Figure 3: At the two Mediterranean mountain sites (Amplero and Alinya) and partially at Matra, PPFD explained more than 90% of the variability in NEE in spring and autumn, when soil water availability was high, but not during the summer drought. Conversely, the fraction of variability in NEE explained by PPFD was generally lower with cool and wet conditions in spring and autumn and higher during summer at the three Alpine sites (Monte Bondone, Seebodenalp, Neustift), Auchencorth Moss and, although less pronounced, at the two sub-arctic sites, Varriö and Stordalen. The fraction of variability in NEE explained by PPFD was also affected by management, the r^2 of the fitted relationships in Figure 3 decreasing in response to mowing or grazing. This was most evident for the

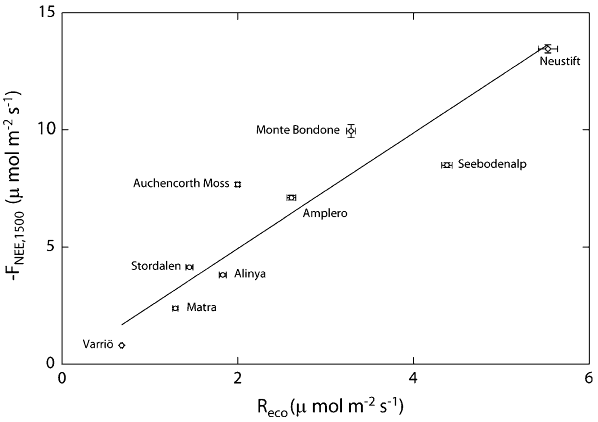

Figure 2. Ecosystem respiration (R_{eco}) versus net ecosystem CO_2 exchange at a photosynthetically active radiation of 1500 µmol m^{-2} s^{-1} ($F_{NEE,1500}$) for data pooled over the vegetation period. Error bars refer to ±1 standard deviation.

three Alpine meadows (Monte Bondone, Seebodenalp, Neustift), less so for Amplero, Alinya and Matra, where management activities took place during the summer drought.

To elucidate the controls of environmental drivers other than PPFD, as well as biotic factors, on NEE, two key parameters of the response of NEE to PPFD, R_{eco} and $F_{NEE,1500}$, are analyzed in the following. This analysis is done using examples of three selected sites—Amplero, representative of the sites characterized by a pronounced summer drought, Neustift, a typical Alpine meadow, and Auchencorth Moss, representative of extensively grazed northern grasslands.

R_{eco} increased with temperature at Neustift and Auchencorth Moss, but remained relatively constant or even decreased at temperatures above 13°C at Amplero (Figure 4). To mathematically describe

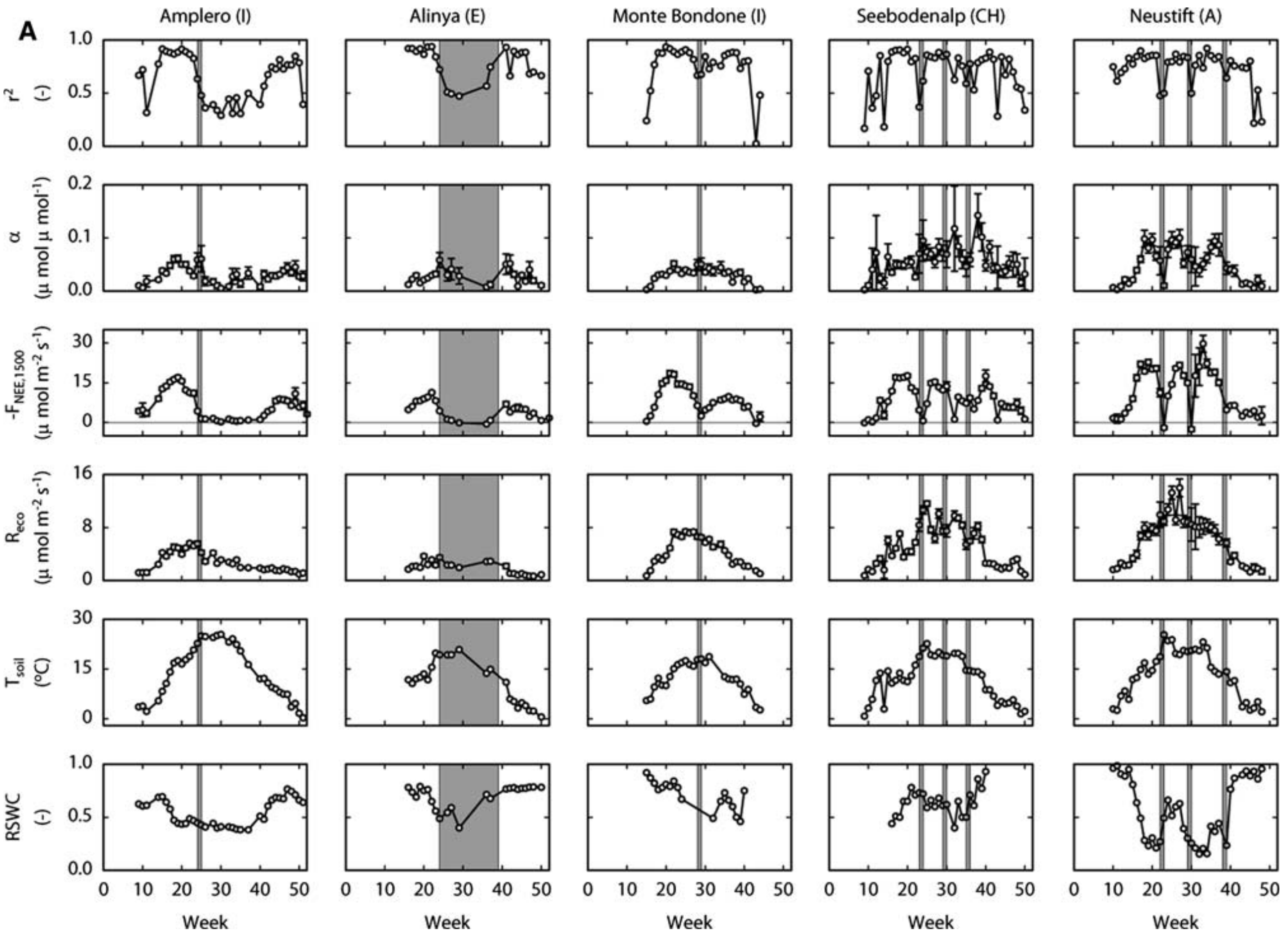

Figure 3. Weekly values (2003) of the correlation coefficient (r^2) for PPFD versus NEE (Eq. 1), the apparent quantum yield (α), the net ecosystem CO_2 exchange at a photosynthetically active radiation of 1500 µmol m^{-2} s^{-1} ($F_{NEE,1500}$) and ecosystem respiration (R_{eco}), as well as weekly average soil temperature (T_{soil}) and relative soil water content (RSWC) at the respective reference soil depth (see Table 1). Gray areas indicate the dates of mowing and grazing, error bars refer to ±1 standard deviation.

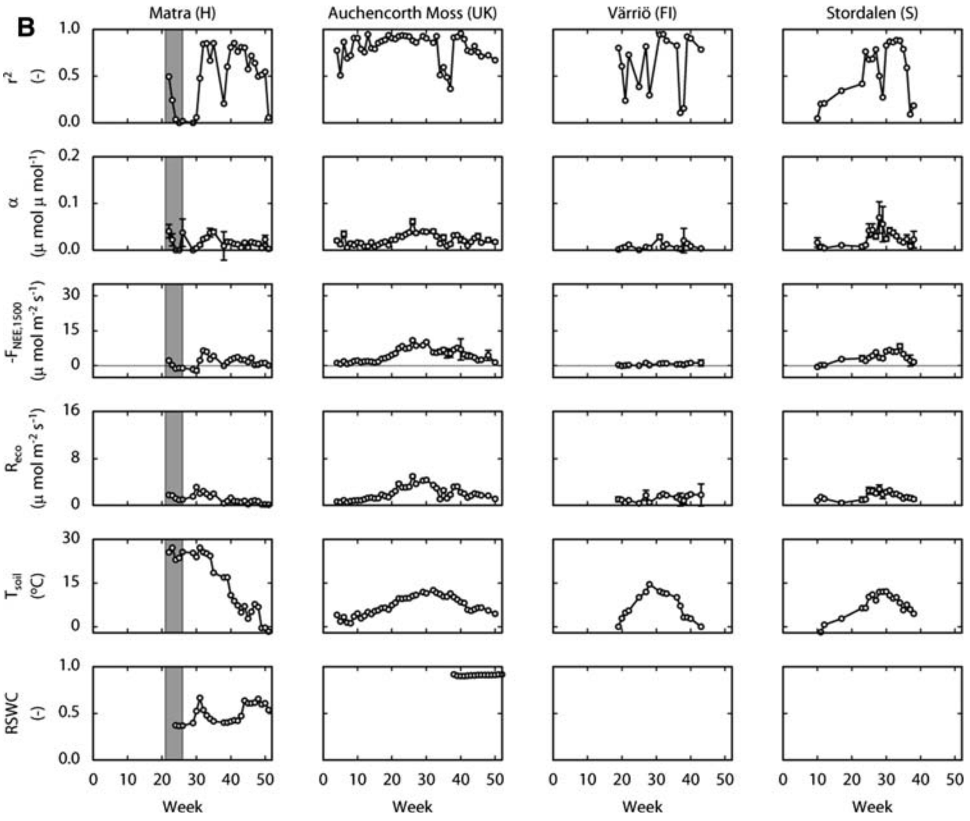

Figure 3. continued

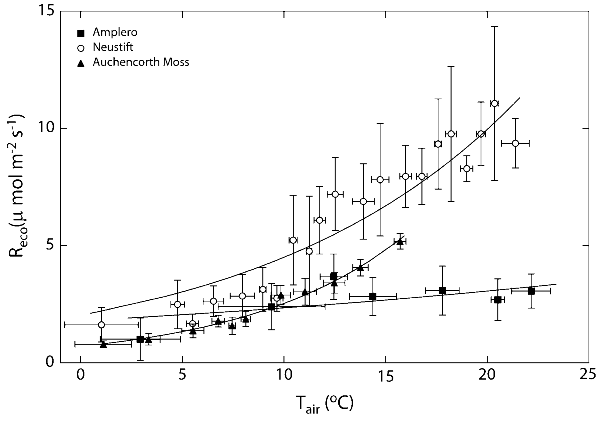

Figure 4. Ecosystem respiration (R_{eco}) as a function of air temperature (T_{air}). Symbols are bin-averages of equally sized blocks of data, lines represent fits (see Table 3 for parameters) to raw data using Eq. (2). Error bars refer to ±1 standard deviation of bin-averages.

the response of R_{eco} to temperature we used a simple exponential model, that is,

$$R_{eco} = A \exp(BT_a), \tag{2}$$

where A is the soil respiration rate (μmol m^{-2} s^{-1}) at 0°C, T_a the air temperature (°C), and B a temperature sensitivity parameter (°C^{-1}), related to the Q_{10} as $B = \ln(Q_{10})/10$. Optimizing the two free parameters of Eq. (2), A and B, against measured R_{eco} showed that 72 and 92% of the variability in R_{eco} were explained by temperature (air and soil temperature alike) for Neustift and Auchencorth Moss, respectively, but only 19% for Amplero (Table 3). The poor explanatory power of temperature for Amplero, as opposed to Neustift and Auchencorth Moss, was due to the fact that at this site R_{eco} and temperature were out of phase, R_{eco} peaking in spring and autumn, not in summer (Figure 3). An analysis of the residuals (data not shown) revealed that this bias may be compensated for by including the amount of aboveground biomass into parameter A of Eq. (2):

$$A = k_A\, BM_{ag} + d_A. \tag{3}$$

where k_A and d_A are the slope (m^2 g^{-1}) and y-intercept (μmol m^{-2} s^{-1}), respectively, of a linear relationship between A and the aboveground biomass (BM_{ag}, g m^{-2}). Combining Eqs. (2) and (3) improved the fraction of explained variability in R_{eco} greatly for Amplero (51%) and somewhat for Neustift (81%), while remaining unchanged at 92% for Auchencorth Moss (Table 3). Although at

Table 3. Regression Statistics and Parameters for Eqs. (2–5)

		Amplero	Neustift	Auchencorth Moss
R_{eco} = f(T_a) Eq. (2)	r^2	0.19	0.72	0.92
	RMSE	1.01	1.78	0.34
	A	1.795 ± 0.363	2.036 ± 0.153	0.704 ± 0.049
	B	0.027 ± 0.010	0.079 ± 0.005	0.128 ± 0.006
R_{eco} = f(T_a,BM_{ag}) Eqs. (2 and 3)	r^2	0.51	0.81	
	RMSE	0.78	1.45	
	k_A	0.006 ± 0.001	0.004 ± 0.001	
	d_A	0.951 ± 0.222	1.449 ± 0.199	
	B	0.027 ± 0.010	0.068 ± 0.005	
R_{eco} = f(T_a,BM_{ag},RSWC) Eqs. (2 , 3, and 4)	r^2	0.65		
	RMSE	0.66		
	k_A	0.004 ± 0.001		
	d_A	0.639 ± 0.189		
	k_B	0.121 ± 0.039		
	d_B	0.005 ± 0.010		
$F_{NEE,1500}$ = f(GAI) Eqs. (5a–b)	r^2	0.81	0.76	0.83
	RMSE	3.14	3.63	1.57
	a	−9.50 ± 0.725	−4.44 ± 0.275	−6.57 ± 0.590
	b	3.72 ± 0.782	−19.16 ± 0.614	5.43 ± 1.205

Parameters are given as means with standard errors derived from a bootstrapping analysis.
Abbreviations: R_{eco}*—ecosystem respiration (μmol* m^{-2} s^{-1}*),* T_a*—air temperature (°C),* BM_{ag}*—aboveground biomass (g* m^{-2}*), RSWC—relative soil water content (dimensionless),* $F_{NEE,1500}$*—net ecosystem* CO_2 *exchange at a photosynthetic photon flux density of 1500 μmol* m^{-2} s^{-1} *(μmol* m^{-2} s^{-1}*), GAI—green area index (*m^2 m^{-2}*),* r^2*—coefficient of determination, RMSE—root mean squared error (μmol* m^{-2} s^{-1}*), A—parameter of Eq. (2) (μmol* m^{-2} s^{-1}*), B—parameter of Eq. (2) (°*C^{-1}*),* k_A*—parameter of Eq. (3) (*m^2 g^{-1}*),* d_A*—parameter of Eq. (3) (μmol* m^{-2} s^{-1}*),* k_B*—parameter of Eq. (4) (dimensionless),* d_A*—parameter of Eq. (4) (°*C^{-1}*), a—parameter of Eq. (5a–b) (μmol* m^{-2} s^{-1}*),* d_A*—parameter of Eq. (5a–b) (μmol* m^{-2} s^{-1}*).*

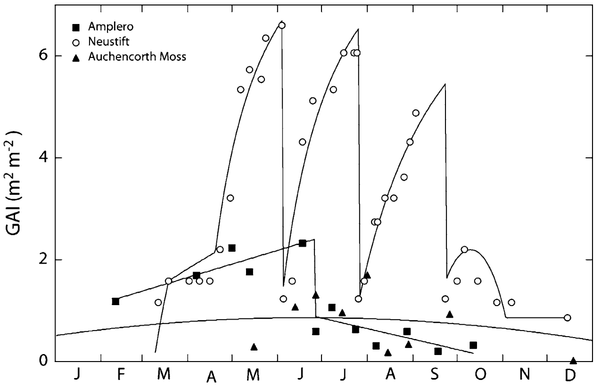

Figure 5. Seasonal course of the green area index (GAI, m^2 m^{-2}) during 2003. Symbols refer to measurement dates, lines to piece-wise best fits.

this stage residuals were randomly distributed and exhibited no correlation with any other potential abiotic or biotic influence factor for Neustift and Auchencorth Moss (data not shown), residuals of Amplero were correlated ($r^2 = 0.51$, $P < 0.001$) with the RSWC. A linear increase of B with increasing RSWC that is,

$$B = k_B \text{ RSWC} + d_B, \tag{4}$$

where k_B and d_B are the slope (dimensionless) and y-intercept (°C^{-1}), respectively, of a linear relationship between B and the RSWC (dimensionless), provided the best fit to data, increasing the fraction of explained variability in R_{eco} for Amplero to 65% (Table 3).

As might be expected from the temporal correlation between the amount of photosynthetically active plant area (GAI, m^2 m^{-2}, Figure 5) and $F_{NEE,1500}$ (Figure 3), there was a close relationship between these two: $F_{NEE,1500}$ increased in an approximately linear fashion with GAI for Amplero and Auchencorth Moss (Figure 6). For Neustift $F_{NEE,1500}$ increased linearly with GAI until values of about 4.3 m^2 m^{-2}, at higher GAI's it saturated at a value of around −19 μmol m^{-2} s^{-1} (Figure 6). Using appropriate relationships, that is,

$$F_{NEE,1500} = a \text{ GAI} + b \text{ for Amplero and Auchencorth Moss, and} \tag{5a}$$

$$F_{NEE,1500} = \max\{a \text{ GAI}, b\} \text{ for Neustift,} \tag{5b}$$

where parameters a and b have units of μmol m^{-2} s^{-1}, GAI turned out to be the single most important factor determining the variability in $F_{NEE,1500}$, explaining 81, 76 and 83% of the variability in

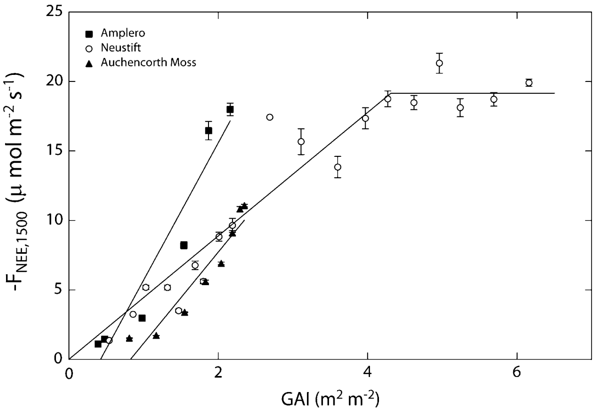

Figure 6. The net ecosystem CO_2 exchange at a photosynthetically active radiation of 1500 μmol m^{-2} s^{-1} ($F_{NEE,1500}$) as a function of the green area index (GAI, m^2 m^{-2}). Symbols are bin-averages of equally sized blocks of data, lines represent fits (see Table 3 for parameters) to raw data using Eqs. (5a–b). Error bars refer to ±1 standard deviation of bin-averages.

$F_{NEE,1500}$ for Amplero, Neustift, and Auchencorth Moss, respectively (Table 3). Residuals were distributed randomly and exhibited no correlation with either temperature (both soil and air) or RSWC (data not shown).

DISCUSSION

In a comprehensive literature survey, Ruimy and others (1995) analyzed 1362 data sets of the response of NEE to PPFD (so-called light response curves). For C_3 grasslands ($n = 68$), they determined average values of α and $-F_{NEE,1500}$ of 0.017 mol mol^{-1} and 25.5 μmol m^{-2} s^{-1}, respectively, whereas no value could be determined for R_{eco} which was thus assumed zero. With α ranging from 0.015 to 0.045 (average 0.025) mol mol^{-1} and $-F_{NEE,1500}$ from 0.8 to 13.5 (average 6.4) μmol m^{-2} s^{-1} (Table 2) the light response curves of the investigated mountain grassland ecosystems are only somewhat steeper at low light intensities (that is, higher α), but reach clearly lower minimum values at high light intensities. This difference may be attributed to the fact that most of the C_3 grasslands in the study of Ruimy and others (1995) were forage grasses, such as ryegrass or tall fescue, sown on fertile lowland agricultural soils, which are obviously much more productive than the (semi-) natural mountain grasslands investigated here. Better correspondence in terms of $F_{NEE,1500}$ and α is observed with studies on semi-natural or natural grasslands, such as temperate (Novick and others 2004), alpine and sub-alpine grasslands (Kato and others 2004a, b; Li and others 2008; Rogiers and others 2005), tropical (Wilsey and others 2002), Mediterranean (Xu and Baldocchi, 2003) and temperate (Nieven and others 2005) pastures, or tundra ecosystems (Whiting and others 1992; Vourlitis and others 2000), where, roughly, α ranges from 0.01 to 0.04 and $-F_{NEE,1500}$ from 1 to 12 μmol m^{-2} s^{-1}. Large differences in maximum weekly light response curve parameters between intensively managed and semi-natural European grasslands have also been reported by Gilmanov and others (2007). There is yet another difference to the more productive grasslands studied by Ruimy and others (1995), insofar as that their higher $-F_{NEE,1500}$ is not accompanied by proportionally higher respiration costs. With $-F_{NEE,1500}$ to R_{eco} ratios in the range of 4–7, the grasslands reviewed by Ruimy and others (1995) are much more similar to many crop ecosystems in the same study, which on average exhibited a $-F_{NEE,1500}$ to R_{eco} ratio of 6–7. Again the investigated mountain grasslands, in terms of the $-F_{NEE,1500}$ to R_{eco} ratio (range 1.2–3.8, average 2.5, Figure 2, Table 2), compare much better with the above-mentioned (semi-) natural grasslands, even with grasslands dominated by C_4 species (for example, Gilmanov and others 2003).

Given that the absorption of photons is key to the assimilation of CO_2 (Larcher 2001), it comes as no surprise that the availability of PPFD is often the single most important abiotic influence factor for ecosystem-scale CO_2 fluxes, explaining well in excess of 50% of the variability in NEE (for example, Gilmanov and others 2007; Li and others 2008; Ruimy and others 1995), which is confirmed in the present study (Figure 1, Table 2). The role of PPFD in determining NEE changes markedly during the course of the vegetation period, PPFD being a better predictor for NEE during periods favorable for ecosystem CO_2 uptake, that is, well developed canopy and minor limitations by other abiotic influence factors (Li and others 2008; Vourlitis and others 2000; Wilsey and others 2002; Xu and Baldocchi 2003; Kato and others 2004b). Accordingly, PPFD explains the major part of the variability in NEE in spring and autumn for the three sites experiencing a pronounced summer drought (Amplero, Alinya, Matra), whereas most of the variability of NEE is explained by PPFD in (peak) summer for the investigated Alpine and northern ecosystems (Figure 3). Exceptions from this seasonal pattern are mostly due to management practices, mowing or grazing reducing the amount of assimilating plant matter and thus the relative importance of PPFD in determining NEE (Maljanen and others 2001; Nieven and others 2005; Rogiers and others 2005).

With the enzymatic reaction speed usually increasing exponentially with temperature (Larcher 2001), it is to be expected and has been demonstrated repeatedly (for example, Wohlfahrt and others 2005a) that temperature exerts a major control over R_{eco}, despite the multitude of respiration sources involved. This temperature dependency may be confounded by other factors, such as the availability of respirable substrate or soil water, in situations where these become limiting (Davidson and others 1998; Högberg and others 2001; Reichstein and others 2003; Wan and Luo 2003; Whitehead and others 2003; Bahn and others 2008). In our study, temperature was the single most important influence factor for R_{eco} at Neustift and Auchencorth Moss, but not at Amplero, where the amount of aboveground matter and the RSWC explained a larger or at least similar fraction of the variability in R_{eco} (Figure 4, Table 3). At Amplero this was due to R_{eco}, RSWC and aboveground biomass being low during summer, when temperatures are the highest (Figure 3). Findings along this line have been reported also by Xu and Baldocchi (2003) for a Mediterranean grassland, who argued that this reflects the reduction of assimilate supply and availability for both auto- and heterotrophic respiration during drought conditions. It appears that the aboveground biomass and RSWC are reasonable proxies for the supply and availability of respirable substrate (Reichstein and others 2002). At Neustift, where a large amount of aboveground biomass is available (Figure 5, Table 3), aboveground respiration may contribute significantly to R_{eco} (Wohlfahrt and others 2005a) and therefore the variation in the amount of aboveground biomass modulates the variability in R_{eco}. In contrast, the amount of aboveground biomass and RSWC exhibit little seasonal variation at Auchencorth Moss (Figures 3 and 5), where these factors accordingly do not contribute to the explained fraction in R_{eco} (Table 3).

In accordance with other studies on ecosystems with a pronounced dry period (for example, Reichstein and others 2002; Xu and Baldocchi 2003; Flanagan and Johnson 2005), a reduction in the temperature sensitivity of R_{eco} within decreasing water availability was observed for Amplero. This might represent a physiologic adaptation to drier conditions, as well as reflect a shift in the activity between root and microbial respiration or within the microbial community itself, related to both the decrease in assimilate input and soil water availability.

As noted already by Wohlfahrt (2004), immediately after cutting or grazing R_{eco} remains relatively high (Figure 3), which cannot be solely explained by the associated rise in soil temperature (Bahn and others 2006) caused by the increased radiation absorption at the soil surface. This phenomenon also contradicts our understanding of the role of the assimilate supply in controlling R_{eco}, which should be expected to be greatly reduced with most of the aboveground biomass being lost (Wan and Luo 2003). Because the aboveground biomass is used as a proxy for the assimilate input into the ecosystem in Eq. (3), this model provides a poor fit to ecosystem respiration immediately after cutting. Possible mechanisms responsible for the sustained R_{eco} might be the decomposition of fresh dead plant matter remaining in the field after cutting, an increased efflux of CO_2 through the soil surface caused by a more efficient turbulent exchange in the shortened canopy, as well as higher specific plant respiration rates due to the initiation of repair mechanisms of severed, as well as the reconstruction of lost plant matter (Wohlfahrt 2004).

The single most important influence factor for the net ecosystem CO_2 exchange (NEE) at saturating light intensity, $F_{NEE,1500}$, was the amount of assimilating plant area (GAI), explaining around 80% of the variability in $F_{NEE,1500}$ for all three sites investigated in detail (Figure 6, Table 3). For Amplero and Auchencorth Moss, whose GAI did not exceed values of 2.5 $m^2\ m^{-2}$, $F_{NEE,1500}$ increased approximately linearly with GAI, which has been observed for several grassland ecosystems (for example, Suyker and Verma 2001; Flanagan and others 2002; Xu and Baldocchi 2003; Li and others 2005). In contrast at Neustift, where GAI's of up to 6.5 $m^2\ m^{-2}$ were reached, $F_{NEE,1500}$ saturated at a GAI of around 4.3 $m^2\ m^{-2}$ (Figure 6), reflecting the trade-off between increasing self-shading and increasing assimilatory area (Wohlfahrt and others 2003). This saturation-type response is typical for many crops (for example, Suyker and others 2004, 2005) and reflects the high amounts of biomass/GAI which result from the, at least for mountain grassland ecosystems, relatively intensive management of this site.

SUMMARY AND CONCLUSION

The data presented in this article show that the investigated European mountain grassland ecosystems have, in terms of NEE, little in common with grasslands sown on fertile soils in low-land locations, which exhibit higher maximum carbon gains at lower respiratory costs. Better correspondence was observed with many (semi-) natural grassland ecosystems around the world, despite contrasting climatic and edaphic conditions, land use, vegetation structure and composition. Overall, the availability of PPFD was the single most important abiotic influence factor for NEE. Its role changed markedly during the course of the season, PPFD being a better predictor for NEE during periods favorable for CO$_2$ uptake, which was spring and autumn for the sites characterized by summer droughts and (peak) summer for the Alpine and northern study sites. This general pattern was interrupted by grassland management practices, that is, mowing and grazing, when the variability in NEE explained by PPFD decreased in concert with the amount of aboveground biomass. Temperature was the abiotic influence factor that explained most of the variability in ecosystem respiration at the Alpine and northern study sites. At the sites characterized by a pronounced summer drought, soil water availability and aboveground biomass, two proxies for drought-induced reductions in substrate supply and availability, were more or equally important as compared to temperature. The amount of assimilating plant area was the single most important biotic variable determining the maximum ecosystem carbon uptake potential, that is, the NEE at saturating PPFD.

It may thus be concluded that, through triggering rapid changes in the amount and area of the aboveground plant matter, the timing and frequency of land management practices (mowing and grazing) is crucial for the short-term sensitivity of NEE of the investigated mountain grassland ecosystems to climatic drivers.

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