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**Land use affects the  
net ecosystem CO<sub>2</sub>  
exchange**

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# Land use affects the net ecosystem CO<sub>2</sub> exchange and its components in mountain grasslands

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## Abstract

Land-use change has been strongly affecting mountain grasslands, however, its controls on the net ecosystem exchange of CO<sub>2</sub> (NEE) and its components have not yet been well documented. We analyzed chamber-based estimates of NEE, gross primary productivity (GPP), ecosystem respiration (R) and light use efficiency (LUE) of six mountain grasslands differing in land use, as measured during the growing seasons from 2002 to 2008. The main findings of the study are that: (1) land use affected seasonal NEE, GPP, R and LUE, which all decreased from managed to unmanaged grasslands; (2) these changes were explained by altered leaf area index (LAI), biomass and physiology; (3) diurnal variations of NEE were primarily controlled by photosynthetically active photon flux density (GPP) and soil and air temperature (R), seasonal variations were associated with changes in LAI; (4) parameters of light response curves were generally closely coupled, and the ratio R/GPP was nearly constant across the sites; (5) similarly to our study, GPP and R for other grasslands on the globe decreased with land-use intensity, while their ratio remained largely unchanged. We conclude that land use exerts a major influence on the net ecosystem CO<sub>2</sub> exchange and its components in mountain grasslands.

## 1 Introduction

Due to the importance of the terrestrial carbon cycle for the global climate system there is a considerable interest in understanding the factors that control the carbon balance of terrestrial ecosystems (Canadell et al., 2007; IPCC, 2007). In European mountain regions, grasslands are an important component of the landscape. Differences and changes in land management can be expected to affect the ecosystem carbon (C) sequestration potential of these ecosystems. Several studies have shown that temperate grasslands can act as both sinks and sources of CO<sub>2</sub> (Novick et al., 2004; Gilmanov et al., 2007; Stoy et al., 2008; Wohlfahrt et al., 2008b). Land-use changes have the

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potential to modify ecosystem source/sink relationships, which in turn will feed back on atmospheric CO<sub>2</sub> concentrations (Houghton, 1995, 1999; IPCC, 2007). Over the past decades, socio-economic changes have led to land-use changes in mountain grasslands (Cernusca et al., 1999; Tappeiner et al., 2003), which affect nitrogen availability (Zeller et al., 2000; Robson et al., 2007), species composition (Tasser et al., 1999), leaf and canopy gas exchange at peak biomass (e.g. Bahn et al., 1999; Wohlfahrt et al., 2003) and soil and root respiration (Bahn et al., 2006, 2008). Up to now the diurnal, seasonal and interannual variation of net ecosystem CO<sub>2</sub> exchange (NEE) and its components have not been documented for grasslands differing in land use. This reflects a general scarcity of comparative studies of NEE on adjacent ecosystems (i.e. with comparable climate, geology and soil) differing in land-use (Stoy et al., 2008; Don et al., 2009).

Measurements of NEE are needed in order to determine the sink-source status of ecosystems, and to analyze how the CO<sub>2</sub> exchange varies with the seasonal and interannual variation in environmental conditions (Flanagan et al., 2002). Control of NEE is complex, often involving phenological variability, temporal variation in moisture availability, seasonal and interannual temperature variation, and canopy structure and variation in light intensity (e.g. Monson et al., 2002). Surface-based flux measurements are being made at more than 500 sites worldwide and form a global flux network (Baldocchi et al., 2001; Baldocchi, 2008). The Fluxnet approach for assessing NEE is based on the eddy covariance (EC) method, which is most accurate when the atmospheric conditions are steady and the underlying surface is homogeneous (Baldocchi, 2003). These requirements currently limit this method to relatively homogeneous and flat terrain and greatly complicate the study of NEE in landscapes with complex topography (Schimel et al., 2002). This is why the majority of the investigated ecosystems from the global flux network are ecosystems with flat terrain and a homogeneous canopy structure. As an alternative to the EC method, chamber-based measurements may be suitable for monitoring NEE from short-plant ecosystems located on mountain slopes (Risch and Dougas, 2005; Li et al., 2008). One of the strengths of the chamber ap-

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proach is the possibility to control and manipulate environmental factors, which offers an opportunity to separate their individual effects on NEE and to partition NEE into its key components, i.e. gross primary productivity (GPP) and ecosystem respiration (R) while avoiding assumptions that commonly underlie the separation of the components as based on EC data (e.g. Wohlfahrt et al., 2005b).

In this paper, we present chamber-based measurements of NEE and its components for six mountain grasslands, including two meadows, two pastures and two abandoned grasslands differing in site fertility, as obtained during seven consecutive growing seasons (2002–2008). Aim of this study was (1) to assess the importance of the major biotic and abiotic drivers determining the diurnal and seasonal variation of NEE in relation to land use, (2) to explore relationships between GPP, R and light use efficiency (LUE) across seasons and sites, and (3) compare the major components of NEE, i.e. GPP and R, for different types of grasslands around the globe. We tested the hypotheses that (1) NEE and its components GPP and R are primarily controlled by photosynthetically active photon flux density (PF<sub>D</sub>), temperature, LAI, biomass and canopy physiology, and decrease from meadows to pastures and a nutrient-poor abandoned grassland, and (2) there is a close relationship between GPP, R and LUE across seasons and study sites.

## 2 Material and methods

### 2.1 Study sites

The study sites are located in the Austrian Central Alps near the village Neustift (47°07' N, 11°19' E) in the Stubai Valley. Investigations were carried out during the growing seasons (May to November) 2002–2008 on a meadow at the valley bottom (970 m a.s.l.), a mountain meadow (1750–1820 m a.s.l.), two pastures (1930 and 1950 m a.s.l.), a nutrient-rich abandoned grassland (1960 m a.s.l.), and a nutrient-poor abandoned grassland (2000 m a.s.l.).

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Except for the valley bottom meadow all sites are located on slopes with inclinations of 19–29° (Table 1), which is typical for grasslands in mountain regions. The sites cover an annual average temperature range from 3.0 to 6.3°C and an annual precipitation from 850 to 1097 mm (Table 1). The valley bottom meadow is cut three times per year and fertilized with manure annually (Wohlfahrt et al., 2008a), the mountain meadow once a year and fertilized with manure every 2–3 years (Bahn et al., 2006). The pastures are grazed from May to mid-September. CO<sub>2</sub>-fluxes of the two pastures were very similar, consequently data from the two sites were pooled and are referred to as pastures. The two unmanaged grasslands were abandoned in 1983. The nutrient-rich abandoned grassland was reforested and fertilized once in 1988. The trees were not included in the flux measurements. For soil types and vegetation composition refer to Table 1.

## 2.2 Assessment of the net ecosystem CO<sub>2</sub> exchange

Measurements were conducted between 2002 and 2008 in episodic campaigns every three to four weeks. During each campaign, chamber measurements of NEE were conducted over a diurnal course for each site. We measured NEE with home-made manually operated temperature-controlled closed transparent plexiglass chambers, as described by Wohlfahrt et al. (2005a). Chambers (0.4–0.7 m high) were placed on frames (0.6 m<sup>2</sup> ground area) made of polyethylene that had been inserted 3 cm into the soil at the beginning of each season. Three frames were placed at each site. Measurements were usually carried out within 120 s during daytime and within 180 to maximum 300 s when flux rates were low (i.e. at levels of low or no light).

When placing the chamber on the frame a hole at the top of the chamber was kept open to avoid pressurization, in addition a vent connected to a tube at the lower part of the chamber prevented pressure differences to the atmosphere during measurements. Air temperature inside the chamber was maintained within ±2°C relative to ambient by using cool packs, packed on a metal frame at the rear of the chamber. CO<sub>2</sub> concentrations were measured with an infra-red gas analyser (LCA-2, ADC, Hoddesdon, UK)

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from 2002 to 2005 and CO<sub>2</sub>-Sensor (GMP343, Vaisala, Helsinki, Finland) from 2006 to 2008. During all measurements the following parameters were recorded: air temperature outside and inside the chamber (temperature module 110, Voltcraft, Germany), air humidity (HM70, Vaisala, Helsinki, Finland), soil temperature (HOBO data logger, Onset Computer, Bourne, MA, USA) and incident photosynthetically active photon flux density (PPFD) (G1118 GaAsP, Ga Photodiode diffusion type, Hamamatsu Photonics GmbH, Germany).

NEE ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) was calculated as

$$\text{NEE} = \frac{(d\text{CO}_2/dt) * T * P * 10^3}{[V_m * (273.15 + T) * P_0]} * (V/A) * 10^6 \quad (1)$$

where  $d\text{CO}_2/dt$  ( $\mu\text{mol mol}^{-1} \text{ s}^{-1}$ ) is the change in CO<sub>2</sub> mole fraction inside the chamber over time,  $P$  is the atmospheric pressure (kPa),  $V_m$  is the molar volume of CO<sub>2</sub> ( $\text{m}^3 \text{ mol}^{-1}$ ),  $T$  is the chamber temperature ( $^{\circ}\text{C}$ ),  $P_0$  is the air pressure correction (kPa),  $V$  is the chamber volume ( $\text{m}^3$ ), and  $A$  is the chamber base area ( $0.6 \text{ m}^2$ ).

Kutzbach et al. (2007) found that for their closed chamber system nonlinear regression models were more appropriate for estimating CO<sub>2</sub> fluxes than linear ones. In contrast, for our chamber system we observed consistent and highly significant linear changes of CO<sub>2</sub> concentrations over the comparatively short time of chamber closure, and therefore applied linear regressions in flux calculations.

An evaluation of the ecosystem chamber was made by a cross comparison with an eddy covariance system on flat terrain on the valley bottom meadow. The comparison was made using diurnal courses of NEE measured on 10 days between May and November 2002. The estimates of CO<sub>2</sub> fluxes obtained by these two methods correspond well. NEE measured with chambers showed 12 and 23% higher flux rates during day- and nighttime, respectively, than estimated by the eddy covariance method. Hammerle et al. (2007) carried out a comparison at the mountain meadow and found an underestimation on average by 19% by the EC method. Similarly, a number of earlier

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studies observed higher flux rates obtained by chamber-based approaches as compared to the eddy covariance approach, which were in the range of 6–26% for daytime and 4–30% for nighttime fluxes (e.g. Goulden et al., 1996; Dugas et al., 1999; Lavigne et al., 1997; Angell et al., 2001; Dore et al., 2003; Zamolodchikov et al., 2003; Wohlfahrt et al., 2005a). Possible reasons for these discrepancies are differences in spatial sampling/footprint area (Lavigne et al., 1997), as well as an underestimation of EC-based respiration fluxes through advection or insufficient turbulence/ mixing at night (Goulden et al., 1996; Lavigne et al., 1997). Chamber artefacts as related to the influence of pressure on respiration (Davidson et al., 2002) or influences on microclimate were avoided by the chamber design (cf. above) and therefore considered as minor.

### 2.3 Parameters of light response curves

To relate NEE to PFD we fitted the dataset obtained during each field campaign and site to the following rectangular hyperbolic model (Ruimy et al., 1995):

$$NEE = \frac{-\alpha PFD GPP_{sat}}{\alpha PFD + GPP_{sat}} + R \quad (2)$$

where NEE represents net ecosystem exchange of CO<sub>2</sub> ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $\alpha$  the apparent quantum yield ( $\text{mol CO}_2 \text{ mol photons}^{-1}$ ), PFD the photosynthetically active photon flux density ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $GPP_{sat}$  the asymptotic value of the gross primary production at high irradiance ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), and R denotes ecosystem respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).

For comparison across ecosystems we used Eq. (2) to calculate NEE and GPP at PFD of  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  ( $NEE_{2000}$ ,  $GPP_{2000}$ ). R was interpolated to a reference soil temperature of  $10^\circ\text{C}$  ( $R_{10}$ ) by best fitting linear and exponential models. LUE was calculated from the initial slope of the light response curve obtained for each diurnal course.

## 2.4 Measurement of biomass and leaf area index

Biomass and leaf area index were assessed at all sites by clipping of three square plots of  $0.25 \text{ m}^2$  at regular intervals throughout the vegetation periods from 2002 to 2008. The harvested plant material was separated into leaves, stems, reproductive organs, dead plant matter and cryptogams (mainly mosses). Silhouette area was determined with an area meter (LI-3100, Li-Cor, Lincoln, USA). Dry biomass was determined after drying at least for 24 h at  $60^\circ\text{C}$ .

## 3 Results

Minimum and maximum rates of net ecosystem  $\text{CO}_2$  exchange (NEE) as measured during all campaigns were highest for the meadows and fertilized abandoned grassland (Fig. 1), which all exhibited a high above-ground biomass (Table 1). Lowest peak net fluxes of  $\text{CO}_2$  were measured for the pastures and the unfertilized abandoned grassland that supported relatively low above-ground biomass and leaf area index (LAI). After mowing and grazing there was a transient net release of  $\text{CO}_2$  from the meadows and the pastures also during daylight (Fig. 1), which lasted for approximately 6–10 days (not shown). For all study years, highest rates of net  $\text{CO}_2$  uptake coincided with values of peak biomass, occurring between June (valley bottom meadow) and August (abandoned sites), maximum NEE ranging from  $-16.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$  (late part of July 2004) to  $-30 \mu\text{mol m}^{-2} \text{ s}^{-1}$  (June 2003). There were marked differences in the light response curves of NEE between the two abandoned sites in July and August (Fig. 1). The nutrient-rich abandoned grassland showed much higher values of NEE at any given temperature and light intensity, as compared to the nutrient-poor abandoned grassland.

Across sites, ecosystem respiration (R) ranged from 0.6 (unfertilized abandoned grassland in October 2003 at  $T_{\text{air}}=-3^\circ\text{C}$  and  $T_{\text{soil}}=2.9^\circ\text{C}$ ) to  $22.1 \mu\text{mol m}^{-2} \text{ s}^{-1}$  (valley bottom meadow in July 2003 at  $T_{\text{air}}=13.5^\circ\text{C}$  and  $T_{\text{soil}}=13.7^\circ\text{C}$ ). Across seasons

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and sites, R generally increased linearly and exponentially with soil ( $R^2=0.28-0.78$ ,  $p < 0.01-0.06$ ) and air ( $R^2=0.25-0.66$ ,  $p < 0.01-0.06$ ) temperature (data not shown). At the pasture R decreased after a reduction of above ground biomass due to grazing (data not shown).

5 The seasonal variation of NEE in the grasslands studied was associated with variations in photosynthetically active photon flux density (PFD), temperature, above-ground biomass, plant area index (PAI) and LAI. A stepwise multiple regression across all sites and years explained 68% of NEE, 75% of gross primary productivity (GPP) and 60% of R for these grasslands by the factors PFD, air and soil temperature, above-ground biomass, LAI, type of grassland, measurement year and the time of the season. PFD  
10 was the most important factor determining NEE and GPP, explaining 61 % ( $p < 0.001$ ) and 67% ( $p < 0.001$ ) of the respective variability. Soil temperature was the most prominent parameter determining R by 33 % ( $p < 0.001$ ). While during the heat wave 2003 Western parts of Europe suffered from drought, the Austrian Alps remained largely un-  
15 affected and NEE was not moisture limited (Foelsche, 2004; Wohlfahrt et al., 2008b). At the sites studied here biomass was high in 2003 and peak values of NEE and R exceeded those from 2002 to 2008.

NEE, GPP, R and light use efficiency (LUE) were significantly related to LAI (Fig. 2) (for regression statistics cf. Table 2). At all sites, except the pastures, optimum values  
20 for LAI ranged from 2.7 to 4.8 m<sup>2</sup> m<sup>-2</sup>. R at a reference temperature of 10°C (R<sub>10</sub>) was positively related to LAI for all sites (Fig. 2, Table 2).

Across all years seasonal peak values of GPP, R and light use efficiency (LUE), measured at optimum LAI, decreased significantly from the meadows to the pastures and the N-poor abandoned grassland, whereas fertilization of abandoned grassland  
25 (N-rich) caused an increase of these parameters (Fig. 3a, b, e). When normalized for LAI, GPP also decreased significantly from the meadows to the pastures and the N-poor abandoned grassland (Fig. 3c). Normalized R tended to decrease in the same manner, and was significantly lower on the N-poor abandoned grassland as compared to the other sites (Fig. 3d). For the ratio R/GPP there was no significant trend across

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sites, the highest ratio occurring on the N-poor abandoned grassland (Fig. 3f). When pooling all data across seasons and years, we observed a similar trend as for peak season values: GPP, R and LUE decreased from the meadows to the pastures and the N-poor abandoned grassland (data not shown). Across study sites and years there were positive correlations between GPP, R and LUE (Fig. 4).

## 4 Discussion

A number of previous studies have shown that NEE is affected by interactions of microclimate, canopy structure and plant physiology (for herbaceous communities e.g. Tappeiner and Cernusca, 1998; Wilsey et al., 2002; Wohlfahrt et al., 2003). In most ecosystems light is the prime driver and explains most variability of NEE (Ruimy et al., 1995; Flanagan et al., 2002; Wilsey et al., 2002; Li et al., 2005, 2008; Zhao et al., 2006). In all the grasslands studied here, the diurnal variation of NEE was mostly determined by PFD during daytime and by soil and air temperature during nighttime. The seasonal and inter-annual variation was also affected by above-ground biomass and LAI. The extreme summer of 2003 was characterised in many parts of Europe by hot and dry days and rainfalls in the evenings (Foelsche 2004; Ciais et al., 2005), which at our sites led to a high production of above-ground biomass and LAI and particularly high values of NEE, GPP and R during 2003 (Fig. 1). This finding indicates that unusually warm years need not generally cause a reduction of GPP (Ciais et al., 2005; Reichstein et al., 2006), but can potentially also enhance productivity at sites with sufficient water supply (Jaksic et al., 2006; Mirzae et al., 2008).

LAI is a unique biophysical factor accounting for differences in phenological development, assimilation and biomass growth in plant canopies. By constituting the main assimilatory area, LAI exerts an import influence on canopy photosynthesis (Tappeiner and Cernusca, 1996; Saigusa et al., 1998) and thus provides assimilates to the roots and soil microorganisms (Reichstein et al., 2003; Bahn et al., 2008, 2009). Both, mowing and grazing, cause a substantial reduction of leaf area and thus GPP, turning the

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meadows and the pastures from sinks to short-term sources of CO<sub>2</sub> (Fig. 1). For the valley bottom meadow of our study it took on average 16 days after the first cut to become (on a daily basis) a net sink for CO<sub>2</sub> again (Wohlfahrt et al., 2008a). This pattern repeated itself after the second and third cut, whereas daily average rates of net CO<sub>2</sub> uptake and loss before and after cutting, respectively, decreased from the first to the third cut. Other studies in warm temperate grasslands showed that between 6 to 11 days are required, before net carbon gain (on a daily basis) is resumed (Dugas et al., 1999; Novick et al., 2004).

At all sites, both NEE and GPP at a PFD of 2000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  were closely related to LAI, the relationships saturating at LAI of 3–6  $\text{m}^2 \text{m}^{-2}$ . This is typical for productive grasslands, for which maximum GPP observed at LAI of 2–5  $\text{m}^2 \text{m}^{-2}$  (Gilmanov et al., 2007; Veenendaal et al., 2007; Wohlfahrt et al., 2008b). At the pastures studied here, grazing maintained LAI below a critical value of 4, which avoided trade-offs between increasing assimilatory area and associated self-shading effects.

The parameters of NEE light response curves reflect both canopy structure and physiology (e.g. Gu et al., 2002; Wohlfahrt et al., 2003; Flanagan and Johnson, 2005; Gilmanov et al., 2007) and inherently determine the response of NEE to environmental drivers and land use. In our study, across all years seasonal mean as well as seasonal peak values of GPP<sub>2000</sub>, R<sub>10</sub> and LUE decreased significantly from managed to unmanaged sites (Fig. 3a, b, e). Such a decrease could potentially be caused by differences in leaf area, its spatial arrangement, as well as species physiology. Accounting for effects of leaf area by normalizing GPP to LAI, we observed a reduction of GPP<sub>2000</sub> per unit leaf area with decreasing intensity of land management, in particular N supply. This finding is in agreement with ecophysiological studies documenting a reduction of leaf photosynthetic capacities with decreasing intensity of grassland management (Bahn et al., 1999), which have been attributed to changes in species composition and nutrient availability.

Also normalized R<sub>10</sub> tended to decrease from the meadows and the N-rich abandoned grassland to the pastures and the N-poor abandoned grassland (Fig. 3d).

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Ecosystem respiration is the sum of respiration of aboveground biomass and soil respiration. Soil respiration is considered to be the main contributor to R in most ecosystems, particularly grasslands (Wohlfahrt et al., 2005a). Grassland soil respiration has been shown to be closely related to LAI and GPP (Bahn et al., 2008). Likewise, our study demonstrates a close link between GPP and R across sites and study years (Fig. 4), which confirms earlier observations for a range of grasslands (Li et al., 2005; Gilmanov et al., 2007; Wohlfahrt et al., 2008b). Our study indicates that the ratio of  $R_{10}$  over  $GPP_{2000}$  is generally not affected by land management, however, may be somewhat higher on nutrient poor sites (Fig. 3f).

To test the generality of our finding we compared maximum GPP and R for ecosystems differing in land use from around the globe (Fig. 5). Similar to our study,  $GPP_{max}$  and  $R_{max}$  decreased from meadows to pastures and abandoned and natural grasslands (Fig. 5a). The ratio  $R_{max}$  over  $GPP_{max}$  (Fig. 5b) was relatively constant across all types of ecosystems, which indicates a close coupling of R to site productivity. This global comparison confirms the trend suggested by our study and corroborates the observation that land use exerts a major influence on the components of NEE.

From our study we conclude that in mountain grassland land use affects the net ecosystem  $CO_2$  exchange and its components via changes in leaf area index, biomass and physiology.

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**Table 1.** General characterisation of the study sites.

Grassland type	Meadows	Pastures	Abandoned			
Altitude (m)	1000	1850	1950	1870	2000	1970
Aspect	–	E-SE	SE	S-SE	S-SE	S-SE
Inclination (°)	0	19	30	29	29	20
MAT (°C)	6.3	3.0	3.0	3.0	3.0	3.0
MAP (mm)	850	1097	1097	1097	1097	1097
Land management	Organic fertilisation three cuts, grazed in autumn	Organic fertilisation one cut, grazed in late summer	Grazed from May to Mid-September	Grazed from May to Mid-September	abandoned since 1983 fertilized 1989	abandoned since 1983
Soil type <sup>a</sup>	Fluvisol	Dystric cambisol	Dystric cambisol	Dystric cambisol	Dystric cambisol	Dystric cambisol
Vegetation type	<i>Pastinaco Arrheneterum</i>	<i>Trisetum flavescens</i>	<i>Seslerio-Caricetum Sempervirentis</i>	<i>Alchemilla</i>	<i>Vaccinio Callunetum</i>	<i>Seslerio-Caricetum with dwarf shrubs</i>
Dominant species	<i>Dactylis glomerata</i> <i>Leontodon hispidus</i> <i>Poa pratensis</i> <i>Ranunculus acris</i> <i>Taraxacum officinale</i> <i>Trifolium pratense</i> <i>Trifolium repens</i>	<i>Alchemilla vulgaris</i> <i>Anthoxanthum odoratum</i> <i>Festuca rubra</i> <i>Leontodon hispidus</i> <i>Trifolium repens</i>	<i>Alchemilla vulgaris</i> <i>Carex sempervirens</i> <i>Leontodon hispidus</i> <i>Lotus corniculatus</i> <i>Plantago lanceolata</i> <i>Plantago media</i> <i>Ranunculus montanus</i> <i>Sesleria albicans</i> <i>Sesleria albicans</i>	<i>Alchemilla vulgaris</i> <i>Anthoxanthum odoratum</i> <i>Carex sempervirens</i> <i>Festuca rubra</i> <i>Leontodon hispidus</i> <i>Lotus corniculatus</i> <i>Sesleria albicans</i> <i>Trifolium repens</i>	<i>Alchemilla vulgaris</i> <i>Avenella flexuosa</i> <i>Homogyne alpina</i> <i>Nardus stricta</i> <i>Vaccinium vitis-idaea</i>	<i>Anthyllis vulneraria</i> <i>Calluna vulgaris</i> <i>Festuca rubra</i> <i>Vaccinium myrtillus</i> <i>Vaccinium vitis-idea</i>
Study years	2002–2005	2002–2008	2002–2004	2006–2008	2002–2003	2003–2008
Above-ground biomass (g/m <sup>2</sup> )						
spring	311–607	190–313	157–334	198–374	291–376	106–215
summer	449–549	244–440	122–180	129–231	310–390	392–402
autum	266–517	224–261	119–138	91–148	105–240	217–386

<sup>a</sup> FAO classification; MA, mean annual; T, temperature; P, precipitation.

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**Land use affects the net ecosystem CO<sub>2</sub> exchange**

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**Table 2.** Regression statistics of the relationships between net ecosystem CO<sub>2</sub> exchange at PFD of 2000 μmol m<sup>-2</sup> s<sup>-1</sup> (NEE<sub>2000</sub>), gross primary productivity at PFD of 2000 μmol m<sup>-2</sup> s<sup>-1</sup> (GPP<sub>2000</sub>), respiration at a reference temperature of 10°C (R<sub>10</sub>) and light use efficiency (LUE) in response to leaf area index (LAI).

Site	NEE <sub>2000</sub> vs. LAI		GPP <sub>2000</sub> vs. LAI		R <sub>10</sub> vs. LAI		LUE vs. LAI	
	R <sup>2</sup>	p value	R <sup>2</sup>	p value	R <sup>2</sup>	p value	R <sup>2</sup>	p value
Valley bottom meadow	0.50	< 0.001	0.55	< 0.001	0.72	< 0.001	0.71	< 0.001
Mountain meadow	0.55	< 0.001	0.54	< 0.001	0.56	< 0.001	0.57	< 0.001
Pastures	0.63	< 0.001	0.50	0.002	0.78	< 0.001	0.56	< 0.001
Abandoned	0.71	< 0.001	0.63	0.001	0.56	< 0.001	0.63	< 0.001

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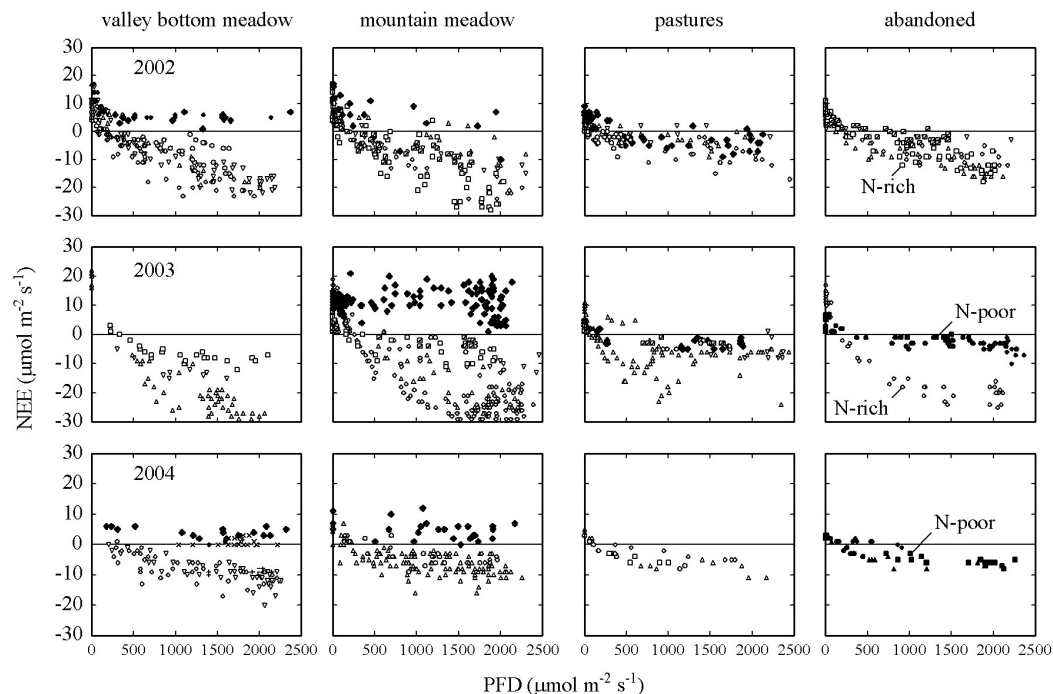
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## Land use affects the net ecosystem CO<sub>2</sub> exchange

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**Fig. 1.** NEE in relation to photon flux density (PFD) of two meadows, two pastures and two abandoned grasslands during the growing seasons 2002–2004. Negative values denote net CO<sub>2</sub> uptake by the canopy, positive values a net loss of CO<sub>2</sub> to the atmosphere. Each data point shows a single set of chamber measurements. The measurements were taken during clear days. The following symbols are used: × March, + April, ∇ May, ◇ June, △ July, □ August, ○ September, ⌘ October, ◇ November; closed symbols indicate NEE after mowing and grazing on the meadows at the valley bottom (1000 m) and the mountain slope (1850 m), as well as the pastures. For the abandoned sites open and closed symbols indicate values for the nutrient-rich and the nutrient-poor abandoned grassland, respectively.

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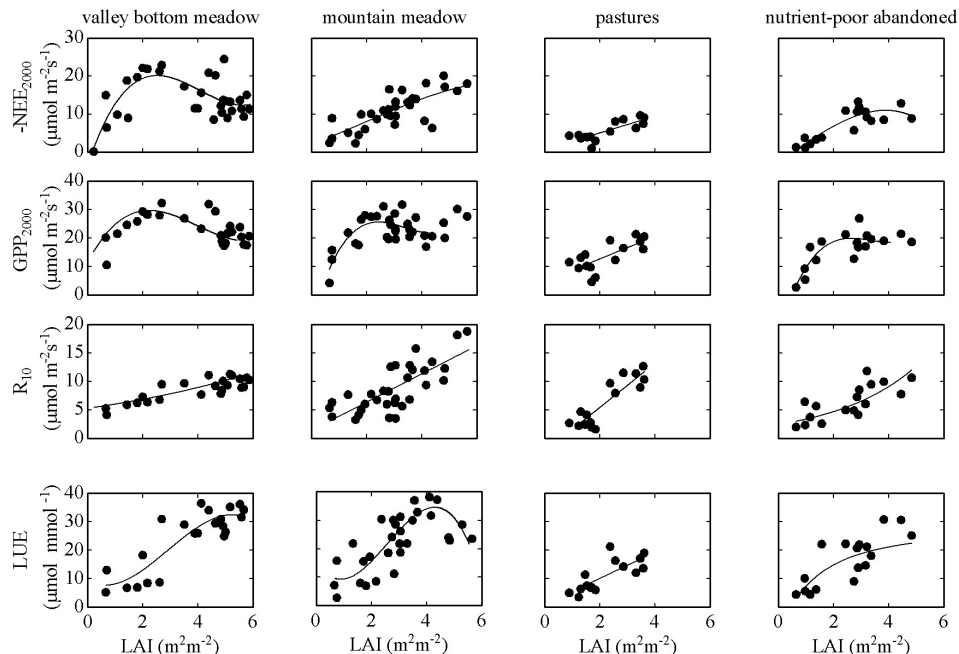
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**Fig. 2.** Relationships between net ecosystem CO<sub>2</sub> exchange at photon flux density (PFD) of 2000 μmol m<sup>-2</sup> s<sup>-1</sup> (NEE<sub>2000</sub>), gross primary productivity at PFD of 2000 μmol m<sup>-2</sup> s<sup>-1</sup> (GPP<sub>2000</sub>), ecosystem respiration at a reference temperature of 10°C (R<sub>10</sub>) and light use efficiency (LUE) in response to leaf area index (LAI) at the study sites. Regressions are based on all available data during the growing seasons from 2002 to 2008.

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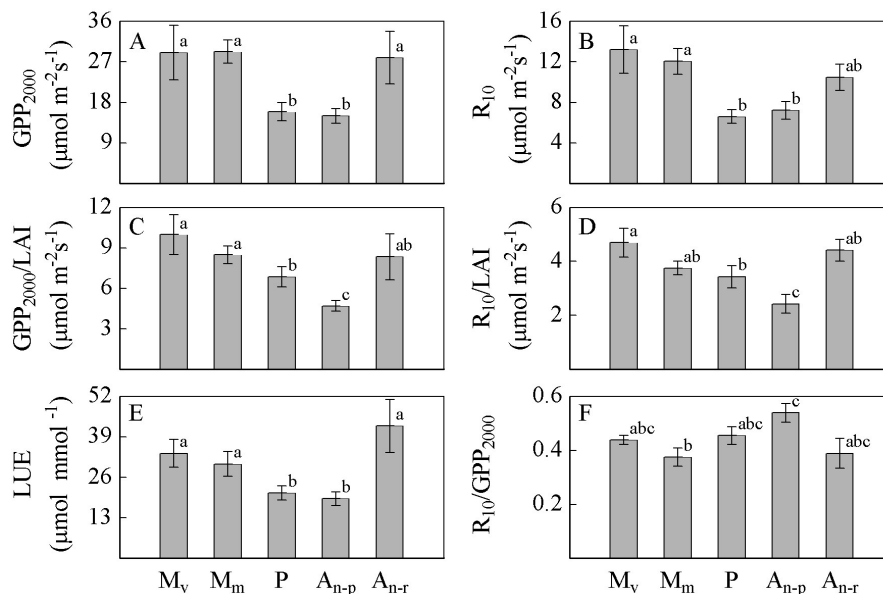
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**Fig. 3.** Mean peak season values of **(A)** gross primary productivity per unit ground area at photon flux density of  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  ( $GPP_{2000}$ ), **(B)** ecosystem respiration at a reference temperature of  $10^\circ\text{C}$  ( $R_{10}$ ), **(C)**  $GPP_{2000}$  per unit leaf area, **(D)**  $R_{10}$  per unit leaf area, **(E)** light-use efficiency (LUE), **(F)**  $R_{10}/GPP_{2000}$  at optimum LAI based on all field campaigns across all study years. Sites are indicated as:  $M_v$  (valley bottom meadow),  $M_m$  (mountain meadow),  $P$  (pastures),  $A_{n-r}$  (nutrient-rich abandoned grassland),  $A_{n-p}$  (nutrient-poor abandoned grassland). Significantly different means are indicated by different letters (oneway ANOVA). Error bars represent standard errors,  $M_v$   $n = 4$  (May 2002),  $M_m$   $n = 7$  (August 2002),  $P$   $n = 7$  (August 2002),  $A_{n-p}$   $n = 6$  (August 2003),  $A_{n-r}$   $n = 2$  (March 2002).

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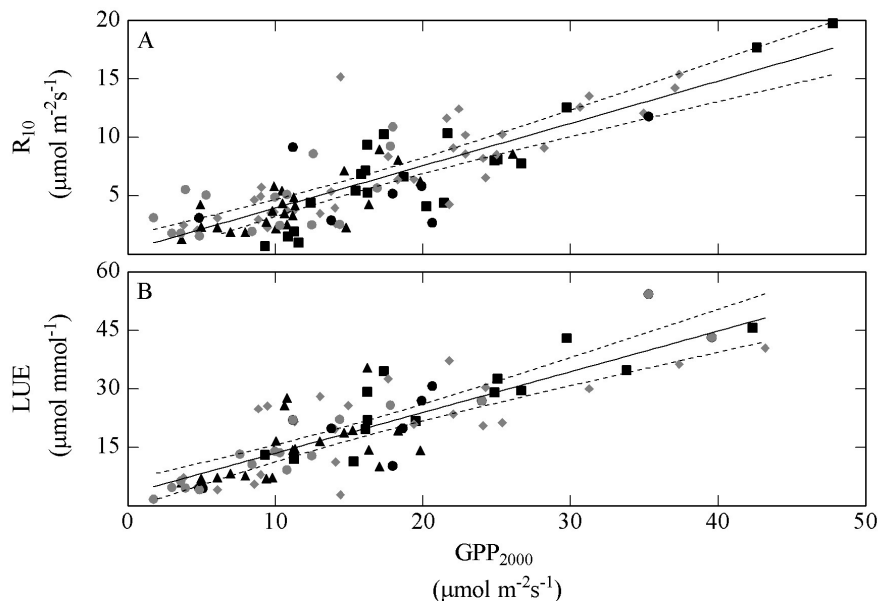
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**Fig. 4.** Relationship of gross primary productivity at photon flux density of 2000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  ( $\text{GPP}_{2000}$ ) and **(A)** ecosystem respiration at a reference temperature of 10°C ( $R_{10}$ ) and **(B)** light use efficiency (LUE). The equations for the fitted lines for all sites and years are:  $R_{10}=0.36 \text{ GPP}_{\text{max}}+0.32$  ( $R^2=0.69$ ;  $p < 0.01$ ) and  $\text{LUE}=0.88 \text{ GPP}_{2000}+2.86$  ( $R^2=0.66$ ;  $p < 0.01$ ). Dotted lines represent 95% confidence intervals. Sites are indicated by following symbols:  $\blacksquare$  valley bottom meadow,  $\blacklozenge$  mountain meadow,  $\blacktriangle$  pastures,  $\bullet$  nutrient-rich abandoned grassland,  $\bullet$  nutrient-poor abandoned grassland.

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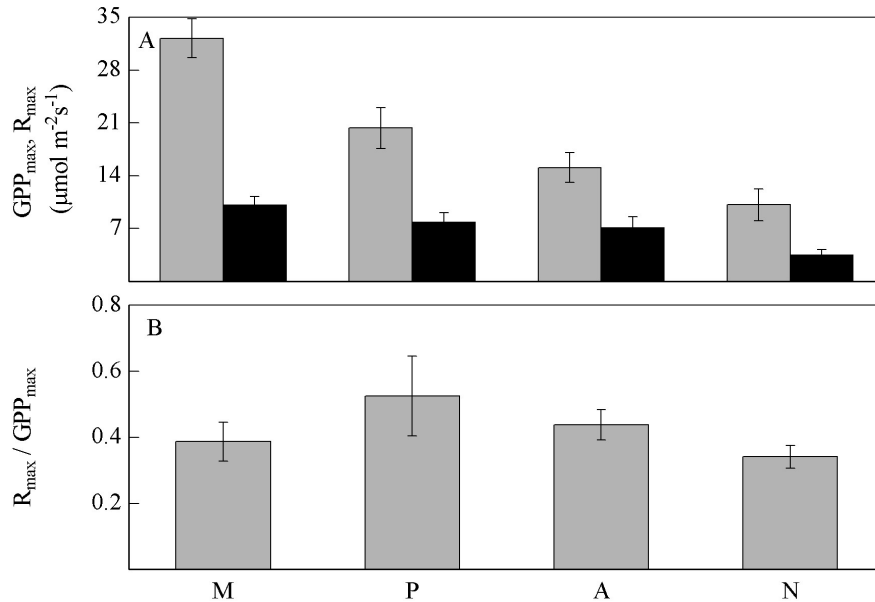
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**Fig. 5.** (A) Maximum gross primary productivity ( $\text{GPP}_{\text{max}}$ ) (grey bars) and maximum ecosystem respiration ( $R_{\text{max}}$ ) (black bars), (B)  $R_{\text{max}}/\text{GPP}_{\text{max}}$  for different ecosystems across the globe. Ecosystems are indicated as: *M* (meadows), *P* (pastures), *A* (abandoned), *N* (natural grasslands, including steppes and prairies, tundras and savannas). Error bars represent standard errors, meadows  $n = 28$  (Maljanen et al., 2001; Falge et al., 2002; Wilsey et al., 2002; Li et al., 2003; Barcza et al., 2003; Wohlfahrt 2004; Rogiers et al., 2004; Byrne et al., 2005; Lawton et al., 2006; Zhao et al., 2006; Gilmanov et al., 2007; Otieno et al., 2009); pastures  $n = 19$  (Grace et al., 1998; Falge et al., 2002; Wilsey et al., 2002; Hunt et al., 2004; Santos et al., 2004; Priante-Filho et al., 2004; Santos et al., 2004; Rogiers et al., 2004; Byrne et al., 2005; Nieveen et al., 2005; Jaksic et al., 2006; Gilmanov et al., 2007; Susiluoto et al., 2008; Don et al., 2009); abandoned  $n = 13$  (Ripley and Redmann, 1978; Miranda et al., 1997; Soegaard and Nordstroem, 1999; Suyker et al., 2001; Flanagan et al., 2002; Hanan et al., 2003; Zamolodchikov et al., 2003; Flanagan et al., 2005; Gilmanov et al., 2007; Don et al., 2009; Otieno et al., 2009); natural grasslands  $n = 18$  (Angell et al., 2001; Obrist et al., 2003; Corradi et al., 2005; Gilmanov et al., 2005; Baldocchi et al., 2006; Zhao et al., 2006; Susiluoto et al., 2008).

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