Land use affects the net ecosystem CO$_2$ exchange and its components in mountain grasslands

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Abstract

Changes in land use and management have been strongly affecting mountain grassland, however, their effects on the net ecosystem exchange of CO$_2$ (NEE) and its components have not yet been well documented. We analysed 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 and management, and thus site fertility, for the growing seasons of 2002 to 2008. The main findings of the study are that: (1) land use and management affected seasonal NEE, GPP and R, which all decreased from managed to unmanaged grasslands; (2) these changes were explained by differences in leaf area index (LAI), biomass and leaf-area-independent changes that were likely related to photosynthetic physiology; (3) diurnal variations of NEE were primarily controlled by photosynthetically active photon flux density and soil and air temperature; seasonal variations were associated with changes in LAI; (4) parameters of light response curves were generally closely related to each other, and the ratio of R at a reference temperature/ maximum GPP was nearly constant across the sites; (5) similarly to our study, maximum GPP and R for other grasslands on the globe decreased with decreasing land use intensity, while their ratio remained remarkably constant. We conclude that decreasing intensity of management and, in particular, abandonment of mountain grassland lead to a decrease in NEE and its component processes. While GPP and R are generally closely coupled during most of the growing season, GPP is more immediately and strongly affected by land management (mowing, grazing) and season. This suggests that management and growing season length, as well as their possible future changes, may play an important role for the annual C balance of mountain grassland.

1 Introduction

Due to the importance of the terrestrial carbon cycle for the global climate system there is 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. Several studies have shown that temperate grasslands can act as both sinks and sources of CO$_2$ (Gilmanov et al., 2007; Novick et al., 2004; Stoy et al., 2008; Wohlfahrt et al., 2008b). Differences and changes in land management can be expected to affect the carbon sequestration rate of these ecosystems (Cernusca et al., 2008), which in turn will feed back on atmospheric CO$_2$ 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 (Robson et al., 2007; Zeller et al., 2000), species composition (Tasser et al., 1999), leaf and canopy gas exchange (e.g. Bahn et al., 1999;

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Tappeiner et al., 1999; Wohlfahrt et al., 2003) and soil and root respiration (Bahn et al., 2006, 2008).

While relationships between the net ecosystem CO_2 exchange (NEE) of mountain grasslands and its abiotic and biotic drivers have been analysed in some detail (Fu et al., 2009; Gu et al., 2003; Hirota et al., 2009; Kato et al., 2004a, b; Wohlfahrt et al., 2008b, Yashiro et al., 2010), to our knowledge, there has so far been no study on whether and how land use change and land management might affect the diurnal, seasonal and interannual variation of NEE and its component processes gross primary productivity (GPP) and ecosystem respiration (R). 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 (Don et al., 2009; Stoy et al., 2008).

Measurements of NEE are needed in order to determine the source-sink status of ecosystems, and to analyse how C exchange varies with 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). Micrometeorological flux measurements are being made at more than 500 sites worldwide and form a global flux network (FLUXNET; 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 complex terrain (Schimel et al., 2002). As an alternative to the EC method, chamber-based measurements may be suitable for monitoring NEE from short-plant ecosystems located in complex terrain, such as mountain slopes (Li et al., 2008; Risch and Dougas, 2005). One of the strengths of the chamber approach is the possibility to control and manipulate environmental factors, which offers an opportunity to separate individual effects of environmental factors on NEE and to partition NEE into its key components, i.e. GPP and 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 meadows, pastures and 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 and management, (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) differences in NEE and its component processes GPP and R between differently managed mountain grassland ecosystems are primarily driven by differences in the amount of photo-synthetically active leaf area and its CO_2 assimilation potential, that (2) NEE and its component processes thus decrease as management intensity (in particular fertilisation) decreases (meadows>pastures>abandoned grasslands), and that (3) these changes occur in a similar manner for all component processes, which results in conservative ratios between CO_2 uptake and release.

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) on a meadow at the valley bottom (970 m a.s.l.) in the years 2002–2005, a mountain meadow (1750–1820 m a.s.l.) in the years 2002–2004 and 2005–2008, two pastures (1930 and 1950 m a.s.l.) in the years 2002–2004 and 2005–2008, a nutrient-rich abandoned grassland (1960 m a.s.l.) in the years 2002–2003, and a nutrient-poor abandoned grassland (2000 m a.s.l.) in the years 2003–2004 and 2005–2008.

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 (values recorded at nearby weather stations) from 850 to 1097 mm (Table 1). The valley bottom meadow is cut three times per year and fertilised with manure annually (Wohlfahrt et al., 2008a), the mountain meadow is cut once a year and fertilised with manure every 2–3 years (Bahn et al., 2006). The pastures are grazed from May to mid-September. Cattle are moved around within the pastures by the farmer in order to ensure relatively even grazing within the entire area. As a consequence, the unfenced plots where NEE measurements were made had time to recover (and regrow) between grazing periods. Once grazing started again, an immediate response to grazing was thus observed. CO_2-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 was reforested and fertilised once in 1988. The trees were not included in the flux measurements. For soil type and vegetation compositions refer to Table 1.

2.2 Assessment of net ecosystem CO_2 exchange

Measurements were conducted between 2002 and 2008 in episodic campaigns every three to four weeks. Throughout all campaigns the sites were sampled on the same day or within two to three consecutive days during stable weather conditions. During each campaign, chamber measurements of NEE were conducted over a diurnal course for each site. In order to document the diurnal course, from 2002 to 2005 the measurements began immediately before sunrise and ended about three hours after sunset. From 2006 to 2008 the measurements started in the night and ended at midday (mostly between 2:00 am and 12:00 am). All ecosystem respiration measurements reported in this paper were thus made during nighttime. We measured NEE with home-made manually operated temperature-stabilised 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^2 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 and were alternately recorded once per hour with one chamber system. In total, 30 to 50 single measurements per day were taken. It was randomly chosen with which plot the sampling started. Measurements were usually carried out within 120 s during daytime and within 180 to not more than 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. On hot summer days 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_2 concentrations were measured with an infra-red gas analyser (LCA-2, ADC, Hoddesdon, UK) from 2002 to 2005 and CO_2-Sensor (GMP343, Vaisala, Helsinki, Finnland) 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, Finnland), soil temperature (HOBO data logger, Onset Computer, Bourne, MA, USA) and incident photosynthetically active photon flux density (PFD) (G1118 GaAsP, Ga Photodiode diffusion type, Hamamatsu Photonics GmbH, Germany).

NEE (μmol CO_2 m^{-2} s^{-1}) was calculated as

$$NEE = \frac{(d CO_2/dt) \cdot T \cdot P \times 10^3}{[V_m \cdot (273.15 + T) \cdot P_0]} \cdot (V/A) \times 10^6 \quad (1)$$

where $d CO_2/dt$ (μmol mol^{-1} s^{-1}) is the change in CO_2 mole fraction inside the chamber over time, P is the atmospheric pressure (kPa), V_m is the molar volume of CO_2 (m^3 mol^{-1}), T is the chamber temperature (°C), P_0 is the standard atmospheric pressure (kPa), V is the chamber volume (m^3), and A is the chamber base area (0.6 m^2). In this study, negative fluxes represent a net CO_2 uptake by the ecosystem, positive ones the reverse.

Kutzbach et al. (2007) found that for their closed chamber system nonlinear regression models were more appropriate for estimating CO_2 fluxes than linear ones. In contrast, for our chamber system we observed consistent and highly significant linear changes of CO_2 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_2 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 of 19% by the EC method. Similarly, a number of earlier 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. Angell et al., 2001; Dore et al., 2003; Dugas et al., 1999; Goulden et al., 1996; Lavigne et al., 1997; Wohlfahrt et al., 2005a; Zamolodchikov et al., 2003). 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 due to advection or insufficient turbulent mixing at night (Goulden at al., 1996; Lavigne et al., 1997). Chamber artefacts are mainly related to the influence of pressure on soil respiration (Davidson et al., 2002) and modifications of the microclimate, which were however minimised as described above.

To take the comparison one step further, we tested how well daily NEE corresponded between eddy covariance-based and chamber-based data, thus comparing integrated daily values rather than individual data points. Daily average NEE based on chamber data was calculated for 7 day time periods using site specific environmental conditions and NEE light response curves measured during the course of a single day within this 7 day period. Daily average NEE based on the EC data was derived from gap-filled data as described in Wohlfahrt et al. (2008a). As depicted in the Fig. 1, the chamber method underestimated daily NEE measured by eddy covariance at the valley bottom meadow on average by only 5%.

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 the net ecosystem exchange of CO_2 (μmol m^{-2} s^{-1}), α the apparent quantum yield (mol CO_2 mol photons^{-1}), PFD the photosynthetically active photon flux density (μmol m^{-2} s^{-1}), GPP_{sat} the asymptotic value of the gross primary production (GPP) at high irradiance (μmol m^{-2} s^{-1}), and R denotes ecosystem respiration (μmol m^{-2} s^{-1}).

For comparison across ecosystems we used Eq. (2) to calculate NEE and GPP at PFD of 2000 μmol m^{-2} s^{-1} (NEE_{2000}, GPP_{2000}). R was interpolated to a reference soil temperature of 10 °C (R_{10}) by best fitting linear and exponential models. LUE was calculated by a linear regression fitted to the light response curves at low incident light intensities – the slope of the linear regression corresponds to the LUE.

Daily integrals of NEE were derived by applying Eq. (2) with input data (PFD) from 10 day periods around each measurement campaign. These 10-day periods were the same for all sites – the daily integrals of NEE are thus comparable and reflect differences between sites that were independent of the diurnal and day-to-day variability of PFD.

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 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 °C.

3 Results

Minimum and maximum rates of net ecosystem CO_2 exchange (NEE) as measured during all campaigns were highest for the meadows and fertilised abandoned grassland (Fig. 2), which all exhibited a high above-ground biomass (Table 1). Lowest peak net fluxes of CO_2 were measured for the pastures and the unfertilised abandoned that relatively low abandoned grassland. grassland, supported above-ground biomass and leaf area index (LAI). For all study years, highest rates of net CO_2 uptake coincided with values of peak biomass, mountain meadow, mountain meadow, occurring between June (valley bottom meadow) and August (abandoned sites), maximum NEE ranging from −16.5 μmol m^{-2} s^{-1} (late part of July 2004) to −30 μmol m^{-2} 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. 2). In the year when both abandoned sites were studied simultaneously, 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 (unfertilised abandoned grassland in October 2003 at T_{air} = −3 °C / T_{soil} = 2.9 °C) to 22.1 μmol m^{-2} s^{-1} (valley bottom meadow in July 2003 at T_{air} = 13.5 °C / T_{soil} = 13.7 °C). Across seasons and sites, ecosystem respiration 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).

Daily average NEE, as compared for the same time periods across sites, mostly decreased from valley bottom meadow to mountain meadow to pastures and abandoned grasslands (Fig. 3a, b). For unmanaged periods, at all study sites, daily NEE followed a marked seasonal trend varying from −4.47 (valley bottom meadow), −4.20 (mountain meadow), −2.13 (pastures) and −1.36 g C m^{-2} d^{-1} (abandoned) in spring and summer to 2.77, 1.89, 2.11 and 3.70 g C m^{-2} d^{-1}, respectively, in autumn (Fig. 3a, b). Correspondingly, average daily integrated gross primary productivity (GPP) exceeded R for unmanaged periods in spring and summer on the meadows and pastures, while the reverse was generally true in autumn, when GPP was more strongly reduced relative to the summer months than R (Fig. 4). Daily average GPP and R of the abandoned sites generally clustered around the 1:1 line of Fig. 4. Mowing and grazing resulted in a transient net release of CO_2 from the meadows and the pastures (Fig. 3c), which lasted for approximately 6–10 days (not shown).

Pooling all NEE data across the season, their variation 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 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 (0.33, $p < 0.001$). While during the heat wave 2003 Western parts of Europe suffered from drought, the Austrian Alps remained largely unaffected 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. 5) (for regression statistics cf. Table 2). At all sites, except the pastures, optimum values for LAI ranged from 2.7 to 4.8 m^2 m^{-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 these parameters increased on the fertilized abandoned grassland (N-rich) (Fig. 6a, b, e). When normalized for LAI, GPP also decreased significantly from the meadows to the pastures and the N-poor abandoned grassland (Fig. 6c). 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. 6d). The ratio R/GPP was not significantly different between sites, except between the mountain meadow and the nutrient poor abandoned grassland, the highest ratio occurring on the N-poor abandoned grassland (Fig. 6f). 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. 7).

4 Discussion

A number of previous studies have shown that NEE is affected by interactions of microclimate, canopy structure and the photosynthetic and respiratory physiology of plants (for grasslands e.g. Flanagan and Johnson, 2005; Gu et al., 2003; Tappeiner and Cernusca, 1998; Wohlfahrt et al., 2003). In most ecosystems light is the prime driver and explains most variability of NEE (Flanagan et al., 2002; Li et al., 2005, 2008; Ruimy et al., 1995; Wilsey et al., 2002; Zhao et al., 2006). PFD, air and soil temperature, above-ground biomass, LAI, type of grassland, measurement year and the time of the season (see results section)

explained 68% of NEE, 75% of GPP and 60% of R in our study. 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 unexplained variability in the stepwise multiple regression indicates that NEE was related to a number of factors, including the spatial variability in nutrient availability and species composition and related effects on above- (Bahn et al., 1999) and belowground processes (Bahn et al., 2006). Contrary to results from studies in water limited systems (Wilsey et al., 2002), it appears that soil water availability did not induce seasonal variation in NEE at our sites in years with typical amount of precipitation. The extreme summer of 2003 was characterised in many parts of Europe by hot and dry days (Ciais et al., 2005; Foelsche 2004), which at our sites led to a high production of above-ground biomass and LAI and particularly high values of NEE, GPP and R (Fig. 2). 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 site 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. Leaf area exerts a major influence on canopy photosynthesis (Saigusa et al., 1998; Tappeiner and Cernusca, 1996), which also provides assimilates for the respiration of roots and soil microorganisms (Bahn et al., 2008, 2009; Reichstein et al., 2003). Both, mowing and grazing, cause a substantial reduction of leaf area and thus GPP (Fig. 4), turning the meadows and the pastures from sinks to short-term sources of CO_2 (Fig. 3). For the valley bottom meadow (three cuts per year) of our study it took on average 16 days after the first cut to become (on a daily basis) a net sink for CO_2 again (Wohlfahrt et al., 2008a). This pattern repeated itself after the second and third cut, whereas daily average rates of net CO_2 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).

Our study showed that land use and management were responsible for the differences in NEE between sites (Fig. 3). Generally, NEE, GPP and R increased with management intensity (Figs. 3 and 4). The fertilised meadows showed the highest, the unmanaged (unfertilised) abandoned grassland the lowest values of NEE. For unmanaged periods in spring and summer NEE was more strongly determined by CO_2-uptake than release (Fig. 4). In contrast, during unmanaged periods in autumn, NEE was more affected by CO_2-release.

At all sites, both NEE and GPP at a PFD of 2000 μmol m^{-2} s^{-1} were closely related to LAI, the relationships saturating at LAI of 2.7–4.8 m^2 m^{-2}. This is typical for productive grasslands, for which maximum GPP was observed at LAI of 2–5 m^2 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 key parameters of light response curves of NEE include GPP at maximum incident light (GPP$_{2000}$), R at a reference temperature (R$_{10}$) and the initial slope of the curve (LUE), which were all affected by land management and land-use change. In our study, across all years seasonal mean as well as seasonal peak values of GPP$_{2000}$, R$_{10}$ 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 the photosynthetic physiology of the dominant species. Accounting for effects of leaf area by normalizing GPP to LAI, we observed a reduction of GPP$_{2000}$ 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 are related to changes in species composition and nutrient availability.

Also normalized R_{10} tended to decrease from the meadows and the N-rich abandoned grassland to the pastures and the N-poor abandoned grassland (Fig. 6d). 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, 2009). Likewise, our study demonstrates a close link between GPP and R across sites and study years (Fig. 7), which confirms earlier observations for a range of grasslands (Gilmanov et al., 2007; Li et al., 2005; Wohlfahrt et al., 2008b). Our study indicates that the ratio of R_{10} / GPP_{2000} is generally not affected by land management, however, may be somewhat higher on nutrient poor sites (Fig. 6f).

To test the generality of our findings, we compared maximum GPP and R for ecosystems differing in land use from around the globe (Fig. 8). Similar to our study, GPP_{max} and R_{max} decreased from meadows to pastures and abandoned and natural grasslands (Fig. 8a). We assume that the main reason for lower fluxes at unmanaged systems is the lower soil fertility in comparison to the managed systems, which are usually fertilised leading to higher flux rates of GPP and R. We found no significant relationship between GPP_{max} or R_{max} and the mean annual temperature and/ or precipitation at the sites, suggesting that climatic effects did not confound the observed land-management and land-use effects. The ratio R_{max} / GPP_{max} (Fig. 8b) was relatively constant across all types of ecosystems, which indicates a close coupling of maximum R to potential site productivity and *vice versa*. This global comparison confirms the trend observed in our study and thus the notion that the intensity of land use exerts a major influence on the components of NEE, while leaving their ratio largely unaffected.

5 Conclusions

From our study we conclude that in mountain grassland, and most likely also in grassland in general, land use and management may importantly affect the net ecosystem CO_2 exchange (NEE) and its component fluxes gross primary productivity (GPP) and ecosystem respiration (R). In our study, these effects were mediated by differences in leaf area index, biomass and leaf-area-independent changes that were likely related to photosynthetic physiology. NEE and its component fluxes decreased with decreasing intensity of management and thus site fertility. The ratio of R at a reference temperature/ maximum GPP remained remarkably constant across gradients of land-use intensity both within the present study of adjacent sites and for a global compilation of grasslands. During short periods following mowing or grazing, the studied grasslands turned from carbon sinks to sources. As such changes in the source-sink relations also occur as part of the seasonal dynamics of NEE, future studies should address possible trade-offs between effects of land-use changes and those related to phenology and growing season length in a climate change context.

Acknowledgments

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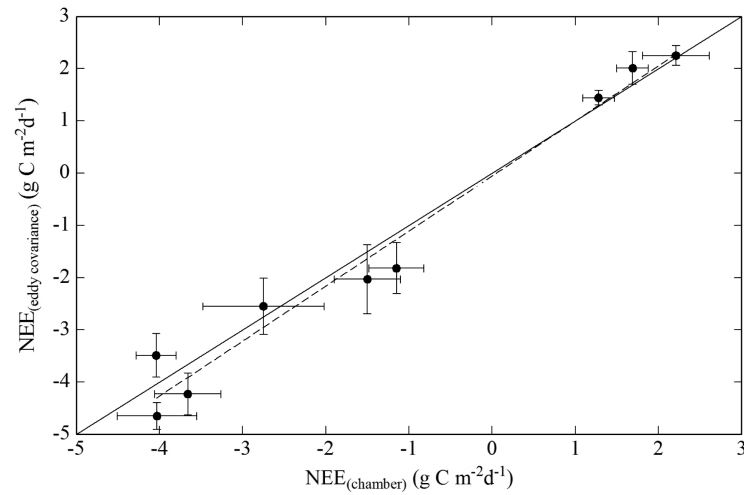
Fig. 1.

Comparison between 7-day average daily integrated net ecosystem exchange of CO_2 (NEE; g C m^{-2} s^{-1}) derived from chamber and eddy covariance data at the valley bottom meadow. The solid line is the 1:1 line, the dotted line corresponds to a linear regression (NEE$_{(eddy\ covariance)}$ = 1.05 NEE$_{(chamber)}$ − 0.05; R^2=0.97). Error bars represent standard errors and reflect temporal variability in gap-filled NEE (eddy covariance) and in meteorological input parameters of light response curve models (Eq. 2), which were used to simulate NEE based on chamber data.
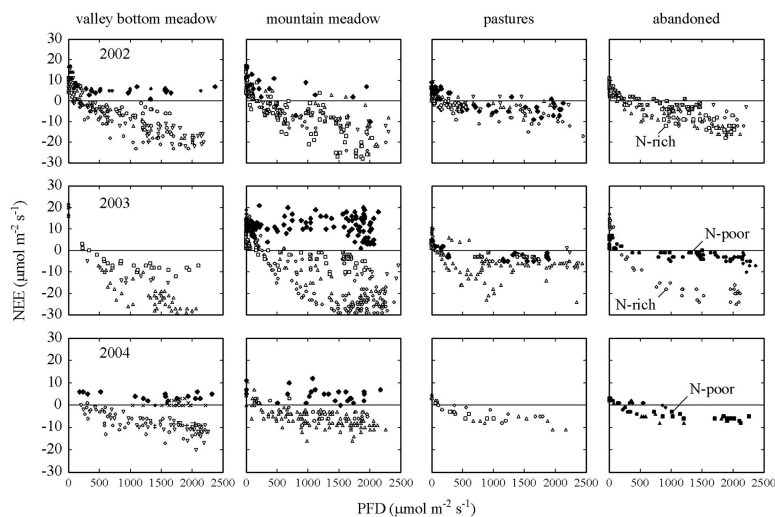
Fig. 2.
NEE in relation to photon flux density (PFD) for two meadows, two pastures and two abandoned grasslands during the growing seasons 2002–2004. Negative values denote net CO_2 uptake by the canopy, positive values a net loss of CO_2 to the atmosphere. Each data point shows a single set of chamber measurements. The measurements were taken during clear days. The following symbols are used: × March, + April, ∇ May, ◇ June, Δ June, □ 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 (1850m), 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.
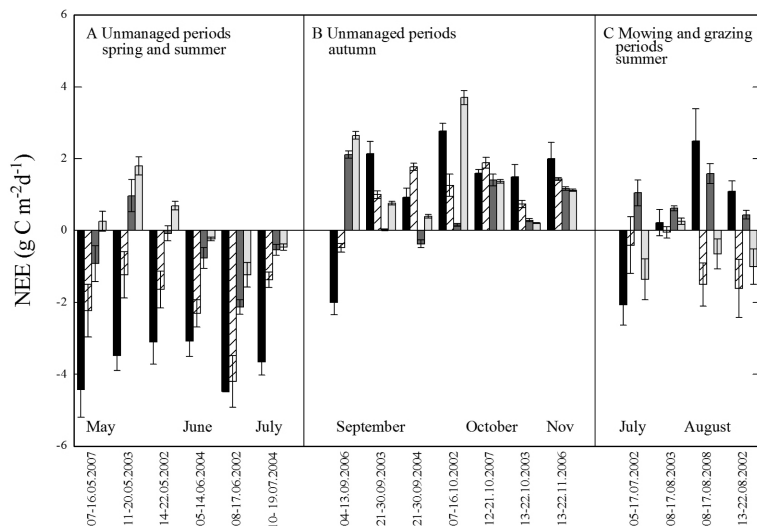
Fig. 3.
Daily integrated average net ecosystem exchange of CO_2 (NEE; g C m^{-2} s^{-1}) of (**A, B**) unmanaged, and (**C**) mowing and grazing periods from 2002 to 2008. Groups of bars refer to the same 10-day time periods for all sites as explained in the text. NEE was calculated using Eq. (2) based on 10-day periods during which at least one complete day of chamber measurements was available, and using site-specific microclimatic conditions as input. Sites are indicated by black bars (valley bottom meadow), criss-cross bars (mountain meadow), dark grey bars (pastures) and light grey bars (abandoned). Error bars represent standard errors and reflect the temporal variability in meteorological input parameters to Eq. (2).
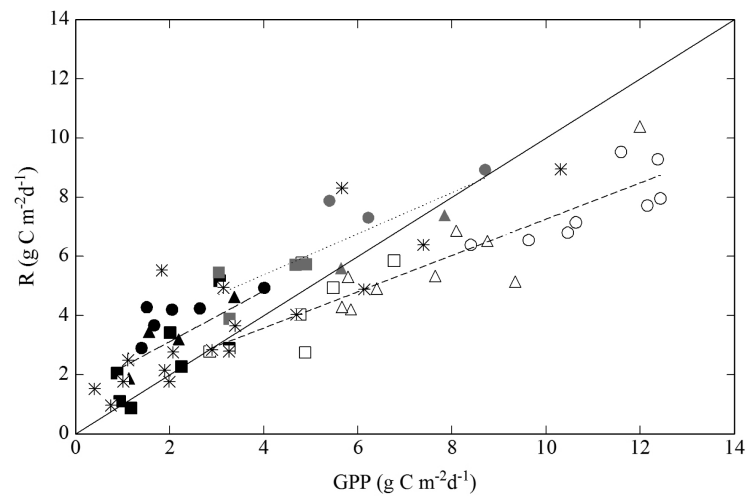
Fig. 4.
Relationship of daily integrated average gross primary productivity (GPP) and ecosystem respiration (R) at all sites for unmanaged and mowing and grazing periods from 2002 to 2008, as based on the approach for Fig. 3. Sites and management periods are indicated by symbols: circles (valley bottom meadow), triangles (mountain meadow), quadrats (pastures) and stars (abandoned); open symbols (unmanaged periods, spring and summer), closed symbols (un-managed periods, autumn) and grey symbols (mowing and grazing periods, summer). The solid line is the 1:1 line, the dotted regression lines indicate linear relationships, as described by R = a× GPP + b. a, b and R^2 of the linear regressions are as follows: 0.61, 1.13 and 0.80 for unmanaged periods in spring and summer, 0.86, 1.41 and 0.44 for unmanaged periods in autumn, and 0.69, 2.60, 0.71, respectively, for mowing and grazing periods (during summer).
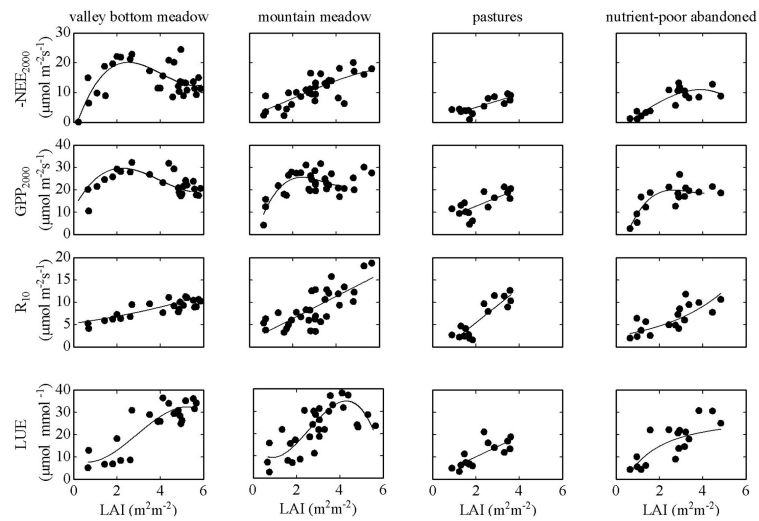
Fig. 5.
Relationships between the net ecosystem CO_2 exchange at a photon flux density (PFD) of 2000 µmol m^{-2} s^{-1} (NEE$_{2000}$), the gross primary productivity at a PFD of 2000 µmol m^{-2} s^{-1} (GPP$_{2000}$), the ecosystem respiration at a reference temperature of 10 °C (R$_{10}$) and the light 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. For regression statistics see Table 2.
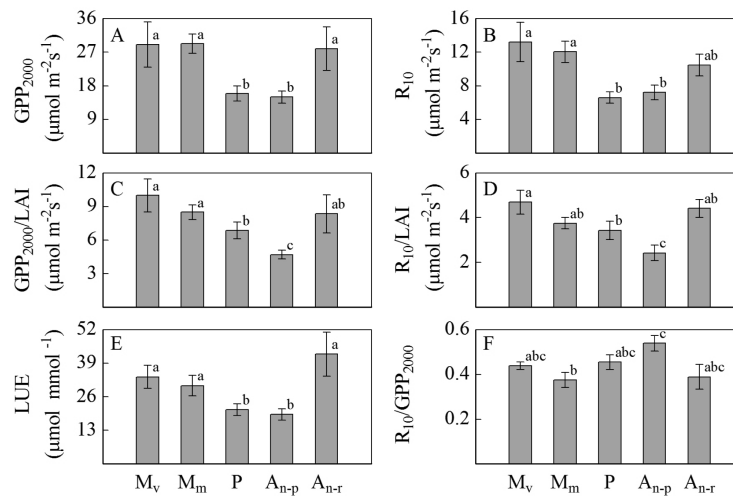
Fig. 6.
Mean peak season values of (**A**) gross primary productivity per unit ground area at a photon flux density of 2000 μmol m^{-2} s^{-1} (GPP$_{2000}$), (**B**) ecosystem respiration at a reference temperature of 10 °C (R$_{10}$), (**C**) GPP$_{2000}$ per unit leaf area, (**D**) R$_{10}$ per unit 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 to 2005), M$_m$: n=7 (August 2002 to 2004 and 2006 to 2008), P: n=7 (August 2002 to 2004 and 2006 to 2008), A$_{n-p}$: n=6 (August 2003 to 2004 and 2006 to 2008), A$_{n-r}$: n=2 (March 2002 to 2003).
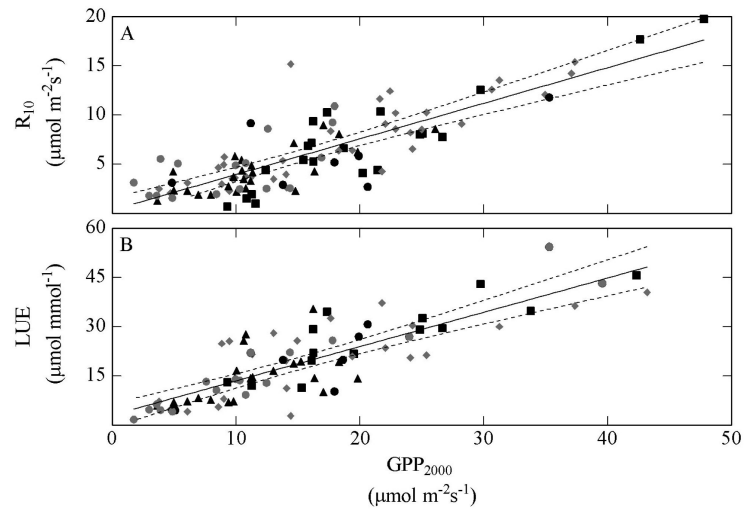
Fig. 7.
Relationship of the gross primary productivity at a photon flux density of 2000 μmol m^{-2} s^{-1} (GPP$_{2000}$) and (A) the ecosystem respiration at a reference temperature of 10 °C (R$_{10}$) and (B) the light use efficiency (LUE). The equations for the fitted lines for all sites and years are: R$_{10}$ = 0.36 GPP$_{max}$ + 0.32 (R^2 = 0.69; p < 0.01) and LUE = 0.88 GPP$_{2000}$ + 2.86 (R^2 = 0.66; p < 0.01). Dotted lines represent 95% confidence intervals. Sites are indicated by following symbols: ■ valley bottom meadow, ◆ mountain meadow, ▲ pastures, ● nutrient-rich abandoned grassland, ● nutrient-poor abandoned grassland.
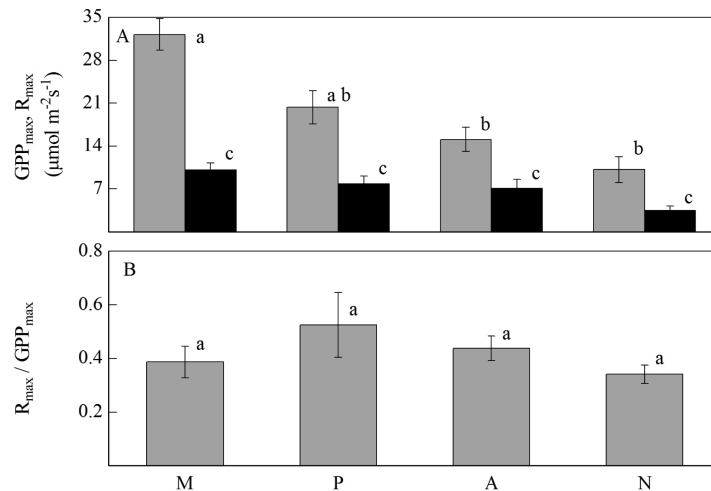
Fig. 8.
(**A**) Maximum gross primary productivity (GPP_{max}) (grey bars) and maximum ecosystem respiration (R_{max}) (black bars), (**B**) ratio of R_{max} and GPP_{max} for different ecosystems across the globe. Ecosystems are indicated as: M (meadows), P (pastures), A (abandoned), N (natural grasslands, including steppes and prairies, tundras and savannas). Significantly different means are indicated by different letters (oneway ANOVA). Error bars represent standard errors, meadows n=28 (References: Barcza et al., 2003; Byrne et al., 2005; Falge et al., 2002; Gilmanov et al., 2007; Lawton et al., 2006; Li et al., 2003; Maljanen et al., 2001; Otieno et al., 2009; Rogiers et al., 2004; Wilsey et al., 2002; Wohlfahrt 2004; Zhao et al., 2006), pastures n=19 (References: Byrne et al., 2005; Don et al., 2009; Falge et al., 2002; Gilmanov et al., 2007; Grace et al., 1998; Hunt et al., 2004; Jaksic et al., 2006; Nieveen et al., 2005; Priante-Filho et al., 2004; Rogiers et al., 2004; Santos et al., 2004; Susiluoto et al., 2008; Wilsey et al., 2002), abandoned n=13 (Reference: Don et al., 2009; Flanagan et al., 2002; Flanagen et al., 2005; Gilmanov et al., 2007; Hanan et al., 2003; Miranda et al., 1997; Otieno et al., 2009; Ripley and Redmann, 1978; Soegaard and Nordstroem, 1999; Suyker et al., 2001; Zamolodchikov et al., 2003), natural grasslands n=18 (References: Angell et al., 2001; Baldocchi et al., 2006; Corradi et al., 2005; Gilmanov et al., 2005; Obrist et al., 2003; Susiluoto et al., 2008; Zhao et al., 2006).

Table 1

General characterisation of the study sites.

Grassland type	Meadows		Pastures		Abandoned	
Altitude (m)	970	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	3	3	3	3
MAP (mm)	850	1097	1097	1097	1097	1097
Land management	Organic fertilisation three cuts, grazed in autum	Organic fertilisation one cut, grazed in late summer	Grazed from May to Mid-September	Grazed from May to Mid-September	abandoned since 1983 fertilised 1989	abandoned since 1983
Soil type[a]	Fluvisol	Dystric cambisol	Dystric cambisol	Dystric cambisol	Dystric cambisol	Dystric cambisol
Vegetation type	Pastinaco Arrhenteretum	Trisetetum flavescentis	Seslerio-Caricetum Sempervirentis	Allchemillo Poetum supinae	Vaccinio Callunetum	Seslerio-Caricetum with dwarf shrubs
Dominant species	Dactylis glomerata Poa pratensis Ranunculus acris Taraxacum officinale Trifolium pratense Trifolium repens Trifolium repens	Alchemilla vulgaris Anthoxanthum odoratum Festuca rubra Leontodon hispidus Trifolium repens	Alchemilla vulgaris Carex sempervirens Leontodon hispidus Lotus corniculatus Plantago lanceolata Plantago media Ranunculus montanus Sesleria albicans	Alchemilla vulgaris Anthoxanthum odoratum Carex sempervirens Festuca rubra Leontodon hispidus Lotus corniculatus Sesleria albicans Trifolium repens	Alchemilla vulgaris Avenella flexuosa Homogyne alpina Nardus stricta Vaccinium vitis-idaea	Anthyllis vulneraria Calluna vulgaris Festuca rubra Vaccinium myrtillus Vaccinium vitis-idea
Study years	2002–2005	2002–2004 2006–2008	2002–2004	2006–2008	2002–2003	2003–2008
Above-ground biomass (g/m²) *						
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

[a]FAO classification; MA, mean annual (values from two nearby weather stations, representing the situation of the valley bottom and the high mountain sites, respectively); T, temperature; P, precipitation.

*
Ranges refer to the minimum and maximum values in the given observation period.

Table 2

Regression statistics of the relationships between the net ecosystem CO_2 exchange at a PFD of 2000 µmol m^{-2} s^{-1} (NEE_{2000}), the gross primary productivity at a PFD of 2000 µmol m^{-2} s^{-1} (GPP_{2000}), the ecosystem respiration at a reference temperature of 10 °C (R_{10}) and the light use efficiency (LUE) in response to leaf area index (LAI). The following functions were used: NEE_{2000} vs. LAI: cubic and linear, GPP_{2000} vs. LAI: cubic and linear, $R10$ vs. LAI exponential- and linear, LUE vs. LAI: cubic and linear.

Site	NEE_{2000} vs. LAI		GPP_{2000} vs. LAI		R_{10} vs. LAI		LUE vs. LAI	
	R^2	p value	R^2	p value	R^2	p value	R^2	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