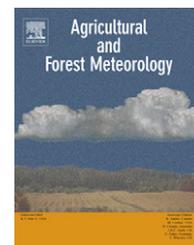


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Patterns in CO₂ gas exchange capacity of grassland ecosystems in the Alps

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ABSTRACT

Direct investigations of carbon exchange by grassland vegetation along elevation gradients from 620 m a.s.l. to 1960 m in the Alps were undertaken in the Berchtesgaden National Park, Germany and in Stubai Valley, Austria during 2002 and 2003, focusing on vegetation development in response to seasonal change in climate, where vegetation is not immediately influenced by grazing activity. The data were analyzed via model inversions with an empirical hyperbolic light response model and a physiological carboxylase-based process model. Differences were found in 'high' versus 'low' elevation sites in photosynthetic and respiratory capacity as well as their relationship to temperature environment and vegetation structure. Differentiation of the grassland types, which has a parallel in observations of grassland gas exchange worldwide as illustrated for the network projects CarboEurope and AmeriFlux, apparently depends on land use management, climate stress, nitrogen availability and plant community composition and dynamics. The importance of developing a better understanding of the observed differences or shifts in grassland ecosystem behavior in the context of assessing landscape, regional and continental scale water and carbon balances is discussed. The utility and need for simultaneous study of grasslands via eddy covariance and chamber methodologies, for parallel analysis of data with different models, and for supplementing field gas exchange observations with ancillary measurements of leaf structural and chemical composition in order to achieve new insight is emphasized.

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1. Introduction

Mountain regions covering ca. 20% of the earth surface act as an important water storage reservoir, supplying fresh water to half of humankind via major river systems (Messerli and Ives, 1997; Mountain Agenda, 1997, 1998). They are also hotspots of biodiversity (Körner and Spehn, 2002), provide food and forest products, and are centers for tourism and recreation. Multiple-

use mountain environments, which are critical in terms of sustained use of the biosphere, are sensitive to changes in atmospheric composition, in deposition and in other climate factors, and are, therefore, subject to rapid change and potentially to degradation. The importance of improving our understanding of alpine ecosystems and the need to simultaneously study natural processes, land use, resource management, and socio-economics in mountain regions was

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recognized decades ago by the Man and Biosphere Programme (MAB) of UNESCO (Haber et al., 1983; Tobias, 1991; Erdmann and Nauber, 1995).

Although ecological processes along elevation gradients in mountain regions have been studied for decades (Tranquillini, 1979; Körner, 1999; Larcher, 2003), gaps remain in our knowledge, due in part to the logistic difficulties of carrying out comprehensive ecological studies in such terrain. In Europe, changing agricultural policies influence the ecosystems in alpine regions with a trend toward abandonment of traditionally maintained high elevation grasslands and pastures, as their maintenance becomes less and less economically favorable (Bätzing, 1996; Cernusca, 1999). As a result, changes are taking place not only in the composition and structure of the vegetation, but also in ecosystem processes which influence the hydrological, carbon, and nutrient cycles in these regions and potentially alter ecological stability (Tappeiner et al., 1998; Tasser et al., 2001). An open question that requires more detailed clarification is whether the potentials of vegetation for water use and, thereby, for production change significantly at high elevation in comparison to valley sites, and if so, what factors are responsible for such changes.

Körner et al. (1989) demonstrated from water balance studies of grasslands in the Alps and in the Caucasus that annual evapotranspiration decreases at high elevation, leading to greater runoff. They concluded that the decrease can be explained by the length of the growing season, and that average grassland daily evapotranspiration was similar at all elevations. On the other hand, Cernusca and Seeber (1989a,b) found decreases in the surface area of green biomass in high elevation pastures (decreased LAI) and associated decreases in evapotranspiration measured via Bowen-ratio methods. Overall, the studies suggest that water use by grasslands may be influenced by compensating effects along elevation gradients, but that there is reason to believe that carbon dioxide exchange in general at canopy level may decrease with elevation. Management methods, however, may strongly mask natural trends. Bahn et al. (1999) demonstrated that leaves of plants in abandoned areas had lower nitrogen content on a mass basis and that this leads to lower net photosynthesis rates, which is also reflected at the canopy scale (Wohlfahrt et al., 2003). Likewise, on abandoned areas, roots tend to have lower N contents and respiration rates (Bahn et al., 2006). N mineralization and thus N availability is lower on abandoned as compared to managed alpine grassland (Zeller et al., 2000).

Understanding the carbon cycle and its dynamics in alpine ecosystems is important because it provides an indicator of stability or change (Odum, 1969, 1985; Reimers, 1983), e.g., in response to environmental stress or altered landuse. The carbon cycle along mountain elevation gradients, however, is tightly coupled to changes in energy balance and hydrology as well as landuse (Cernusca, 1999). Thus, research begun in the context of MAB (Cernusca, 1989) and continued in subsequent European projects has had the same goals as found in recent network studies at eddy covariance measurement sites, namely to observe the long-term characteristics of carbon, water and energy fluxes associated with different ecosystem types along climate gradients (Baldocchi et al., 1996). On slopes of mountainous areas, eddy covariance methodology is not

applicable in assessments of carbon balance and alternative methods must be found, e.g., monitoring via chamber methodologies.

Direct investigations of carbon exchange capacity of grassland vegetation along elevation gradients from 620 m a.s.l. to 1960 m in the Alps were undertaken in the Berchtesgaden National Park, Germany and in Stubai Valley, Austria within the framework of the European CARBOMONT project. We report here results from studies during 2002 and 2003 that focus on vegetation development in response to seasonal change in climate and where vegetation is not directly influenced by grazing activity, i.e., where an overview in the potential for CO₂ uptake by the vegetation is obtained. Establishing this point is important, since models for upscaling of ecosystem response to landscapes and regions commonly assume that grasslands at high elevation function in a similar fashion to their lowland counterparts. The measurements of net ecosystem CO₂ exchange were carried out with the same portable temperature-controlled and ventilated chambers at all sites, ensuring comparability of data from the different field locations.

Owen et al. (2007) examined long-term eddy covariance data from 35 sites with an empirical hyperbolic light response model and a physiological carboxylase-based process model with the goal of linking the results to large-scale models or other data analysis applications. We have applied the methods from Owen et al. (2007) to our gas exchange chamber measurements in order to estimate parameters describing gas exchange capacity along mountain elevation and land use gradients, and with the intention of comparing these results with those from Central European eddy covariance grassland study sites. Our goals in this paper are (1) to apply to chamber data the analysis methods previously used with eddy covariance data for model parameter estimation, (2) to demonstrate relationships between the empirical and process-based parameters obtained for grasslands along elevation gradients in the Alps, (3) to examine patterns in CO₂ uptake as related to climate factors, LAI, leaf physiology and elevation, and (4) to determine whether recognizable patterns occur among the grasslands studied. On this basis, we hope that future spatial modeling efforts at landscape to global scales can consider ways to improve simulations of vegetation/atmosphere CO₂ exchange in mountain regions.

2. Materials and methods

2.1. Site descriptions

The study was carried out from May 2002 to November 2003 in Berchtesgaden National Park, Germany at altitudes from 620 to 1750 m and in Stubai Valley, Austria at altitudes from 1000 to 1960 m.

2.1.1. German sites

The Berchtesgaden National Park (210 km²) is located in southeastern Germany between 12°47' and 13°05'E and 47°27' and 47°45'N, and borders on Austria's province of Salzburg. It includes a nearly natural alpine region situated in the northern limestone Alps. The landscape is characterized by

steep valleys and glacial moraines. Altitude ranges from 603 m at the lowland lake of Königssee to 2713 m at the summit of Watzmann Mountain. At high elevation, typical mountain climate conditions prevail. The mean annual temperature ranges, from +7 °C at Königssee to –2 °C on the Watzmann summit. Annual precipitation varies between 1500 and 2200 mm, with a mean of ca. 1900 mm (National Park Climate Stations). Vegetation in the Berchtesgaden National Park is strongly affected by elevation gradients. Mixed mountain forest occurs up to 1400 m, although Norway spruce (*Picea abies*) stands dominate due to planting during the last centuries. The subalpine zone from 1400 to 2000 m includes spruce-larch forests (*Picea abies* and *Larix decidua*). Above 1700 m, dwarf pines (*Pinus mugo*) and alpine meadows prevail. Approximately 70% of land cover in the park is forest, 17% is managed pasture and meadows, and the remaining areas include bare soil and rocks, wetlands and human settlements.

The Berchtesgaden field studies were carried out at four measurement sites, at elevations of 620, 1020, 1420 and 1750 m. The grassland vegetation at the first three of these sites was managed, while the highest elevation site (Kederbichl) was a naturally occurring grass-dominated herbaceous understory of the open *Larix decidua* forest. At the Schönau meadow site (620 m), the vegetation was cut once in 2002 (day of year – DOY – 212) and twice in 2003 (DOY 167 and 191) for winter hay production. Hirschengarten (1020 m) and Kuhrint (1420 m) are pastures where the spruce forest was cleared during the 19th century, and where grazing occurs during mid-summer. In order to compare the spring phase of vegetation development as well as maximum LAI reached along the elevation gradient, observations at Kuhrint during 2003 focused on the period before mid-July, when cattle were brought to pasture. At Hirschengarten during 2002, the period for natural growth without grazing was extended by building an enclosure. Thus, at Schönau, Hirschengarten and Kederbichl, gas exchange behavior during natural senescence in late season during 2002 could be examined. Except for Kederbichl, annual fertilization (not quantified) occurs via the animal activity or via manure application (Schönau). Soils of the higher elevation sites are classified as Rendzinas, while the soil at the Schönau site was a Cambisol (FAO).

2.1.2. Austrian sites

Stubai Valley is situated at approx. 47°07'N, 11°17'E and covers an altitudinal range from 660 to 3450 m at the summit of the Schrankogel Mountain. Vegetation in the Stubai Valley includes alpine grasslands and subalpine coniferous forests at higher elevations and cultivated areas at the bottom of the valley. Approximately 5% of the area is continuously inhabited and land is used as pasture, for hay production or for crops; ca. 50% of the surface is covered by glaciers, while 30% is alpine meadows or pastures, and the rest of the valley consists of forest dominated by Norway spruce (cf. mapping by the ECOMONT project, in Cernusca, 1999). The Stubai Valley field studies were carried out at four measurement sites at elevations of 1000, 1750, 1950 and 1960 m. Average air temperature and annual precipitation range from 6.3 °C and 850 mm to 3.0 °C and 1100 mm at the valley bottom and the treeline (1800–2000 m), respectively. As the meadow at the valley bottom is quite flat, an eddy covariance station was

installed here for testing and calibration of the chamber measurements, which were located within the center of the tower footprint (cf. Wohlfahrt et al., 2005). Inclination of the high elevation sites range between 20° and 30°. Soils of the higher elevation sites have been classified as Cambisols, soils at the valley bottom as Fluvisols (FAO). The vegetation of the meadows at the elevation of 1000 and 1750 m were cut between one to three times a year (cuts on DOY 155, 208, and 275 at the 1000 m intensive meadow; cut on DOY 190 at the 1750 m extensive meadow). The vegetation of the intensive meadow at the valley bottom at 1000 m is classified as a *Pastinaco-Arrhenatheretum*, vegetation of the extensive meadow at 1750 m a.s.l. as a *Trisetetum flavescens*, the pasture at 1950 m a.s.l. as an *Alchemillo Poetum supinae*, and the abandoned and reforested pasture at 1960 m a.s.l. as a *Vaccinio-Callunetum* community.

2.2. Meteorological and harvest data

Meteorological measurements were carried out at each site with standard instrumentation, recording observations at an hourly time step and at 2 m height. Data included global radiation, photosynthetic photon flux density (Q), air temperature, soil temperature near the soil surface (0–5 cm), relative humidity, and wind speed. Vapor pressure deficit (VPD) was calculated from air temperature and relative humidity. Air pressure and atmospheric CO₂ concentration were recorded together with chamber fluxes during measurement campaigns (see Section 2.3). Soil water content was not documented, but rainfall was frequent during both summers. Noticeable indication of water stress could not be observed at any time. Details of microclimate at individual measurement sites during the month of July are compared in Table 1.

Aboveground biomass was sampled in the immediate vicinity of the measurement plots at the end of each measurement campaign. At each location, three samples of vegetation similar in appearance to that included in the measurement plots were harvested from a 20 cm × 20 cm square. Biomass was determined separately for green dry weight (separately for green leaf and stem) and dead dry weight (separately for dead leaf and stem). During various periods, LAI of the grassland stands was determined directly with a LiCor leaf area meter (LiCor, Lincoln, Nebraska). A regression established between measured biomass and LAI was used to estimate LAI for all remaining observation periods.

2.3. F_{NEE} measurements and F_{GPP} estimates

Net ecosystem exchange of CO₂ (F_{NEE}) was measured using manually operated, closed gas exchange canopy chambers as described by Droessler (2005) and Wohlfahrt et al. (2005). The 78 cm × 78 cm × 40 cm chambers were constructed of transparent plexiglass (3 mm XT type 20070; light transmission 95%). Dark chambers, for measuring ecosystem respiration (F_{RE}), were constructed of opaque PVC. Using extensions, chamber height was adjusted to the canopy height. Chambers were placed on frames made of polyethylene that had been inserted 7 cm into the ground at the beginning of the vegetation growth period. They were sealed with a flexible

Table 1 – Meteorological conditions at the grassland sites in Berchtesgaden National Park, Germany and Stubai Valley, Austria during the month of July in the years shown

	Berchtesgaden, Germany					Stubai Valley, Austria				
	Schoenau 620 m (2002)	Schoenau 620 m (2003)	Hirschen- garten 1020 m (2002)	Kuhroint 1420 m (2002)	Kuhroint 1420 m (2003)	Kederbichl 1750 m (2002)	Meadow 1000 m (2002)	Meadow 1750 m (2002)	Pasture 1950 m (2002)	Pasture Abandoned 1960 m (2002)
Q_{Mean} ($\text{mol m}^{-2} \text{day}^{-1}$)	39.8	38.3	24.9	27.6	29.4	28.7	42.2	44.0	44.0 ^a	44.0
VPD_{Mean} daily max (kPa)	11.7	16.6	7.9	9.6	10.2	5.3	N/A	7.6	N/A	N/A
VPD_{max} (kPa)	23.4	33.7	20.3	21.5	23.9	10.2	N/A	18.9	N/A	N/A
$T_{\text{air,Mean}}$ daily min ($^{\circ}\text{C}$)	12.0	11.9	9.4	10.0	10.0	7.7	10.5	8.7	11.6	9.1
$T_{\text{air,Mean}}$ daily max ($^{\circ}\text{C}$)	23.0	25.1	19.8	18.0	18.4	15.0	23.3	16.4	18.3	15.9
$T_{\text{air,Mean}}$ ($^{\circ}\text{C}$)	17.2	18.1	13.8	13.6	14.0	11.3	16.5	12.4	15.3	12.5
$T_{\text{surf,Mean}}$ daily min ($^{\circ}\text{C}$)	16.5	16.4	15.0	12.5	12.8	8.4	14.8	11.9	12.4	11.5
$T_{\text{surf,Mean}}$ daily max ($^{\circ}\text{C}$)	19.1	19.4	17.8	17.0	15.4	13.1	19.0	17.6	19.6	13.2
$T_{\text{surf,Mean}}$ ($^{\circ}\text{C}$)	17.8	17.9	16.3	14.5	14.1	10.6	16.7	14.4	16.6	12.3
Monthly precipitation (mm)	193	187	195	N/A	N/A	150	142	150	143	143

N/A = not available.

^a Q sensor failed during July, as only 400 m horizontal distance separate the pasture with the abandoned pasture, the Q value was assumed the same.

rubber gasket. Tests indicated that leakage did not occur (see Droessler, 2005 for details), however, this could not be examined regularly in the case of systematic field measurements. Three frames were placed at each site. The number was limited by logistic considerations related to frequency of sampling as well as the desire to obtain comparisons between sites. Increased pressure in the chamber was avoided by (i) a 12 mm diameter opening at the top of the chamber which was closed after the chamber had been placed onto the frame and (ii) a 4 mm diameter venting tube inserted at the bottom of the chamber and through the sealing gasket. Circulation of air within of the chamber was provided by two fans yielding a wind speed of 1.2 m s^{-1} . Change in chamber CO_2 concentration over time was assessed with a portable, battery operated IRGA (LCA2, ADC, UK). Measurements were carried out in most cases within 3 min of placing the chamber on the frames (when the rate of concentration change was approximately linear), except at rates of F_{NEE} close to 0 where they lasted up to 5 min. Depletion of CO_2 in the chamber during measurement was ca. 20–30 ppm. Influence of the concentration change on estimated gas exchange rates was ignored. By mounting frozen ice packs on the backside of the chamber in the air flow, temperature during measurements could be stabilised within 1°C relative to ambient (air and soil temperatures inside and outside of the chambers are monitored during measurement). The frozen ice packs also prevent any rapid build-up of water vapour in the chamber during measurements. Data obtained with the chambers provided results that were closely correlated to F_{NEE} measured by the Stubai Valley eddy covariance tower ($F_{\text{NEE eddy}} = 0.88 \times F_{\text{NEE chamber}} - 0.08$, $R^2 = 0.87$; cf. Wohlfahrt et al., 2005). The differences arise due to differences in spatial sampling as well as methodology, and they have not been resolved further to date (see discussion of Fig. 8 below). Chamber F_{NEE} measurements were conducted at each site every third or fourth week over the course of the growing season in order to develop a picture of the annual changes in ecosystem function in CO_2 exchange. During each measurement campaign, light and dark chamber measurements were conducted from sunrise to sunset over 2 days for each site. Two databases were produced, one for the observed F_{NEE} , and a second for estimated F_{GPP} where the ecosystem respiration added to F_{NEE} was determined by fitting the equation of Lloyd and Taylor (1994) to all dark chamber observations during a campaign.

2.4. Estimation of model parameters

2.4.1. Empirical hyperbolic light response model

Empirical description of the measured F_{NEE} fluxes was accomplished via a non-linear least squares fit of the data to a hyperbolic light response model, also known as the Michaelis–Menten or rectangular hyperbola model (cf. Tamiya, 1951; Gilmanov et al., 2003; Owen et al., 2007; see Fig. 1):

$$F_{\text{NEE}} = -\frac{\alpha\beta Q}{\alpha Q + \beta} + \gamma \quad (1)$$

where F_{NEE} is net ecosystem CO_2 exchange ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), α is the initial slope of the light response curve

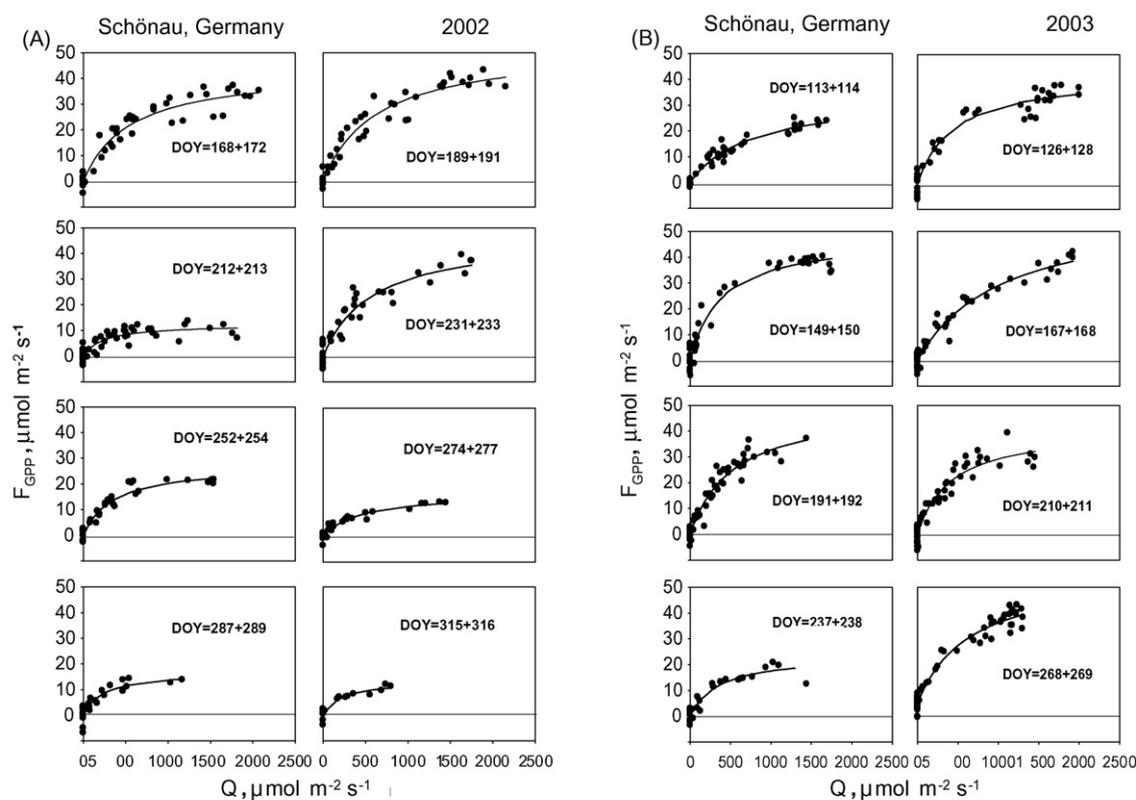


Fig. 1 – Measured fluxes at the Schönau site in Berchtesgaden National Park plotted for each campaign in 2002 (A) and 2003 (B) as a function of incident photosynthetic photon flux density, Q . Also shown are the predicted light response curves obtained in fitting of the hyperbolic light response model. Both measured and predicted data are corrected with average ecosystem respiration (γ in Tables 2 and 3) to obtain the estimates of F_{GPP} shown.

and an approximation of the canopy light utilization efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \mu\text{mol photon m}^{-2} \text{ s}^{-1}$), β is the maximum F_{NEE} of the canopy ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), Q is the photosynthetic photon flux density ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$) measured inside of the gas exchange chamber, γ is an estimate of the average ecosystem respiration (F_{RE}) occurring during the observation period ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), (α/β) is the radiation required for half maximal uptake rate, and $(\beta + \gamma)$ is the theoretical maximum uptake capacity. Since the rectangular hyperbola may saturate very slowly in terms of light, the term $\alpha\beta Q / (\alpha Q + \beta)$ evaluated at a reasonable level of high light ($Q = 2000 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ is used in this study) approximates the maximum F_{GPP} and can be thought of as the average maximum canopy uptake capacity during each observation period, notated here as $(\beta + \gamma)_{2000}$. The parameters α , β , β_{2000} (e.g., F_{NEE} at $Q = 2000$) and γ were estimated for each site using F_{NEE} data for each measurement campaign, which were typically carried out over 2 consecutive days. Data were pooled for these campaigns including all chambers, since there was no known reason to believe that ecosystem behavior would shift during the short period of a campaign, differentiation of fluxes from separate chambers was not of interest, and visual examination of the data suggested that the collection of observations could be interpreted as a single light response (cf. Fig. 1).

2.4.2. Physiology-based process model

The physiology-based process model applied to describe light interception and leaf gas exchange is single-layered and defines sun and shade light classes for canopy foliage. Inputs to the model inversion include global radiation, air temperature, soil temperature at 5 cm, relative humidity, wind speed, air pressure, atmospheric CO_2 concentration, gross primary productivity (e.g., the short-term gross uptake flux F_{GPP}), and leaf area index (LAI). We used the measured F_{RE} from the dark chamber measurements to estimate the F_{RE} ongoing during the light measurements; and then obtained $F_{GPP} = F_{NEE} + F_{RE}$. LAI is calculated as linearly extrapolated versus time from periods with biomass harvests. Radiation distribution in the model onto sun and shaded leaves is described according to Chen et al. (1999) with Ω assumed at 0.9 for grassland. The light interception of the sunlit and shaded leaves is used along with absorption and emission of long-wave radiation, convective heat loss and latent heat loss through transpiration to calculate the energy balance of leaves in two classes (sunlit and shaded). The simulation of gross photosynthesis follows Farquhar and von Caemmerer (1982) as modified for field applications by Harley and Tenhunen (1991). Model inversions for parameter estimation are based on Ribulose-1,5-bisphosphate-carboxylase-oxygenase (Rubisco) enzyme reactions where the rate of CO_2 fixation is limited by either the regeneration of Ribulose-1,5-biphosphate (RuBP) at low light

Table 2 – Best-fit parameters of the empirical hyperbolic light response model and physiology-based model for F_{NEE} and F_{GPP} at Schönau and their statistical characteristics for days in 2002

DOY date	n (n)	α	β	β_{2000}	γ	S.E. α	S.E. β	S.E. γ	R^2	Vcuptake1*	S.E. Vcuptake1*	LAI
168 + 172 (June 17,21)	44 (34)	0.080	43.6	13.9	20.3	0.013	2.95	1.08	0.93	140	4.7	2.9
189 + 191 (July 8,10)	45 (35)	0.082	52.5	23.6	16.2	0.012	3.32	1.04	0.95	150	4.3	3.5
212 + 213 (July 30,31)	49 (34)	0.052	12.3	5.7	16.7	0.017	1.43	0.60	0.76	55	3.9	1.7
231 + 233 (August 19,21)	41 (36)	0.081	47.3	21.7	14.9	0.013	4.2	0.97	0.92	218	13.3	2.2
252 + 254 (September 9,11)	38 (25)	0.077	27.3	10.8	12.4	0.011	1.79	0.57	0.94	103	4.1	2.5
274 + 277 (October 1,4)	29 (21)	0.038	16.7	8.1	5.6	0.007	1.54	0.42	0.93	50	2.2	3.0
287 + 289 (October 14,16)	26 (17)	0.071	17	7.7	7.4	0.026	2.89	0.83	0.81	75	6	2.4
315 + 316 (November 11,12)	16 (10)	0.063	13.5	7.7	4.5	0.026	2.48	0.64	0.90	65	3.6	2.7

DOY is day of year; n is the number of F_{NEE} determinations included in empirical model fits; (n) number of determinations in the light used in physiological model fits; parameters α , β , and γ are defined in Eq. (1). β_{2000} is an estimated value for F_{NEE} at the light level of 2000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$; S.E. is the standard error; LAI is the leaf area index established after harvest of the enclosed vegetation in study plots.

intensity and/or high internal CO_2 concentration; or by Rubisco activity and CO_2/O_2 -concentration at saturated light and low internal CO_2 concentration (cf. Reichstein, 2001). Further details about the physiological model are described in Owen et al. (2007).

Leaf physiological parameters determining temperature dependent response of leaves and stomatal response were held constant at values established in leaf gas exchange studies with non-water limiting conditions (cf. Owen et al., 2007). In the first step of the analysis, seasonal variation of alpha ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}/\mu\text{mol photon m}^{-2} \text{ s}^{-1}$), the average leaf light utilization efficiency without photorespiration, and Vcuptake2* (indicating model inversion for two parameters, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf area s}^{-1}$), the average leaf carboxylation capacity at 25 °C, were estimated via model inversion studies with individual site F_{GPP} data (see Section 2.3 above). As in the case of the empirical model analysis, parameter determination was carried out for each campaign, pooling all days and all chamber measurements at each site.

As described in Owen et al. (2007), the number of parameters for the physiological model were then reduced to one, with alpha dependent on Vcuptake. This eliminates noise in the parameter estimation that arises from the influence of different weather (prevailing high or low light

during measurements) on the inversion routine. From all of the parameter estimates across sites and measurement campaigns, a linear relationship between alpha and Vcuptake* was found to describe correlation in the two parameters (Eq. (2)):

$$\alpha = \text{Vcuptake} * 0.0006 \quad (2)$$

Using Eq. (2), the parameter Vcuptake1* (single parameter model inversion, notation consistent with Owen et al., 2007) was estimated for each site and for each measurement campaign.

3. Results

Results of inverting the simple hyperbolic light response model based on 1-h time scale F_{NEE} gas exchange and Q observations are shown for the parameters α , β , β_{2000} and γ in Tables 2–6 for Berchtesgaden and Tables 7–10 for Stubai Valley campaigns. Also given is the estimated value of LAI for each measurement period. Considering all campaigns at both sites, R^2 ranged between 0.42 and 0.99, but was greater than 0.8 in 87% and greater than 0.9 in 73% of the cases shown (a case includes the flux rate observations during a campaign at a

Table 3 – Best-fit parameters of the empirical hyperbolic light response model and physiology-based model for F_{NEE} and F_{GPP} at Schönau and their statistical characteristics for days in 2003

DOY date	n (n)	α	β	β_{2000}	γ	S.E. α	S.E. β	S.E. γ	R^2	Vcuptake1*	S.E. Vcuptake1*	LAI
113 + 114 (April 23,24)	44 (35)	0.045	33.7	17.4	7.1	0.005	2.25	0.54	0.95	105	4.6	2.7
126 + 128 (May 6,8)	45 (30)	0.095	42.4	20.9	13.8	0.016	2.52	0.87	0.95	149	4.8	3.0
149 + 150 (May 29,30)	52 (34)	0.125	48.2	27.0	13.4	0.018	2.16	0.74	0.96	135	6.5	4.7
167 + 168 (June 16,17)	50 (33)	0.057	59.1	22.8	16.2	0.006	4.73	0.96	0.65	164	14.5	2.9
191 + 192 (July 10,11)	62 (42)	0.094	50.0	26.2	13.3	0.011	4.09	0.61	0.95	151	5.2	3.2
210 + 211 (July 29,30)	63 (36)	0.099	41.2	22.4	11.7	0.014	3.14	0.62	0.93	149	5.4	2.7
237 + 238 (August 25,26)	44 (26)	0.067	23.8	7.6	12.6	0.012	1.58	0.47	0.94	88	5.0	2.3
268 + 269 (September 25,26)	60 (39)	0.053	34.2	19.7	6.2	0.007	2.65	0.36	0.97	95	2.1	3.1

DOY is day of year; n is the number of F_{NEE} determinations included in empirical model fits; (n) number of determinations in the light used in physiological model fits; parameters α , β , and γ are defined in Eq. (1). β_{2000} is an estimated value for F_{NEE} at the light level of 2000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$; S.E. is the standard error; LAI is the leaf area index established after harvest of the enclosed vegetation in study plots.

Table 4 – Best-fit parameters of the empirical hyperbolic light response model and physiology-based model for F_{NEE} and F_{GPP} at Hirschengarten and their statistical characteristics for days in 2002

DOY date	n (n)	α	β	β_{2000}	γ	R^2	Vcuptake1*	LAI
128 + 129 (May 8,9)	60 (42)	0.104	35.9	23.0	7.6	0.95	247	1.9
149 + 152 (May 29, June 1)	43 (31)	0.083	51.7	31.4	8.0	0.97	168	2.7
169 + 171 (June 18,20)	54 (37)	0.088	47.1	22.6	14.5	0.97	147	3.4
190 + 192 (July 9,11)	47 (28)	0.086	34.8	19.0	9.9	0.95	109	3.8
211 + 214 (July 29, August 2)	64 (40)	0.090	36.3	18.7	11.5	0.95	97	4.4
232 + 234 (August 20,22)	60 (47)	0.091	31.2	17.2	9.4	0.95	85	4.6
253 + 255 (September 10,12)	51 (34)	0.046	55.9	27.9	6.9	0.94	81	5.0
275 + 276 (October 2,3)	64 (43)	0.053	18.6	11.7	4.1	0.96	50	3.3
288 + 290 (October 14,16)	42 (42)	0.027	32.1	15.6	4.5	0.95	47	2.9

Column headings as given for Tables 2 and 3.

Table 5 – Best-fit parameters of the empirical hyperbolic light response model and physiology-based model for F_{NEE} and F_{GPP} at Kuhrint and their statistical characteristics for days in 2003

DOY date	n (n)	α	β	β_{2000}	γ	R^2	Vcuptake1*	LAI
127 (May 7)	22 (15)	0.050	24.5	9.8	9.9	0.87	80	0.7
146 + 147 (May 26,27)	43 (19)	0.035	129.3	31.7	13.7	0.94	89	4.7
170 + 171 (June 19,20)	44 (21)	0.122	70.9	37.6	17.4	0.75	181	5.1
188 + 189 (July 7,8)	57 (29)	0.103	52.4	27.4	14.3	0.87	147	4.4

Column headings as given for Tables 2 and 3.

Table 6 – Best-fit parameters of the empirical hyperbolic light response model and physiology-based model for F_{NEE} and F_{GPP} at Kederbichl and their statistical characteristics for days in 2002

DOY date	n (n)	α	β	β_{2000}	γ	R^2	Vcuptake1*	LAI
171 (June 20)	42 (32)	0.144	14.8	6.6	7.5	0.96	62	1.5
190 (July 9)	55 (39)	0.135	18.3	8.6	8.5	0.85	45	3.9
211 (July 30)	43 (28)	0.087	21.8	11.5	7.9	0.94	53	3.4
229 (August 17)	45 (24)	0.138	16.0	9.7	5.4	0.94	69	4.1
255 (September 12)	58 (36)	0.053	20.7	13.5	3.8	0.97	66	2.1

Column headings as given for Tables 2 and 3.

Table 7 – Best-fit parameters of the empirical hyperbolic light response model and physiology-based model for F_{NEE} and F_{GPP} at Stubai Valley 1000 m meadow site and their statistical characteristics for days in 2002

DOY date	n (n)	α	β	β_{2000}	γ	R^2	Vcuptake1*	LAI
134 + 135 (May 14,15)	36 (28)	0.042	43.1	17.5	10.9	0.94	79	3.6
150 (May 30)	25 (22)	0.060	35.2	18.4	8.8	0.95	68	4.4
154 (June 3)	33 (33)	0.048	40.7	21.0	7.6	0.93	73	4.6
208 (July 27)	13 (12)	0.052	44.7	19.9	11.4	0.96	85	4.7
273 (September 30)	24 (23)	0.016	46.7	13.5	5.4	0.85	46	4.1
303 (October 30)	16 (16)	0.022	16.6	8.6	3.5	0.91	83	1.1
332 (November 28)	13 (13)	0.017	12.1	8.2	0.8	0.71	71	0.7

Column headings as given for Tables 2 and 3.

Table 8 – Best-fit parameters of the empirical hyperbolic light response model and physiology-based model for F_{NEE} and F_{GPP} at Stubai Valley 1750 m meadow site and their statistical characteristics for days in 2002

DOY date	n (n)	α	β	β_{2000}	γ	R^2	Vcuptake1*	LAI
136 (May 16)	19 (14)	0.013	40.0	11.9	3.8	0.97	79	1.3
162 (June 11)	40 (31)	0.025	51.3	20.5	4.8	0.92	72	2.5
231 (August 19)	14 (11)	0.047	61.5	24.3	12.9	0.99	141	3.9
232 (August 20)	19 (19)	0.076	48.9	26.5	10.5	0.97	135	4.1
247 (September 4)	9 (9)	0.081	28.3	10.0	14.1	0.97	78	3.8
275 (October 2)	29 (27)	0.045	17.2	9.7	4.8	0.8	43	0.8

Column headings as given for Tables 2 and 3.

Table 9 – Best-fit parameters of the empirical hyperbolic light response model and physiology-based model for F_{NEE} and F_{GPP} at Stubai Valley pasture site (1950 m) and their statistical characteristics for days in 2002

DOY date	n (n)	α	β	β_{2000}	γ	R^2	$V_{cuptake1}^*$	LAI
141 (May 21)	21 (14)	0.023	4.3	1.1	2.8	0.53	11	1.6
165 (June 14)	22 (19)	0.124	11.5	7.1	3.9	0.78	28	1.6
191 (July 10)	27 (20)	0.025	14.8	5.9	5.6	0.9	35	1.5
220 (August 8)	12 (12)	0.060	13.0	4.9	6.8	0.9	44	1.6
227 (August 15)	34 (30)	0.028	12.8	4.7	5.7	0.67	26	1.6
294 (October 21)	34 (31)	0.038	5.0	3.9	0.8	0.42	38	0.8

Column headings as given for Tables 2 and 3.

single location). To demonstrate the ability of Eq. (2) to describe the data in each case, predicted F_{GPP} at Schönau during both 2002 and 2003 is presented in Fig. 1A and B, where the measured F_{NEE} data are adjusted to F_{GPP} by adding the value of F_{RE} to observed fluxes (Section 2.3). While some unexplained scatter around the predicted response curves is found due to temperature shifts, diurnal hysteresis (Gilmanov et al., 2003, 2005), or simply measurement errors, Q is a very good predictor of response. Even during the campaigns where R^2 decreased below 0.8 (DOY 212 + 213 in 2002 and 167 + 168 in 2003), only a few observations were found to deviate strongly from the predicted relationship. Only very late in the year (DOY 294) at the pasture site at 1950 m in the Austrian Alps (Tables 9 and 10) did the apparent influence of other environmental factors or senescence lead to less reliable parameter values in the Q equation. Thus, in the correlation analyses discussed below, all data indicated in Tables 2–10 were included. The standard error estimates for parameters are eliminated from Tables 4–10, as they were similar to the example given in Tables 2 and 3.

Seasonal patterns for LAI and for $(\beta + \gamma)_{2000}$ for all sites and years are shown in Figs. 2 and 3 (actual values may be derived from Tables 2–10). Interpreting $(\beta + \gamma)_{2000}$ as an estimate of maximum F_{GPP} at the time of observation, the photosynthetic potential of the Schönau meadow varied seasonally during the assessment periods from ca. 12.2 to 40.4 $\mu\text{mol CO}_2 \text{ m}^{-2}$ ground area s^{-1} , depending on stand development and environmental conditions. In other words, the estimated maximum F_{GPP} typically approached ca. 40 $\mu\text{mol m}^{-2}$ ground area s^{-1} under full sunlight and with high leaf area during the growing season, and about 10 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ with lower temperature and radiation during late fall and winter. During summer, $(\beta + \gamma)_{2000}$ increased in Schönau during 2002 to a maximum of ca. 40 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, decreased to ca. 20 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ with

harvesting of the meadow, and then increased again. But an additional trend is evident. Even though LAI increased until senescence in late October, photosynthetic capacity of the meadow decreased after mid-August. At the same location in 2003, high activity again occurred over a long period in spring and summer, aided perhaps by higher temperatures and an early spring in the hot, dry year in Europe during 2003. Early development of the vegetation allowed two cuts of the meadow. The long period of high photosynthetic capacity was again followed by a decrease after mid-August as observed during 2003.

At Hirschengarten (1020 m), a long period of LAI development occurred in the fenced area under study with LAI increasing over the season to more than 6. Senescence of the grass stand occurred only at the beginning of September. During the summer, $(\beta + \gamma)_{2000}$ remained relatively constant over a long period. In this case, the continuing slow LAI increase appeared to offset a decrease in physiological capacity which became more pronounced at the end of the season (low values of $(\beta + \gamma)_{2000}$ in October). At Kuhroint (1420 m), it was only possible to measure gas exchange without the disturbance by grazing cows at the beginning of the season. Rapid increase in LAI during spring of 2002 was accompanied by the highest uptake rates measured at all sites (between 40 and 50 $\mu\text{mol CO}_2 \text{ m}^{-2}$ ground area s^{-1}). In contrast, low CO_2 uptake rates were measured in natural understory grass stands of the open *Larix decidua* forest near tree line at Kederbichl (1750 m). Maximum F_{GPP} was ca. 20 $\mu\text{mol CO}_2 \text{ m}^{-2}$ ground area s^{-1} , even though LAI increased to values of 4 which were sufficient to support twice as much CO_2 uptake at other sites. No influence of late season photosynthetic declines in the grass stands at Kederbichl were apparent, at least not by mid-September when observations were terminated.

Table 10 – Best-fit parameters of the empirical hyperbolic light response model and physiology-based model for F_{NEE} and F_{GPP} at Stubai Valley abandoned site (1960 m) and their statistical characteristics for days in 2002

DOY date	n (n)	α	β	β_{2000}	γ	R^2	$V_{cuptake1}^*$	LAI
142 (May 22)	21 (20)	0.010	7.6	2.8	2.7	0.89	17	1.2
164 (June 13)	36 (33)	0.037	18.9	9.8	5.2	0.91	39	2.5
204 (July 23)	32 (29)	0.020	58.0	15.4	7.9	0.96	52	4.2
205 (July 24)	18 (17)	0.053	24.4	13.2	6.7	0.93	50	4.2
228 (August 16)	12 (12)	0.045	17.7	6.8	8.0	0.97	50	3.2
229 (August 17)	32 (27)	0.034	26.4	12.9	6.2	0.89	52	3.2
284 (October 11)	31 (30)	0.072	12.8	3.2	8.6	0.9	41	0.9

Column headings as given for Tables 2 and 3.

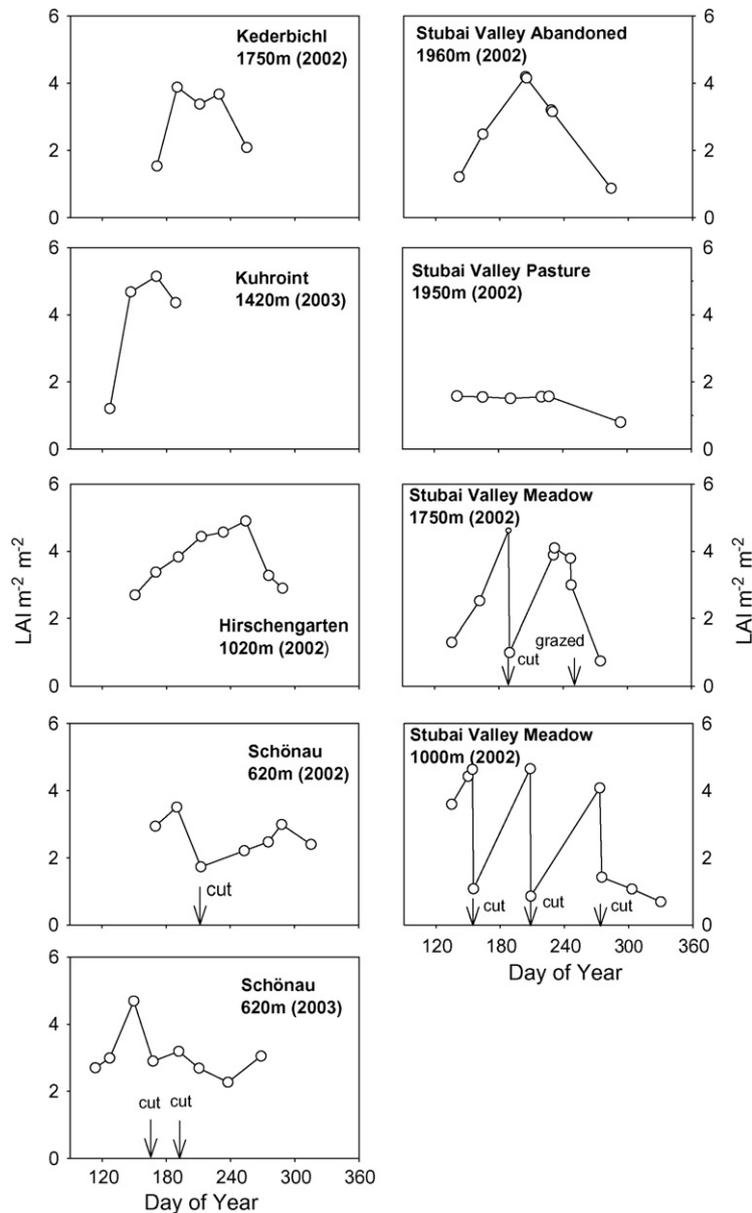


Fig. 2 – Seasonal changes in leaf area index (LAI) from harvests at the study sites in Berchtesgaden National Park, Germany (left column of panels) and in Stubai Valley, Austria (right column of panels). Exact dates for each harvest are given in the text.

Similar seasonal patterns in photosynthetic capacity of grasslands to those in Berchtesgaden were observed in Stubai Valley. At the intensive and extensive meadow sites at 1000 and 1750 m, photosynthetic capacity increased rapidly in springtime. Uptake rates greater than $30 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ ground area s}^{-1}$ were measured with LAI greater than 3. Uptake capacity remained high until mid-August, after which decreases occurred, in this case along with changes in LAI. The decreases in CO_2 uptake at times of harvesting were not studied. At the high elevation sites in Stubai Valley, lower photosynthetic capacity on a ground area basis was observed. The uptake rates of ca. $10 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ ground area s}^{-1}$ at the pasture site, where LAI remained below 2, were the lowest recorded. In the abandoned area, uptake rates and LAI similar

to that observed at Kederbichl in Berchtesgaden National Park were found (ca. $20 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ ground area s}^{-1}$ during mid-season).

The seasonal patterns in $(\beta + \gamma)_{2000}$ are associated with systematic seasonal changes in the shape of the light response of the grassland vegetation. As shown in Fig. 4A, the parameter α , reflecting canopy light utilization efficiency, varies in strong correlation with $(\beta + \gamma)_{2000}$. The relationship shown is not significantly different when comparing the sites in Berchtesgaden and Stubai Valley. The average values observed for ecosystem respiration, γ , are also influenced by the above-ground seasonal activity changes in the meadows. As seen in Fig. 4B, the parameter γ is significantly correlated with $(\beta + \gamma)_{2000}$ with no difference found between locations.

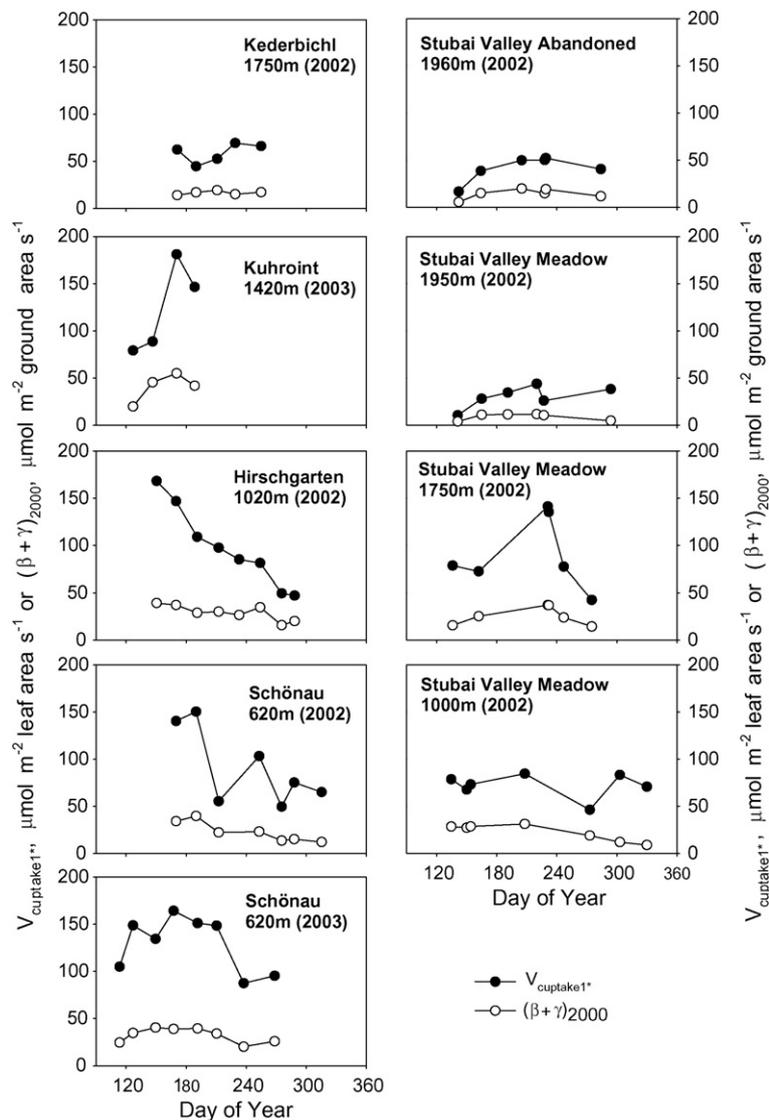


Fig. 3 – Seasonal change in canopy carbon fixation capacity at the study sites in Berchtesgaden National Park, Germany (left column of panels) and in Stubai Valley, Austria (right column of panels), expressed in terms of the empirical hyperbolic light response model $((\beta + \gamma)_{2000}$ in $\mu\text{mol m}^{-2}$ ground area s^{-1}) and the physiology-based model (V_{cuptake1^*} in $\mu\text{mol m}^{-2}$ leaf area s^{-1}).

The scatter around the regression line shown is large, which indicates that the estimated γ does not account for temperature fluctuations occurring during the measurements, rather it is an average value dependent on the sampling employed within a campaign (discussed further below). When considering the overall range of rates observed during the campaigns, light use efficiency and ecosystem respiration rates were slightly lower at the Stubai Valley sites as compared to the grasslands at Berchtesgaden (Fig. 4A and B).

The parameter V_{cuptake1^*} provides a second measure in addition to $(\beta + \gamma)_{2000}$ of carbon fixation capacity of the grassland sites, although it differs because it is standardized at 25 °C, whereas $(\beta + \gamma)_{2000}$ reflects the immediate environmental conditions imposed on the plant stand. Nevertheless, the results in Fig. 3 illustrating seasonal changes in V_{cuptake1^*} suggest some similarity in seasonal changes in both para-

meters. A direct comparison of the empirical and physiology-based model parameters is given in Fig. 5. The parameter V_{cuptake1^*} is in general strongly correlated with $(\beta + \gamma)_{2000}$ (Fig. 5B), while the values of the light use efficiency α (proportional to V_{cuptake1^*} via Eq. (2)) are strongly correlated with the light use efficiency from the empirical model (Fig. 5A).

To gain more insight into factors potentially influencing grassland gas exchange response, i.e. determining the scatter around the regression lines given in Figs. 4 and 5, the grasslands were separated into two groups. At the sites Kederbichl in Berchtesgaden and the pasture and abandoned meadow sites in Stubai Valley, values obtained for $(\beta + \gamma)_{2000}$ did not exceed $24 \mu\text{mol m}^{-2} \text{s}^{-1}$ and V_{cuptake1^*} did not exceed $70 \mu\text{mol m}^{-2} \text{s}^{-1}$. Data from these sites were pooled and we refer to “High Elevation Sites” in the discussion below, although we do not conclude that elevation is the direct

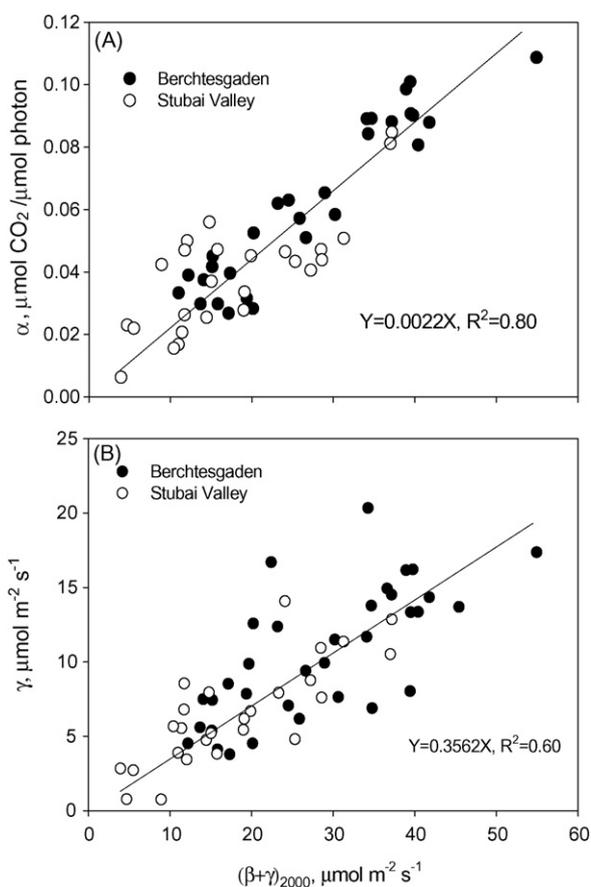


Fig. 4 – Correlation of the hyperbolic light response model parameters α and γ with the carbon fixation capacity estimate $(\beta + \gamma)_{2000}$, considering $(\beta + \gamma)_{2000}$ as a key determinant of grassland response.

cause of the observed differences in flux rates. At all other sites, much larger carbon fixation capacities occurred at least for part of the season. These data were included into a category referred to as “Low Elevation Sites.” Potential causes of the differences in flux rates found for these two groups may include land use, elevation and climate, species composition, and nitrogen availability as discussed further below.

Factors influencing the carbon uptake capacity of the grassland ecosystems are the amount of green biomass or LAI and the physiological activity or reaction rates as determined by temperature. Respiration is similarly influenced by above-ground biomass plus associated belowground biomass and by temperature. Thus, we examined the hypotheses that model parameters may be described as dependent on LAI and on mean air temperature recorded during observations in the case of carbon fixation (γ is included here since it is determined from measurements done in the light), and LAI and mean soil temperature in the case of observed F_{RE} fluxes. We recognize that the hypotheses represent extreme simplifications of complex phenomena.

Results of the respective multi-linear regressions are shown in Figs. 6 and 7 and are summarized in Table 11. The planar surfaces shown in the figures provide a good description of the data with R^2 values between 0.5 and 0.7, except for

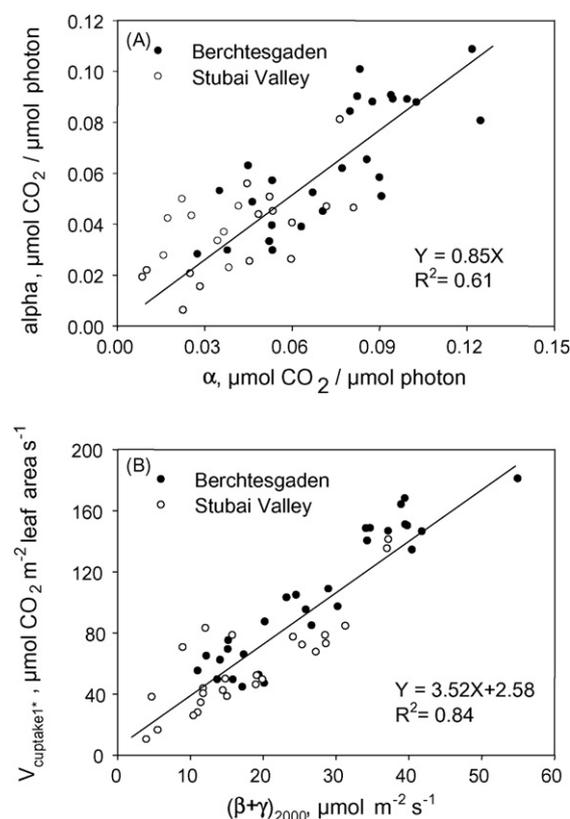


Fig. 5 – Correlations between light utilization efficiency and canopy carbon fixation capacity parameters from the empirical hyperbolic light response model (α and $(\beta + \gamma)_{2000}$) and the physiology-based process model (alpha and $V_{cuptake1^*}$).

$V_{cuptake1^*}$ which exhibited a lower explained sum of squares (ca. 0.3). Although there might be reason to expect the dependencies on LAI and temperature to be non-linear, examination of the residuals showed no systematic tendencies for deviation from the predicted surfaces. Large differences are apparent between the two groups of sites, supporting the separation of data into the two categories shown. Capacity for carbon uptake (Fig. 6; Table 11) was much less influenced by LAI and temperature in the high elevation group. While $V_{cuptake1^*}$ was not significantly influenced by these factors at ‘high elevation’, $(\beta + \gamma)_{2000}$ responded positively to temperature. In the low elevation group, $(\beta + \gamma)_{2000}$ increased strongly with both temperature and LAI, while $V_{cuptake1^*}$ increased only in correlation with air temperature (Table 11). Carbon loss in respiration based either on γ (as the average respiration from all dark chamber measurements during a campaign) or on the measured dark chamber fluxes increased strongly with temperature. Considering all dark chamber fluxes, an influence of LAI is also found to be significant. The shape of all response surfaces in Fig. 7 are similar, even though the respiration capacity at high elevation is less than at low elevation. We conclude from Figs. 4–7 that $(\beta + \gamma)_{2000}$ may be viewed as a key phenomenological parameter for describing seasonal changes in grassland gas

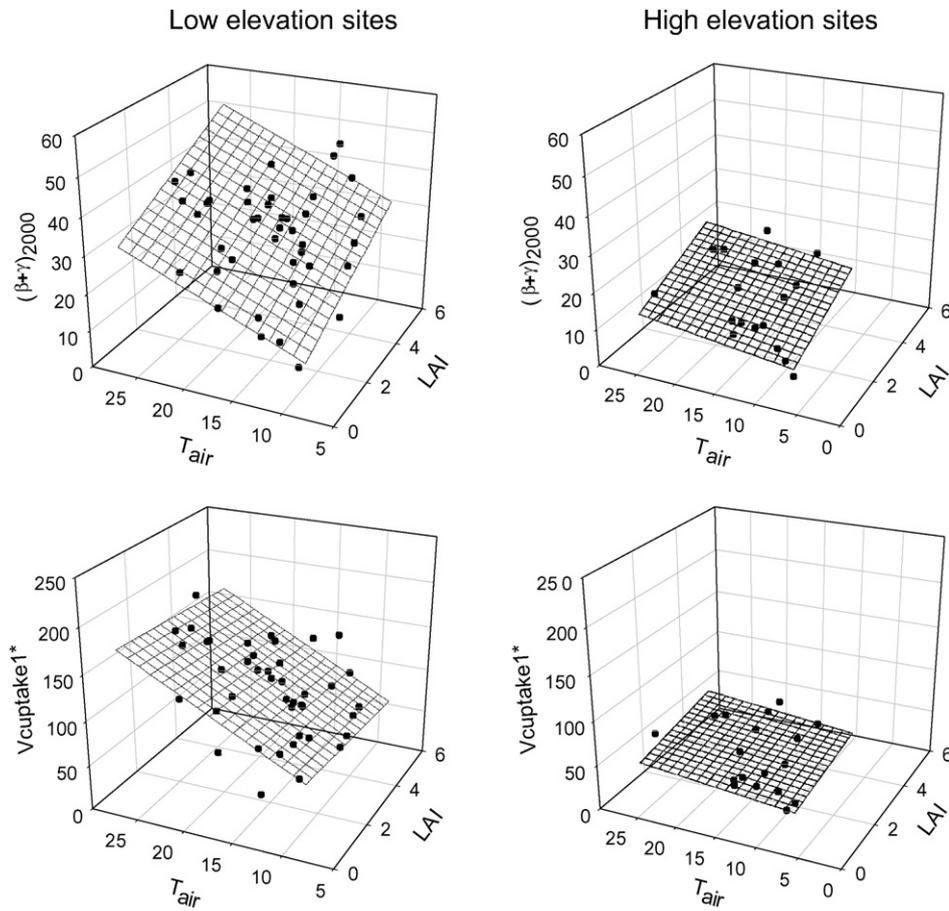


Fig. 6 – Illustration of the apparent influences of temperature and LAI on canopy carbon fixation capacity estimated with the empirical $((\beta + \gamma)_{2000})$ and physiology-based ($V_{cuptake1^*}$) models. Sites are separated into two groups at high and low elevation as described in the text. Equations for the planes shown are given in Table 11. Unit for $(\beta + \gamma)_{2000}$ is $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ ground area s}^{-1}$ and for $V_{cuptake1^*}$ is $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf area s}^{-1}$. T_{air} is the average measured air temperature during all observations of each campaign leading to the parameter determinations.

Table 11 – Coefficients and statistics of the multiple linear regression $Y = a(LAI) + b(T) + c$ applied in the analysis of model parameters to high elevation sites (including Kederbichl in Berchtesgaden and pasture and abandoned sites in Stubai Valley) and low elevation sites (Schönau, Hirschengarten, and Kuhroint in Berchtesgaden and the meadows at 1000 and 1750 m in Stubai Valley)

	Y		a	b	c	R ²
High elevation	$(\beta + \gamma)_{2000}$	T_{air}	3.35 ^{***}	0.28	1.39	0.74
	γ	T_{air}	0.62	0.23 [*]	0.80	0.51
	F_{RE}	T_{soil}	0.46 ^{***}	0.47 ^{***}	-2.02 ^{***}	0.66
	$V_{cuptake1^*}$	T_{air}	5.80	0.79	17.1	0.33
Low elevation	$(\beta + \gamma)_{2000}$	T_{air}	5.47 ^{***}	0.80 [*]	-2.87	0.52
	γ	T_{air}	1.18	0.70 ^{***}	-5.55 ^{**}	0.65
	F_{RE}	T_{soil}	0.52 ^{**}	0.71 ^{***}	-2.11 ^{***}	0.69
	$V_{cuptake1^*}$	T_{air}	1.68	5.08 ^{***}	13.7	0.27

Also shown are the results obtained for analysis of the directly measured respiration fluxes (F_{RE}).

^{*} Significant at $P = 0.05$.

^{**} Significant at $P = 0.01$.

^{***} Significant at $P = 0.001$

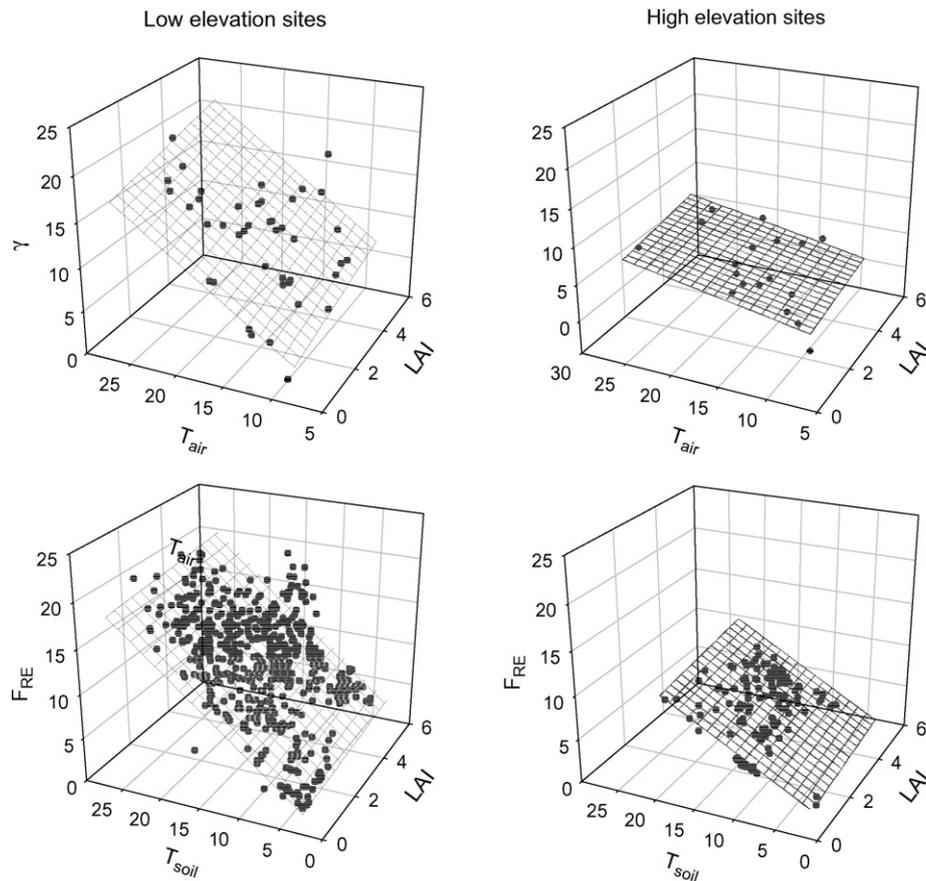


Fig. 7 – Illustration of the apparent influences of temperature and LAI on grassland ecosystem respiration as estimated with the empirical model (γ) and directly from the dark chamber measurements (F_{RE}). Sites are separated into two groups at high and low elevation as described in the text. Equations for the planes shown are given in Table 11. Unit for γ and for F_{RE} is $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ ground area s}^{-1}$. T_{air} is the average measured air temperature during all observations of each campaign leading to the parameter determinations. T_{soil} indicates the observed temperature at 5–10 cm depth during individual chamber dark flux measurements.

exchange behavior in the Alps, but that large temperature and lesser LAI influences must additionally be considered.

4. Discussion and conclusions

4.1. Evaluation of the model description of alpine grassland CO_2 exchange

The empirical hyperbolic light response model has been widely used to describe the photosynthetic response of vegetation based on both data from chambers and from eddy covariance monitoring of net ecosystem CO_2 exchange (Ruimy et al., 1995; Luo et al., 2000; Wohlfahrt et al., 2005; Ammann et al., 2007; Owen et al., 2007). Gilmanov et al. (2003, 2005, 2007) have discussed situations where slightly more complex empirical equations provide advantages in data description, particularly in providing more flexibility in adjusting curvature of the response or in describing daily hysteresis phenomena when the light equations are combined with temperature dependencies. Nevertheless, these empirical formulations all focus on the same response curve character-

istics, identifying light use efficiency, maximum fixation rate and the average level of apparent ecosystem respiration. In the case of the data sets from alpine grasslands studied, the hyperbolic light response model appears to be entirely adequate (cf. Fig. 1 and high R^2 values shown in tables).

In various studies, the time periods over which Eq. (1) has been applied differs. Gilmanov et al. (2007) examined eddy covariance data daily, while Wohlfahrt et al. (2005) described 5 day periods, and Owen et al. (2007) described 10 day periods over the course of a year. In the current study, the period was quite short, usually including observations on 2 consecutive days and where measurements in the dark were also carried out during the daytime period. As such, the parameters are appropriately coupled to the specific environmental conditions on these 2 days and to the ecosystem structure estimated immediately at the end of the experiment. Furthermore, the light and dark measurements (e.g., F_{RE} fluxes) “belong together” and provide an important characterization of the meadows during the light periods. Considerable evidence exists (discussed further below) that F_{RE} and, therefore, γ are influenced by the flow of fixed carbon to the root system, and that this changes with time over the course of night periods (Bahn et al., unpublished).

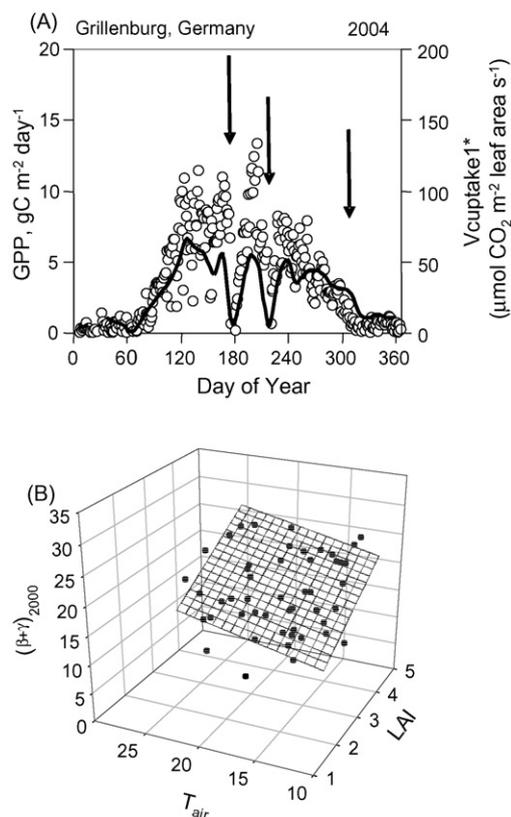


Fig. 8 – (A) Estimated daily GPP during 2004 from eddy covariance measurements for the Grillenburg, Germany meadow used for hay production (open circles; see Owen et al., 2007); and annual course for estimated $V_{cuptake1^*}$ (solid line) obtained from inversion of the physiology-based model described in the methods section. Inversions were carried out for collections of flux observations over 10 day periods. **(B)** Illustration of the apparent influences of temperature and LAI on canopy carbon fixation capacity of the Grillenburg, Germany meadow estimated with the empirical model. $(\beta + \gamma)_{2000}$ is estimated for single days during mid- to late summer as described in the text. Equations for the plane is given along with information about γ and $V_{cuptake1^*}$ in Table 12. Unit for $(\beta + \gamma)_{2000}$ is $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ ground area s}^{-1}$. T_{air} is the average measured air temperature during all half-hour estimates obtained during the daytime (light) period. LAI is estimated for each day from harvest data.

The simultaneous analysis of the same gas exchange data with the physiology-based process model allows us to make an additional first step in the direction of interpreting correlations found with the empirical model. As shown in Fig. 6, potential maximum F_{GPP} for both grassland groups shows a tendency to increase with LAI and with temperature, but the capacity as well as response of high elevation sites is much more limited. We suggest that this may relate to nutrient limitation of the photosynthetic process as found in leaf-level studies (Bahn et al., 1999), by cold temperature effects, and/or by the occurrence and in the plant community of slow growing species. In contrast, $V_{cuptake1^*}$ is indepen-

dent of LAI in both groups of grasslands. This suggests that the photosynthetic function of the average leaf of the grass stands does not change as LAI varies, while increasing LAI leads to higher maximum F_{GPP} . Since $V_{cuptake1^*}$ is not influenced by temperature in the high elevation stands, temperature influences on activity found for $(\beta + \gamma)_{2000}$ are fully described by the response functions included for carboxylase and RuBP regeneration activity in the model.

This is not at all the case for low elevation grasslands. The apparent influence of temperature in this second grassland group may be the result of acclimation of the photosynthetic response over the course of the season, since data are obtained from April through December. Along this line of reasoning, it is apparent from Fig. 3 that seasonal change in photosynthetic capacity does occur, especially during the latter part of the summer. Such shifts where they occur could be accompanied by acclimation and shift in the photosynthetic response curve. Alternatively, and less satisfying, such shifts might indirectly influence the response surface via seasonal changes in the correlation of temperature, LAI and $(\beta + \gamma)_{2000}$ that are difficult to visualize, especially when using data from multiple sites.

In other studies across forest (Janssens et al., 2001; Reichstein et al., 2003; Hibbard et al., 2005) and grassland sites monitored with either eddy covariance techniques or with periodic chamber measurements, soil CO₂ efflux has been found to increase with temperature and with GPP or LAI as a surrogate. The grassland ecosystems studied here exhibit such a response for total ecosystem respiration (Fig. 7). The respiration contribution by aboveground biomass should change similarly to soil CO₂ efflux in response to temperature and LAI, simply increasing the overall magnitude of efflux rates. Increases in LAI contribute to the total flux due to required maintenance respiration of plant organs, but also by increasing assimilate flow to the ecosystem soil compartment. The picture obtained for respiration dependence is essentially the same whether viewed from the perspective of individual measurements of F_{RE} or the parameter γ . The differences in respiration capacity between ‘low’ and ‘high’ elevation category grasslands are quite apparent and mirror the dependencies found for $(\beta + \gamma)_{2000}$.

4.2. Alpine grasslands in relation to general influences on grassland flux rates

Owen et al. (2007) carried out an analysis of eddy covariance data from 18 European and 17 North American and Asian sites, including 3 European grasslands and 4 American grasslands, and applying the same models as used in this study. Unpublished studies to date in our research group have included analysis of 2 additional European grasslands and 2 additional American grasslands. Among these sites observed via eddy covariance methodology, differences of the type described here for alpine grasslands can also be recognized. In particular, fertilized European meadows and those with grazing cattle have high maximum values for $(\beta + \gamma)_{2000}$ ($>35 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and $V_{cuptake1^*}$ ($>100 \mu\text{mol m}^{-2} \text{ s}^{-1}$). An extensively used (lightly fertilized, no grazing) meadow at Grillenburg, Germany (Fig. 8A) as well as a far northern grassland at Jokioinen, Finland exhibit characteristics more similar to the group of high elevation alpine sites

$((\beta + \gamma)_{2000} < 26 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $V_{\text{cuptake1}^*} < 70 \mu\text{mol m}^{-2} \text{s}^{-1}$). All American sites fall into this second category and appear to be relatively natural rather than managed sites, e.g., shortgrass prairie at Lethbridge, Alberta; an abandoned field at Duke University; natural grassland at Fort Peck, Montana, etc. Gilmanov et al. (2007) provided a survey of gas exchange response for 20 European grasslands studied in the European projects focusing on ecosystem carbon balances (GREEN-GRASS, CARBOMONT and CarboEurope). Most sites exhibited flux rates similar to the low elevation alpine sites described here. A very low maximum photosynthetic uptake capacity, similar to the high elevation sites, was found only at a single site in Portugal (Tolja). The observations at Tolja were made during cold winter period of 2004 and during spring 2005, which was an extreme drought year that stunted and then eventually killed the grass vegetation.

We conclude that our group of ‘high elevation’ alpine grasslands exhibit characteristics indicative either of stress or a shift in ecosystem function (for example, nitrogen cycling) as compared to the ‘more average’ group of ‘low elevation’ alpine managed sites. A similar tendency toward reduced flux rates probably applies to natural American grasslands, lowland European grasslands subjected to cold temperature stress and limited water availability, and Central European grasslands with low levels of management intervention, e.g., fertilization. As in the current study for low elevation grasslands (cf. Schönau, Hirschengarten, and Stubai Valley meadows at 1000 and 1750 m in Fig. 3), Owen et al. (2007) found seasonal trends in $(\beta + \gamma)_{2000}$ and V_{cuptake1^*} at some sites, which indicated a slow reduction in photosynthetic capacity in grasslands during the late season even when LAI development reached the same high levels. Grub et al. (1997) found in the case of highly fertilized hay meadows in Switzerland, that seasonal decreases in leaf N content and increases in specific leaf weight occurred. They suggested that such changes could be related to changes in grassland species composition. Better documentation of leaf structural and chemical characteristics (N content as a minimum) is needed in future studies.

4.3. Chamber versus eddy covariance based estimates of model parameters

The parameter estimates obtained by Owen et al. (2007) for grassland sites monitored via eddy covariance methodology agree in general with results for the alpine grasslands obtained with chamber measurements (Section 4.2). Nevertheless, we

reanalyzed data from several of the sites on a daily basis to obtain parameter estimates that are best comparable to those from our measurement campaigns in the Alps. Direct comparison on a short-term basis proves quite difficult, since expected light response curves for ecosystem CO₂ exchange as in Fig. 1 often do not occur, rather linear responses or totally scattered data may be observed. This is easy to understand, since the footprint area during such measurements continually changes and local light conditions at the measurement tower are not always those found within the footprint area. Pooling data for longer periods masks these problems and allows stable model inversions and parameter determinations as illustrated for V_{cuptake1^*} for the meadow at Grillenburg, Germany near Dresden in Fig. 8A (results from Owen et al., 2007). To examine short-term response and to relate parameters to observed temperature and LAI as in Figs. 6 and 7, much more extensive filtering of the data was required. We focused our effort on measurements obtained during summer 2004 in Grillenburg between Day of Year (DOY) 150–290 (May 29 to October 16. This period was chosen, since it was similar to the periods measured in the Alps, we had intensively sampled above- and belowground biomass and LAI, and we were often in the field to observe conditions at first hand.

Well-defined light response curves occurred on only 49 days of the 140-day period examined. These 49 days, in any case a greater number than obtained with chambers at an individual site, were utilized for determination of α , β , and γ with the empirical model, and V_{cuptake1^*} after flux separation with the physiological model (see Owen et al., 2007). All half-hour measurements during the light period were used, LAI was extrapolated from periodic harvests, data for 2 weeks after each harvest were eliminated, and air temperature was evaluated as the mean value during the daylight period. The results for $(\beta + \gamma)_{2000}$ as a function of temperature and LAI are illustrated in Fig. 8B, while the surfaces for other parameters are described in Table 12. The surface shown in Fig. 8B is similar and intermediate to those shown for $(\beta + \gamma)_{2000}$ in Fig. 6. As seen from Table 12, γ was not dependent on temperature or LAI. The seasonal course predicted for V_{cuptake1^*} on a 1-day basis paralleled roughly that shown in Fig. 8A on a 10-day basis. For the selected time period and by eliminating 2 weeks of confusing response after harvest, one can see from Fig. 8A that V_{cuptake1^*} should be relatively constant (as in Table 12). The decrease in V_{cuptake1^*} with LAI (Table 12) may be interpreted as spurious and is probably caused by other seasonal changes. These conclusions are based on 49 days of

Table 12 – Coefficients and statistics of the multiple linear regression $Y = a(\text{LAI}) + b(T) + c$ applied in the analysis of model parameters derived from the Grillenberg, Germany meadow during 2004 and with parameter estimates obtained on a daily basis from eddy covariance flux measurements

	Y		a	b	c	R ²
Grillenberg, 2004	$(\beta + \gamma)_{2000}$	T_{air}	3.97***	0.40*	1.59	0.36
	γ	T_{air}	−0.40	0.05	6.17**	0.04
	V_{cuptake1^*}	T_{air}	−5.56**	0.13	61.84***	0.19

* Significant at P = 0.05.
 ** Significant at P = 0.01.
 *** Significant at P = 0.001.

lower quality data, at least with respect to the expected response behavior of the grassland. The R^2 values obtained in empirical model inversions were in 50% of the cases between 0.8 and 0.9, and in 30% of the cases lower than 0.8.

We conclude from the comparisons among sites and over time at particular sites: (1) that model inversions provide us with a useful tool for going beyond flux observations to eventually define the links between field gas exchange behavior of vegetation and phenomena related to physiological regulation, (2) that inversion studies with both empirical and process-based models are useful, since the first model type remains closer to the observed data and describes patterns, while the second model type allows formulation of hypotheses to explain these patterns, (3) that chamber measurements should not be neglected in ongoing studies of ecosystem carbon balances, and (4) that the conclusions in the current paper represent only a first step in achieving a better comparative understanding of CO_2 flux observations in grasslands via model inversions.

Especially important is the last point. The determined model parameters and response surfaces depend on whether appropriate assumptions have been used in the model inversion procedures, which include assumed temperature functions, assumed conversions for harvested biomass to LAI, assumed leaf angles and clumping, etc. At this time, we cannot be confident that these assumptions apply equally well to all campaigns, all plots and vegetation stands, and to different ecosystem gas exchange measurement methods. Simple differences in the methods to determine LAI may contribute to large differences in V_{cuptake1}^* and subsequent misleading interpretations. Much remains to be learned about the sensitivity of the procedures and their application. Nevertheless, it is encouraging in the context of relating the empirical parameter $(\beta + \gamma)_{2000}$ of the hyperbolic light response model (which is independent of these assumptions) to V_{cuptake1}^* , that the correlation obtained from eddy covariance grassland sites on two continents by Owen et al. (2007; $V_{\text{cuptake1}}^* = 3.19 (\beta + \gamma)_{2000} + 2.28$) is very similar to that reported in Fig. 4.

The chamber studies at alpine meadow sites provide information upon which new hypotheses may be formulated concerning the ordering of grassland types with respect to gas exchange characteristics and potentially carbon flows. Since the same methodology was applied at all sites, our results do show that substantial difference in processes occur at the so-called “low” and “high” elevation grassland sites described in the Alps, supporting conclusions drawn by Tappeiner et al. (1998), Bahn et al. (1999) and Tasser et al. (2001). Detailed clarification of the contributions of land use management, climate stress, nitrogen availability and plant community dynamics to the observed differences in gas exchange potential will require further field studies. Frequency of occurrence of these critical factors in a spatial context will determine whether one can actually refer over the long-term to ‘high’ versus ‘low’ elevation alpine grasslands, or whether new definitions are required. The apparent difference in grassland types is important to understand when attempting to develop a landscape level, regional level or continental scale evaluation of water and carbon balances. However, only with a better explanation as to when the reduced flux rates occur can

we hope to appropriately generalize the results within the framework of spatial models for alpine mountain regions.

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