

Contents lists available at ScienceDirect

Global and Planetary Change



journal homepage: www.elsevier.com/locate/gloplacha

Influences of changing land use and CO₂ concentration on ecosystem and landscape level carbon and water balances in mountainous terrain of the Stubai Valley, Austria

J. Tenhunen ^{a,*}, R. Geyer ^a, S. Adiku ^{a,b}, M. Reichstein ^{a,c}, U. Tappeiner ^d, M. Bahn ^d, A. Cernusca ^d, N.Q. Dinh ^a, O. Kolcun ^a, A. Lohila ^e, D. Otieno ^a, M. Schmidt ^a, M. Schmitt ^d, Q. Wang ^{a,f}, M. Wartinger ^a, G. Wohlfahrt ^d

^a Department of Plant Ecology, University of Bayreuth, 95440 Bayreuth, Germany

^b Department of Soil Science, University of Ghana, Legon, Accra, Ghana

^c Max-Planck-Institute for Biogeochemistry, Hans-Knöll-Str. 10, 07745 Jena, Germany

^d Institute of Ecology, University of Innsbruck, Sternwartestr. 15, Innsbruck, Austria

^e Finnish Meteorological Institute, Air Quality Research, Helsinki, Finland

^f Department of Silviculture, Shizuoka University, Ohya 836, Shizuoka 422-8529, Japan

ARTICLE INFO

Article history: Accepted 8 February 2008 Available online 3 January 2009

Keywords: landscape simulation mountain ecology complex terrain net ecosystem exchange spruce forest sapflow transpiration grasslands alpine meadows up-scaling land use change

ABSTRACT

A process-based spatial simulation model was used to estimate gross primary production, ecosystem respiration, net ecosystem CO_2 exchange and water use by the vegetation in Stubai Valley, Austria at landscape scale. The simulations were run for individual years from early spring to late fall, providing estimates in grasslands for carbon gain, biomass and leaf area development, allocation of photoproducts to the below ground ecosystem compartment, and water use. In the case of evergreen coniferous forests, gas exchange is estimated, but spatial simulation of growth over the single annual cycles is not included. Spatial parameterization of the model is derived for forest LAI based on remote sensing, for soil characteristics by generalization from spatial surveys and for climate drivers from observations at monitoring stations along the elevation gradient and from modelling of incident radiation in complex terrain.

Validation of the model was carried out at point scale, and was based on comparison of model output at selected locations with observations along elevation gradients in Stubai Valley and Berchtesgaden National Park, Germany as well as with known trends in ecosystem response documented in the literature. The utility of the model for describing long-term changes in carbon and water balances at landscape scale is demonstrated in the context of land use change that occurred between 1861 and 2002 in Stubai Valley. During this period, coniferous forest increased in extent by ca. 11% of the vegetated area of 1861, primarily in the subalpine zone. Managed grassland decreased by 46%, while abandoned grassland and natural alpine mats increased by 14 and 11%, respectively.

At point scale, the formulated model predicts higher canopy conductance in 1861 due to lower atmospheric CO_2 concentration which opens stomata. As a result, water use at point scale decreased by ca. 8% in 2002 in the valley bottoms versus 10% at tree line. At landscape level, the decrease in water use by vegetation in 2002 was predicted to be twice as high (ca. 17%) due to increase in subalpine forest, reduction of managed grassland in the valley and on slopes, as well as abandonment of grassland which results in natural succession. Net ecosystem CO_2 exchange (NEE) was predicted to increase (become more negative) at point scale depending on vegetation type by 10 to 20% in 2002 due to increasing atmospheric CO₂ concentration. However, due to the shift from grassland to forest and natural vegetation, landscape level CO₂ exchange did not change. As a result of land use change, the export of carbon in harvested biomass in 2002 was estimated at only 30% of that in 1861. While the need for further validation of model assumptions is recognized. especially changes in ecosystem behavior with changing atmospheric CO₂ concentration, the model analysis indicates a long-term reduction in water use by vegetation and a shift in ecosystem services. The results provide a case study, where land use change may compensate or override the influences of increasing atmospheric CO₂ concentration, maintaining a relatively constant NEE in present time period simulations as compared to 1861, as well as reducing export of carbon from the alpine landscape of Stubai Valley. Use of the model in evaluation of scenarios of future land use change and in relation to vulnerability of ecosystem services are discussed.

© 2009 Elsevier B.V. All rights reserved.

* Corresponding author. Tel.: +49 921 552570; fax: +49 921 552564. *E-mail address:* John.Tenhunen@uni-Bayreuth.de (J. Tenhunen).

0921-8181/\$ - see front matter © 2009 Elsevier B.V. All rights reserved. doi:10.1016/j.gloplacha.2008.12.010

1. Introduction

Mountain regions have been referred to as "Water towers of the 21st century" (Mountain Agenda, 1998), thus, emphasizing that usually precipitation increases rapidly with elevation, water balances in mountain areas are positive, large runoff occurs, and natural water storage is found in mountains as snowfields and glaciers. It is estimated that mountain regions provide 60 to 95% of useful water to human populations, supplying 214 river basins comprising 50% of the land surface. The impacts of human activities in mountain areas can be transmitted to large areas and influence large populations via the hydrological link between upland and lowland areas. The political and social ramifications of land use change in mountain regions, therefore, are large, since the major river basins fed by mountain streams are in most cases shared by more than one country (IGBP, 1997).

The importance of integrated ecosystem research in mountain areas provided the focus of the UNESCO programme "Man and the Biosphere" (MAB). MAB set goals to 1) protect and maintain terrestrial ecosystems that were threatened by intensification of economic development and 2) elucidate the ways in which man had adapted production systems to special environments, e.g., in order to live in high mountain regions. The German contribution (MAB programme area 6 related to "Man's Influence on High Mountain Ecosystems") was devoted to applied landscape ecology, with the intention to apply new approaches in landscape analysis at the Berchtesgaden National Park (founded in 1978 in southeast Bavaria; altitude variation from ca. 603 to 2713 m; 210 km² area). A second cluster of ecosystem research activity developed through exchange of information and ideas between groups working in the Alps in Berchtesgaden, in Austria, and in Switzerland. The task of the programme to facilitate sustainable protection of natural resources required a systematic approach which attempted to combine scientific, economic, social, ethical and cultural perspectives (Erdmann and Nauber, 1995).

In MAB-6, ecological modelling was confronted with the major task of coping with ecosystem process complexity along strong climate gradients in the Alps, but also with spatial and temporal heterogeneity. In Berchtesgaden, the intent was to obtain an overall assessment of water balance for the national park (as a critical longterm management component) based on process information observed at key locations, on generalization in space using a Geographical Information System (GIS), and on simulations of time dependent behavior with dynamic ecosystem models (Haber et al., 1983; Tobias, 1991). The overall tool was intended to provide new potentials for examining scenarios of land use change that result from shifts in socio-economic driving forces.

While progress towards the goals defined within MAB has been made (Köppel, 1995 in the case of Berchtesgaden), the complexity due to terrain and the multiple responses of ecosystems along strong gradients in the Alps has inhibited the development of synthetic approaches. The continued effort reported in this paper, exploits data bases from two long-term research sites, namely Berchtesgaden National Park and Stubai Valley, Austria near Innsbruck, to develop a carbon and water balance model applicable at landscape scale and useful for the evaluation of historical land use change as well as future scenarios. In this context, the simulation model developed within the EU Project CARBOMONT (Effects of land-use changes on sources, sinks and fluxes of carbon in European mountain areas; http://carbomont. uibk.ac.at) is viewed as a tool for providing information on ecosystem services related to carbon and water balances to land use planners and other stakeholder groups.

Over the past 150 years, a massive reduction of agricultural land use has taken place in the Alps, particularly in previously managed areas that have become unfavourable for economic exploitation (Tappeiner et al., 2003, 2006). In Stubai Valley, large pasture areas at high elevation were maintained for summer grazing during 1860 and forest was restricted to the steepest slopes. By 1950 and in subsequent decades, a tendency toward reduced management and less intensive grazing can be recognized, and by 2003 ca. 70% of previously utilized areas were abandoned. The abandoned areas are changing via succession to shrublands and young forest stands. Since World War II, progressive change in land use has occurred in even more advantageous locations, with arable land on slopes being converted to meadows or used for expansion of settlements. While Stubai Valley represents a type of 'standard region' in the context of land use (meadow and forest elements integrated with a tourism base) and land use change in the Alps (cf. Tappeiner et al., 2006), accelerated land use change is shaping landscape structure in many mountain regions of the globe. Even though it is widely acknowledged that land use change is the most dominant component of global change with respect to impacts on terrestrial ecosystems, few studies in complex landscapes have so far attempted to quantify the effect of land use change on biogeochemical cycles. In this context, the objective of the present study is to assess effects of land use change as well as atmospheric CO₂ concentration on gas exchange in a complex landscape which has undergone conspicuous land use change over the past 150 years.

The influence of land use on carbon and water balances of mountainous terrain is determined by the complex behavior of ecosystems along topographic and climate gradients and their response to management practices. To assess such landscape response, a process-based spatial simulation model (PIXGRO) was developed that provides estimates of gross primary production (GPP), ecosystem respiration (Reco), net ecosystem CO₂ exchange (NEE) and water use by the vegetation in Stubai Valley, Austria. The model takes into account the strong influences of relief on radiation input, temperature and humidity, and as far as possible from existing data, the shifts in ecosystem processes along elevation gradients that have been documented. While the model is one-dimensional and applied across landscape maps, it nevertheless provides new insight and a new perspective, since assembling the required data bases for demonstration areas in complex terrain and interpreting ecosystem response in a spatial context remains extremely difficult.

2. Materials and methods

2.1. Site descriptions

The described modeling requires a catalog of information on topography, climate, soils, and vegetation processes. Strong gradients in radiation, temperature, humidity, precipitation and CO₂ pressure occur in the mountain valleys of the Alps. Leaf photosynthesis and respiration, stomatal response, both wood and ecosystem respiration, season length and phenology, carbon allocation, reproductive potential, population dynamics, soil temperature regime, nutrient availability and N-cycling, and microbial activity are among the processes that have been documented to change significantly with elevation in mountain regions (Tranquillini, 1979; Larcher, 2003; Körner, 2003). Two long-term study areas in the Alps provide adequate information to permit formulation of a first version landscape level model of ecosystem carbon and water balances. The primary site which has been studied in a number of European projects is in Stubai Valley near Innsbruck, Austria (Fig. 1A). Additional supporting information and validation of model components was carried out in the Berchtesgaden National Park, Germany (Fig. 1B). Similar climate, vegetation and topography occur at both locations.

2.1.1. Stubai Valley

Stubai Valley is located southwest of the city of Innsbruck between longitude 11° 6' to 11° 25' E and latitude 46° 55' to 47° 15' N with a range in altitude from ca. 660 m to 3450 m (see Figs. 1A and 4B). The average annual air temperature is 6.3 °C at valley sites and ca. 3.0 °C at



Fig. 1. Location of the study sites in the Alps (Insert Map – SV and BNP). A: Stubai Valley – SV – southwest of Innsbruck and B: Berchtesgaden National Park – BNP – southwest of Salzburg in the southeast corner of Germany. Labels *X*₀ to *X*₅ and *Y*₀ to *Y*₆ indicate the test and experimental sites for radiation modelling, sapflow studies, and testing of model performance as illustrated in the photographs of Fig. 4 and described in the text.

treeline (near 1900 m). Average precipitation at University of Innsbruck meteorological stations was estimated at 850 mm in the valley and ca. 1100 mm at treeline. The vegetation is a mosaic of Norway spruce (*Picea abies*) dominated forest and grasslands, with forest stands of *Larix decidua* prevalent at treeline. Deciduous forest stands of *Salix* sp., *Alnus viridis* and *Sorbus aucuparia* are locally important.

The grasslands differ with management intensity, including intensive meadow sites with high fertilization (*Trisetetum flavescentis* community) for hay production during 2 to 3 harvests in summer, extensive meadow sites with low fertilization (Sieversio–Nardetum strictae community) for hay production at high elevation which are mowed at the end of the growing season in late July or in August, managed pastures at and above treeline (Seslerio–Caricetum community), and abandoned pastures and meadows that are undergoing succession with invasion by *Calluna vulgaris*, other shrubs and tree seedlings. Natural alpine grassland mats occur at locations above the managed grasslands.

2.1.2. Berchtesgaden

The Berchtesgaden National Park (210 km²) was established in 1978 by decree of the Bavarian government. It is located in southeastern Germany between longitude 12°47′ and 13°05′ E and latitude 47°27′ and 47°45 N, and borders on Austria's province of Salzburg (Figs. 1B and 4A). In 1990, the park became a UNESCO Biosphere Reserve. The dominant bed-rock in this region is limestone. The altitudes in the Berchtesgaden National Park range from 603 m at the lowland lake Königssee to 2713 m at the summit of the Watzmann Mountain (see Fig. 4A). The mean annual temperature ranges, depending on altitude, from +7 °C (at Königssee) to -2 °C on the Watzmann summit (2713 m). Annual precipitation varies between 1500 and 2200 mm (Berchtesgaden National Park Administration, pers. communication).

Mixed mountain forest occurs up to 1400 m, although this has been replaced over centuries by planted Norway spruce (*P. abies*) due to demands for wood by the local salt producing industry. The subalpine zone at 1400 to 2000 m includes spruce-larch forests (*P. abies* and *L. decidua*). Above 1700 m, dwarf pines (*Pinus mugo*) and alpine meadows prevail. Sapflow studies were carried out on *P. abies* and *P. mugo* (Kolcun, 2005). The data provide important calibration for the influences of elevation on forest gas exchange. Additionally, the development and testing of the radiation model required for mountainous terrain (Wang et al., 2005, 2006) was carried out in Berchtesgaden National Park.

2.2. Simulation model PIXGRO for CO₂ and H₂O fluxes and balances

A true landscape model for CO_2 and H_2O balances in alpine regions should quantify lateral exchanges along topographic gradients due to atmospheric and hydrological transport as well as vertical exchanges. A complete analysis in this context is beyond the scope of the current modelling work. In this first step toward developing a landscape model, heterogeneity in the response of different ecosystem types subjected to strong gradients in climate is considered. Since large differences in land use have occurred over ca. 150 years in Stubai Valley, even a one dimensional treatment of vegetation/atmosphere exchanges and quantifying changes in biomass pools provides new important insights. Furthermore, hydrological flows are impossible to evaluate, since limestone substrates dominate in the areas studied. Nevertheless, estimation of water use by the vegetation provides useful information in terms of catchment hydrological balances (see discussion).

The PIXGRO model structure may be summarized via the components illustrated in Fig. 2. Canopy conductance, canopy transpiration, evapotranspiration, and gross primary production (GPP) are calculated with the vertically-layered, core process model PROXEL_{NEE} (Reichstein, 2001; Reichstein et al., 2003). Since meteorological data along the elevation gradients are only slowly becoming available for longer periods, the first version model makes estimates of vegetation response only for a single season with a known distribution of ecosystem types. In this context, forested areas have a static structure, but grasslands change in aboveground structure during the season as described by classical growth algorithms in the sub-model CGRO. Thus, PROXEL_{NEE} is a sub-model included into the model PIXGRO (Fig. 2), i.e., determines (along with partitioning and whole plant respiration estimates in CGRO) the seasonal development of leaf area



Fig. 2. Schematic diagram of the PIXGRO model, indicating the processes included in the sub-models PROXEL_{NEE} (Reichstein, 2001; Reichstein et al., 2003) and CGRO (Adiku et al., 2006). Not shown but also included in the model is a complete soil water balance and coupling of soil water status to canopy conductance. No water limitations of vegetation response occurred under the climate conditions experienced in Stubai Valley during 2002. In the Stubai Valley application, PIXGRO is used to estimate the CO₂ and H₂O exchange of grasslands along with growth and development (i.e., time dependent changes in biomass and LAI). Additionally, as shown, the PROXEL_{NEE} component of PIXGRO is used together with a sub-model for ecosystem respiration (Reco) to estimate GPP, NEE and water use by forests.

index (LAI) and biomass of grassland communities (cf. Adiku et al., 2006). Also included in the model is a soil water balance, coupling of soil water status to canopy conductance, and routines to estimate canopy water use (Reichstein, 2001; Reichstein et al., 2003).

2.3. PIXGRO application to grasslands in Stubai Valley

2.3.1. Calibration of ecosystem gas exchange

The algorithms included into the model have been described previously with validation for spring barley (Adiku et al., 2006). Extension of the model to grasslands brings with it additional complexity due to the inclusion of multiple species and perennial plants. The model does not address these points specifically, but captures the influences of these traits on ecosystem fluxes, beginning with a focus on GPP and aboveground structural development. Sites with detailed information on gas exchange (NEE) and aboveground carbon pools were used to aid in model formulation and parameterization. The sites included three locations within Stubai Valley (intensive meadow with high fertilization, extensive meadow with low fertilization and an abandoned meadow), a grassland site in Jokioinen, Finland (with eddy covariance monitoring and canopy development), and additional sites in the Fichtelgebirge region of Germany (with only monitoring of time dependent changes in biomass and LAI as validation data sets).

The simulation of gross photosynthesis in PROXEL_{NEE} follows Farquhar and von Caemmerer (1982) as modified for practical field applications by Harley and Tenhunen (1991). Canopy gas exchange rates are obtained by integrating the leaf response over canopy layers and along microclimate gradients. Leaf parameters were obtained by inversion of the canopy model with respect to grassland gas exchange measurements obtained either from eddy covariance or ecosystem chamber studies and according to the methodologies outlined by Wang et al. (2003), Reichstein et al. (2006), Owen et al. (2007) and Li et al. (2008). Eddy covariance data sets used for parameterization are described in Wohlfahrt et al. (2005), Owen et al. (2007) and Lohila et al. (2004). The procedures provided estimates for physiological parameterization of the fertilized intensive meadow sites, since it is at such locations that eddy covariance is measured.

Gas exchange was also measured as NEE using manually operated transparent canopy chambers in a closed system (cf. Wohlfahrt et al., 2005; Li et al., 2008). Using extensions, chamber height was adjusted to canopy height, which was up to 100 cm on the meadows before harvest. During measurements, the chambers were placed on frames made of polyethylene, which had been inserted into the ground at the beginning of the vegetation period. A gas tight seal between chamber and frame was accomplished with a compressable rubber gasket. Circulation of air within the chamber was provided by fans yielding a wind speed of 1.2 m s⁻¹. Change in chamber CO₂ concentration over time was assessed with a portable, battery operated gas analyzer (Li 820, LiCor). By mounting cool packs on the back side of the chamber, temperature during measurements could be stabilised within a mean of 2 °C relative to ambient. Data obtained with the canopy gas exchange system provided results for NEE that were closely correlated to NEE measured by an eddy covariance system at the intensive meadow site in Stubai Valley. Use of a darkened chamber provided direct estimates of ecosystem respiration at different times of day. From the Reco measurements, estimates could be made for GPP. By comparing observations at three sites (intensive, extensive and abandoned meadows), appropriate adjustments in physiological capacity of the canopy model (parameter Vc_{max}) were made as recorded in Table 1 (see also Li et al., 2008).

2.3.2. Calibration of grassland growth model

The CGRO component of PIXGRO was parameterized using harvest data from the intensively managed meadow (960 m elevation) and the abandoned meadow site (1970 m) in Stubai Valley. The simulated fixed CO_2 from PROXEL_{NEE} is converted to carbohydrate and then to dry matter in CGRO by subtracting the growth and maintenance respiration losses according to Jones (1991). Dry matter is partitioned to leaves, stem, and roots according to partitioning coefficients (fixed percentages) that change with the stage of plant development. The coefficients were estimated to account for changes in green leaf and

Table 1

Values and definition of key PIXGRO parameters for grassland. Additional information regarding the algorithms applied are provided in Adiku et al. (2006) and Harley and Tenhunen (1991). Respiration factors are discussed by lones (1991) and partitioning by Charles-Edwards et al. (1986). Parameters for spruce forest are discussed by Falge et al. (2003) and the elevation dependence by Kolcun (2005).

Parameter	Definition		Value	Unit
J _{max}	Electron transport	capacity at 25 °C	21.7	μ mol m ⁻² s ⁻¹
Vc _{max}	Carboxylation capa	city at 25 °C	25-60 ^a	μ mol m ⁻² s ⁻¹
Rd	Respiratory capacit	y at 25 °C	2.1	μ mol m ⁻² s ⁻¹
Ε	Growth respiration	/conversion factor	0.70	g (tissue)/g (CH ₂ O)
Km	Maintenance respir	ation constant	0.0006	g CH ₂ O/g tissue-h
b	Maintenance respir	ation coefficient	0.0693	°C ⁻¹
SLA	Specific leaf area		200	cm ² /g
V	Leaf area senescen	e factor	0.001	cm ² /hr
LFL	Leaf loss rate		0.002	h ⁻¹
STL	Stem loss rate		0.002	h ⁻¹
DL	Dead material loss	rate	0.00004	h ⁻¹ °C ⁻¹
Phenophase threshold	1: Greening		40	°C day above 0 °C
×	2 Regrowth/Vegeta	tive	1000	°C day above 0 °C
	3: Flowering		1500	°C day above 0 °C
	4. Dormancy	4. Dormancy		°C day above 0 °C
Partitioning coefficients dependent of	on plant organ and crop stage (fra	tion of fixed carbohydrate)		
Phenophase	1	2	3	4
Leaf	0	0.30	0.30	0
Stem	0	0.40	0.25	0
Roots	0	0.30	0.40	0
^a The parameter value was 25 for	abandoned meadows and 60 for m	anaged (fertilized) meadows and p	roduces the differences in response sho	wn in Figs 9 and 10

stem dry weight at the intensive meadow and fallow meadow sites in Stubai Valley, with the remainder of fixed carbon allocated to roots and root exudation.

We assumed that dry matter is partitioned to leaves, stems and roots but not to reproductive parts. Only four developmental stages are defined for the grass vegetation, namely (1) the greening period, (2) the regrowth/vegetative stage, (3) flowering and (4) dormancy. The greening period is defined as a short period that enables grass to resume photosynthetic activity when environmental conditions become favorable. Intensive meadows basically remain in the vegetative phase, and their development is reset to the beginning of the vegetative stage each time mowing occurs during summer. We assume that at the end of the season, intensive meadows enter into a dormancy phase without going through a flowering stage.

The fallow grass and natural alpine grasslands at high elevation, however, exhibit all of the developmental stages and reveal characteristics that would occur in grassland in general if there were no harvesting. At single sites, developmental stage may be estimated according to the summed degree-days above a base temperature of zero degrees (Charles-Edwards et al., 1986). This correlative method breaks down in the current application, since grasslands at higher elevation are slow to reach defined thresholds for transition between stages, i.e., heat sums increase ever more slowly as one moves higher and the vegetation remains in the vegetative phase even when stands at lower elevation begin to senesce. Lacking information, a single date for the onset of senescence was chosen in correspondence with the abandoned meadow measurement site. Transition to stage 3 and senescence began for abandoned and natural alpine grasslands on August 3. From this time on, loss of leaves and stems from the aboveground biomass pool occurred.

Management variables included in the model are mowing dates along with postcut-biomass and postcut-LAI, which specify the biomass and LAI of the field just after a mowing event. From observations in Stubai Valley, 50% of postcut-biomass is dead while the remainder is green. Remaining green dry weight was assumed to be 50% leaves and 50% stems. Times of cutting of the intensive and extensive meadows were the same for all locations and were based on the field observations at the research sites during 2002.

2.4. PIXGRO application to forests in Stubai Valley

The PIXGRO model for forests simplifies to the description for PROXEL_{NEE} submodel as described above, since growth is not considered. At the valley floor, we assumed that Norway spruce forest functioned in a similar fashion to lowland spruce forest studied at Tharandt Forest, Germany (Bernhofer et al., 2003; Owen et al., 2007). Physiological capacity of the spruce forest needles was decreased along the elevation gradient (similar to that discussed above for grasslands) in order to obtain reductions in canopy water loss compatible with the measurements of Kolcun (2005, see results section) in Berchtesgaden National Park obtained via sapflow methodology. The relationship of stomatal conductance to assimilation as described by the Ball et al. (1987) approach and applied according to Harley and Tenhunen (1991) remained constant for all locations of the Stubai Valley landscape.

2.5. Spatial framework of the simulations

The final values for parameters used in the simulations are given in Table 1. For each time step in the simulation, PIXGRO results were obtained and stored for each 100×100 m pixel (considered homogeneous) of the landscape maps. Distribution of ecosystem types was determined for 1861 from the Franzian Cartographical Register (second cartographical register of the patrimonial lands of the Habsburg family from 1806 to 1869, 1:25,000) and for 2002 by interpretation of aerial photography (orthophotos 1:10000; Cernusca et al., 1999). Determination of land cover change is based on an integrated-layer model, whereby information on the first landscape registration provides a comparative basis for the next registration, and where each landscape element was examined for changes in spatial extent. The accuracy of the maps is viewed as quite high in the valley area, where centuries of competition for space have provided clear documentation of boundaries and their shifts. The clear definition of boundaries for 1861 at high elevation is less certain, since lower economic gain coupled to the difficulties of working in mountainous terrain may have influenced the available maps.

Land use was simplified to include two categories of forests (montane and subalpine conifers), five categories of grassland (very

Fig. 3. Simplified representation of land use in Stubai Valley during 1861 and 2002 as used in the simulations, including two categories of forests (montane and subalpine conifers), five categories of grassland (very intensive, intensive, extensive, abandoned, and natural alpine meadows), and cover by rock, permanent snow and ice, or urban activities. The vertical direction indicates north on the maps.

intensive, intensive, extensive, former natural or abandoned, and natural alpine meadows), and cover by water, rock, permanent snow or urban activities. The breakdown into area covered by each vegetation type of Fig. 3 is given in Table 2. As seen from the table, the area for intensive and extensive meadows decreased greatly from 1861 to 2002 and contributed to the large increases in subalpine forest, abandoned meadows and natural alpine grass mats. Additionally, large increases in bare rock and decreases in cover by snow and ice occurred.

The digital elevation model used in the simulations was obtained from the Government Surveying Agency of Austria. The soils map is unverified but based on extensive gridded surveys in similar terrain in the Berchtesgaden National Park. Basic relationships between soil types and topography from the Berchtesgaden studies were used to hypothetically map soil type and depth within the topography of Stubai Valley. Inaccuracies in the soil component are considered unimportant in the current simulations, since precipitation input is high, i.e., there are currently no critical feedbacks that link to the soil.

The spatial map for LAI of forests, required to estimate exchange fluxes of individual pixels, was determined via NDVI determined from Landsat Thematic Mapper scenes obtained during 2002. Regression equations describing the LAI to NDVI relationship were determined from ground-based estimates of forest stand LAI within test areas of both Berchtesgaden National Park and Stubai Valley (areas for which LAI estimates are available from forest inventory combined with allometric relationships). The regressions (Berchtesgaden: LAI = 45.1 NDVI – 25.7, R^2 = 0.89; Stubai Valley: LAI = 42.1 NDVI – 22.5, R^2 = 0.89; cf. Bobeva, 2003), which agreed well for spruce forest at the two locations for LAI 2 through 8, were then used to derive the LAI map for the entire Stubai Valley, assuming forest cover to be exclusively Norway spruce.

Elevation dependent gradients in climate factors (e.g., temperature, humidity, etc.) were estimated by linear extrapolation between measurement stations installed on both north and south facing slopes in Stubai Valley. Precipitation was assumed uniform over the catchment at levels recorded at the Neustift valley bottom site. While this is unrealistic, precipitation is high and soil water availability does not influence vegetation response in the simulations. Radiation input is elevation and topography dependent as determined via the modelling approach for mountainous terrain described by Wang et al. (2005, 2006; see also Section 2.6). Matrices for all meteorological drivers were prepared previous to simulation runs

Table 2

Land use in Stubai Valley in 1861 and in 2002 distributed among the	e ecosystem types included in the simulations and	bare rock, urban areas and snow covered are
---	---	---

	Area 1861 (km ²)	Area 2002 (km ²)	Change in area (km ²)	% change related to s	ame class in 1861	% change related to total vegetated in 1861
Montane coniferous forest	18.3	19.8	1.5	8		1
Subalpine coniferous forest	27.9	43.2	15.3	55		10
Very intensive meadow	8.7	7.9	-0.9	- 10		-1
Intensive meadow	23.9	2.5	-21.4	-90		- 14
Extensive meadow	55.6	9.1	-46.6	-84		-31
Abandoned meadows	0.0	21.3	21.3	_		14
Alpine mats	17.6	33.8	16.2	92		11
Bare rock	70.1	92.7	22.6			
Urban	0.1	1.3	1.2			
Snow	34.6	25.4	-9.2			
Total	257	257	0			

(estimated in separate routines and stored outside of the model) and are input to the model according to the hourly simulation timestep. Climate drivers provided to the model were identical for the simulation of response during both 1861 and 2002, although atmospheric CO_2 concentration was decreased from 350 µmol mol⁻¹ to 280 µmol mol⁻¹ for the 1861 simulation.

2.6. Parameterization and validation measurements

Two separate sets of experiments were carried out during summer of 2002 in order to characterize differences in (i) grassland gas exchange along with changes in aboveground biomass and LAI and (ii) forest stand gas exchange along elevation gradients in the Alps. In the case of grasslands, gas exchange was measured as net ecosystem carbon dioxide exchange (NEE) and ecosystem respiration (Reco), using eddy covariance methodology at the valley site and manually operated plexiglass chambers as a closed gas exchange system at different sites (Section 2.3.1, Wohlfahrt et al., 2005; Li et al., 2008). In the latter case, measurement campaigns were carried out at sites along the elevation gradient, enclosing replicate ecosystem sections for short periods over the course of several days and assessing response in relation to environmental factors. After measurements, the aboveground biomass was harvested and separated into component pools (leaves, stems, standing dead, etc.). Since simultaneous measurements of water flux cannot be made with the chamber methods, a fixed relationship between leaf stomatal conductance and photosynthesis rate was assumed (Harley and Tenhunen, 1991), allowing calculation of transpiration and water use. The relationship was established in agreement with eddy covariance derived estimates of canopy conductance at grassland sites. Observational data from the Stubai Valley sites were separated into two sets for parameter estimation and site-specific validation. Additional data for parameterization of the growth model CGRO were obtained from grassland eddy covariance studies and observations at Jokioinen, Finland and at sites in the Fichtelgebirge, Germany (Section 2.3.2). The results of data analysis provided parameter sets for PROXEL_{NEE}, with important differences in uptake capacity as well as in carbohydrate partitioning for different grassland categories.

Alternative methods must be used to characterize forest gas exchange response along elevation gradients. Thus, xylem sapflow according to the constant heating method of Granier (1985, 1987) was measured in Norway spruce stands located between 600 and 1400 m and for *P. mugo* at 1750 m in Berchtesgaden National Park during the summer season of 2002 (Kolcun, 2005). The observed strong decline in water use by forest stands with increasing elevation was analyzed and used to parameterize PROXEL_{NEE}. As in the case of grassland gas exchange, the relationship between leaf stomatal conductance and photosynthesis rate was maintained constant and calibrated according to both leaf gas exchange and eddy covariance studies at other sites (cf. Falge et al., 2003).

Fig. 4A illustrates the specific locations at which xylem sapflow studies were carried out in Berchtesgaden National Park (sites X_1, X_2, X_3 and X_5). At all of the sites in Fig. 4A, testing of the radiation model for complex terrain was also carried out. A meteorological base station (indicated as X_0 in Fig. 4A) provides valley floor radiation values, from which the hourly values at other locations were estimated (Wang et al., 2005, 2006). An example of the results for predicted vs. measured

B Stubai Valley Test Site Locations

Fig. 4. A: Specific locations at which xylem sapflow studies and radiation model testing were carried out in Berchtesgaden National Park (sites X_1 through X_5) and the location of the meteorological base station (indicated as X_0). The sites are located on the eastern flank of the Watzmann mountain (2713 m). The Königsee is seen at the center left at elevation 603 m. Mountains in the background are south of the border with Austria. Graphic from H. Franz, Berchtesgaden. B: The intensive research sites for grassland gas exchange in Stubai Valley at locations Y_0 , Y_1 and Y_2 . The meadow at Neustift (Y_0) is the baseline radiation measurement station. Test output was obtained for the locations Y_0 through Y_6 as described in the text. Mountains in the background southern part of the valley are glaciated and increase in elevation to 3450 m.

Fig. 5. Predicted versus measured PPFD input at the baseline station Schönau in Berchtesgaden National Park and at three test sites located on the Watzmann Mountain indicated in Figs. 1 and 4. In general for both PPFD and global radiation, *R*² values were always greater than 0.9 and RMSE remained very low (cf. Wang et al., 2005, 2006).

photosynthetic photon flux density at the base station and 3 sites on the Watzmann Mountain in Berchtesgaden National Park during summer 2002 are illustrated in Fig. 5. In similar fashion, the intensive research sites for grassland gas exchange in Stubai Valley are indicated in Fig. 4B as locations Y_0 , Y_1 and Y_2 . The meadow at Neustift served as the baseline radiation measurement station from which radiation at other locations was estimated according to the Wang et al. model.

Currently, validation of the model at landscape scale has not been undertaken. Rather, results are presented below that demonstrate point scale response at the pixel locations Y_0 through Y_6 in Stubai Valley, e.g., in different land use types, at different elevations, and in forest on south and north facing slopes. The response at these locations is compared to observations from experimental studies.

2.7. Adjustment of vegetation response to atmospheric CO₂ changes

The response of natural grassland ecosystems to atmospheric CO₂ concentrations within the range of interest in this study, e.g. 280 to

Fig. 6. Simulated transpiration from spruce forest pixels located at Y₃ through Y₆ as indicated at treeline and valley locations (see Fig. 4) over the summer season of 2002.

Fig. 7. Simulated seasonal courses for daily GPP, Reco and NEE of spruce forests for the valley (solid circles) site *Y*₃ and the treeline (open triangles) site *Y*₄ (see Fig. 4) during the summer of 2002. The sites have approximately the same exposure and radiation input but differences in temperature as indicated.

350 μ mol mol⁻¹, has been documented by Anderson et al. (2001), Maherali et al. (2002), and Gill et al. (2002). The results of these studies suggest that for C₃ species under increasing CO₂, adequate nitrogen supply to the vegetation is maintained as a result of N pool shifts, leaf level photosynthesis rates increase linearly with increasing CO₂ concentration and stomatal conductance decreases. Whereas additional minor, species-specific adjustments may occur in leaf gas exchange capacities, the average adjustments in multi-species grasslands are currently unknown. Therefore, a single parameterization was used for leaf response and calibrated to whole ecosystem measured gas exchange rates (chamber data and eddy covariance studies mentioned above). With a single parameterization, the Harley and Tenhunen (1991) model behaves in a fashion compatible with the long-term ecosystem 'reduced CO₂ exposure' studies. It was found that both in the natural grassland studies and in simulations with PIXGRO, NPP increases with increasing CO₂ concentration. Reco in the model depends on leaf respiration which varies over time with leaf

Fig. 8. The simulated temperature response of hourly photosynthesis rate with high radiation input at the spruce forest pixels Y_3 (valley site, solid triangles) and Y_4 (treeline, open circles; see Fig. 4) during the summer of 2002.

biomass, but also on soil CO_2 efflux. Microbial respiration is not explicitly modelled in PIXGRO. Therefore, an approximate adjustment was made in Reco based on observations of Gill et al. (2002, 2006; soil respiration rates ca. 80% of 2002 levels for simulations in 1861).

The characteristics of ecosystem response to increasing CO_2 described above depict behavior in which carbon flow *through* the

Fig. 9. Comparison of measured (solid circles) and simulated (open triangles) net ecosystem CO_2 exchange response to incident PPFD for managed (intensive and extensive with differing degrees of fertilization) and abandoned meadows during periods with high values of LAI in summer 2002.

ecosystem increases. A similar response is described for forest trees in Switzerland by Körner et al. (2005) exposed to atmospheric CO_2 concentration of 530 µmol mol⁻¹ versus ambient. Such response at above ambient concentrations may result due to high levels of atmospheric N deposition which support the ecosystem demand and eliminate nitrogen feedback depression of flux rates. Since N deposition has increased over relatively long periods, and again based on the range of CO_2 increase between 1861 and 2002, we have assumed that forest response may reasonably be treated in the same way as for grasslands.

3. Results

3.1. Forest gas exchange

The observed water use by stands along the elevation gradient in the Berchtesgaden National Park (Kolcun, 2005) revealed decreasing canopy gas exchange capacity with increase in elevation, with spruce maximum transpiration rates above 2 mm day⁻¹ at Bartholomä (630 m – X_1 in Fig. 4), maxima of ca. 1.5 mm day⁻¹ at Hirschengarten (1020 m – X_2 in Fig. 4), similar maxima at Seeangerl (1360 m – X_3 in Fig. 4), and lower maxima of ca. 1 mm day⁻¹ in the scrub pine zone at Kederbichl (1720 m – X_5 in Fig. 4). The test pixels Y_3 and Y_4 for spruce forest in Stubai Valley are similarly exposed. The seasonal course for daily simulated transpiration rates for these locations is illustrated in Fig. 6 (top two panels). The PROXEL_{NEE} model reproduces the observed decrease in transpiration as dependent on elevation. While a reduction in transpiration is also simulated for higher elevation sites on north facing slopes (Fig. 6 lower two panels), the magnitude of water use is lower than at south facing locations. While there are no data for direct validation in this case, the response in general is reasonable and occurs due to lower radiation input and lower maximum temperatures on north facing slopes.

The seasonal course for daily GPP, Reco and NEE of spruce forests is illustrated in Fig. 7 for the valley site Y_3 and the treeline site Y_4 . With approximately the same exposure and radiation input, but differences in temperature as indicated in the figure, GPP and Reco decrease with increasing elevation, leading to an overall reduction in NEE. The rates shown are compatible with those reported from eddy covariance studies at low elevation dense conifer sites which include Norway spruce (Bernhofer et al., 2003). The differences from valley to treeline

Fig. 10. Simulated seasonal courses for daily GPP, Reco, NEE and LAI at intensive meadow (Y_0), extensive meadow (Y_1) and abandoned meadow (Y_2) sites as indicated in Fig. 4 during the summer season of 2002. Open circles indicate measured values for LAI from harvests.

reproduce differences observed between the CarboEurope (http:// www.bgc-jena.mpg.de/bgc-processes/ceip/) Norway spruce sites at Tharandt, Germany (average annual temperature = 7.5 °C) and Bily Kriz, Czech Republic (average annual temperature = 5.0 °C). The shifts in carbon gain are similar to assessments along elevation gradients at the Patscherkofel, Austria reported by Pisek and Winkler (1958 as reported in Tranquillini, 1979, Fig. 26). The response of hourly photosynthesis rate of forest stands to temperature is shown in Fig. 8 for periods with high radiation input. The decrease in maximum uptake rates and shift of the optimum to lower temperature reproduces behavior previously observed for individual branches of conifers by Fryer and Ledig (1972 in Tranquillini, 1979, Fig. 24). Thus, the model performance both at stand and branch level is in agreement with observed behavior in gas exchange for coniferous forests along mountain elevation gradients.

3.2. Grassland gas exchange

Measurements of grassland gas exchange were carried out near the locations Y_0 , Y_1 and Y_2 (Fig. 4). Analysis of these data indicated that CO_2 exchange capacities of the vegetation (e.g., leaf capacity for carboxylation and electron transport) of intensive and extensive meadows were similar, while lower CO_2 exchange capacity was found for abandoned meadows (from canopy model inversion studies). The result is interpreted to mean that leaf nitrogen investments for average leaf material decreases in abandoned sites, a conclusion supported in general from harvest data (Bahn et al., 1999; (see also) Li et al., 2008 for discussion). Output from the PIXGRO model for the sites Y_0 , Y_1 and Y_2 was compared

to chamber measurements for several days as summarized in Fig. 9. In such a comparison, exact correspondence cannot be expected since the exact local site conditions will not be reproduced in the model. Differences in grassland stand structure are probable, and chamber measurements are influenced by short-term fluctuations in microclimate, especially momentary local radiation, which are not represented in the general meteorology used to drive the PIXGRO model. Nevertheless, output from the model on measurement days falls within the scatter of observations and reproduces differences between managed (intensive and extensive) and abandoned meadows. At least in the first approximation, we assume that the gas exchange calibration of the model for important grassland types in the Stubai Valley is adequate.

Model output for the seasonal course in daily GPP, Reco and NEE is shown for the sites Y_0 , Y_1 and Y_2 in Fig. 10. The differences in photosynthetic capacity at abandoned sites are apparent. GPP decreases at extensive meadow sites in comparison to intensive meadow sites, since the latter are located in the valley and are subject to more favorable summer temperatures. The lower temperatures at higher elevation also decrease ecosystem respiration. Harvests occurred for all locations of a land use type on the dates observed at experimental sites during 2002. Leaf area index changes along with carbon gain and decreases after harvests to levels found in the field. As seen in the lower set of panels in Fig. 10, leaf area development in the three grassland types is captured well by the model (open circles indicating the observations at harvests). Water use efficiency in the model is based on eddy covariance studies at a number of sites. Thus, water use is also expected to provide a good approximation of spatial differences in evapotranspiration.

Fig. 11. Daily global radiation input, daily average air temperature, simulated gas exchange from the PIXGRO model and LAI mapped at 100 m resolution for June 17, 2002 in Stubai Valley. The vertical direction indicates north on the maps.

Table 3

Summer season values for evapotranspiration (Et) and transpiration for ecosystem types included in the simulations for the years 1861 and 2002. The upper part of the table provides results averaging pixels (e.g., at point scale), the lower part of the table provides data integrated over the catchment for each vegetation type (landscape scale). Also shown in the relative change in Et and transpiration for 2002 in relation to 1861.

	1861		2002		2002/1861	
Point scale	Season Et (mm)	Season transpiration (mm)	Season Et (mm)	Season transpiration (mm)	Et	Transpiration
Montane coniferous forest	181	81	168	77	0.93	0.95
Subalpine coniferous forest	150	53	142	49	0.95	0.92
Very intensive meadow	277	125	270	123	0.97	0.98
Intensive meadow	232	83	236	88	1.02	1.06
Extensive meadow	227	84	225	85	0.99	1.01
Abandoned meadows	Not present	Not present	214	89		
Alpine mats	238	86	239	92	1.00	1.07
Landscape scale	Season Et (10 ⁶ m ³)	Season Transpiration (10 ⁶ m ³)	Season Et (10 ⁶ m ³)	Season Transpiration (10^6 m^3)	Et	Transpiration
Montane coniferous forest	3.31	1.48	3.33	1.52	1.01	1.03
Subalpine coniferous forest	4.18	1.48	6.14	2.13	1.47	1.43
Very intensive meadow	2.42	1.09	2.12	0.97	0.88	0.88
Intensive meadow	5.55	1.99	0.59	0.22	0.11	0.11
Extensive meadow	12.6	4.67	2.04	0.77	0.16	0.16
Abandoned meadows	Not present	Not present	4.55	1.89		
Alpine mats	4.19	1.51	8.09	3.11	1.93	2.06
Total	32.3	12.2	26.8	10.6	0.83	0.87

3.3. Gas exchange of the Stubai Valley landscape

An example of spatial output from the model for Stubai Valley is illustrated in Fig. 11 for key variables on a sunny summer day (June 17) in 2002. Influences of topography on global radiation and the elevation gradient on average daily temperature are apparent. In response to these climate gradients, decreases occur in GPP, Reco, water exchange and LAI at higher locations. More negative NEE values are found in low elevation sites. The time dependent changes on an hourly basis (not shown) are dramatic in response to weather patterns and harvesting events.

Higher atmospheric CO_2 concentration resulted in more closed stomata and higher leaf CO_2 uptake in the 2002 simulation as compared to 1861 and according to the assumed physiology. The resulting influence on transpiration at point scale was an 8% decrease at valley bottom in 2002 and 10% decrease at tree line as compared to 1861. A seasonal trend occurred with lowest change in transpiration in mid-summer (only 8%) but 12% in spring and fall. The average results at point scale given in Table 3 are slightly different. In the comparison tabulated, the average pixel response in gas exchange is sensitive to land use change, since the average pixel for a vegetation type within the catchment in 1861 and 2002 are located at different elevations. In this case, the comparison indicates that average forest water use is reduced by 5 to 8% in 2002, while average water use at grassland locations remains the same. Water use by forest pixels is considerably less than for grassland pixels both in 1861 and 2002, indicating that conversion from grassland to forest strongly influences overall water balance. In the case of CO_2 gas exchange, subalpine coniferous forests exhibit NEE less negative than intensive and extensive meadows. Thus, the increase in forest at high elevation and loss of grasslands at low elevation and on slopes modified the overall carbon balance.

At landscape scale, e.g. for the entire valley, the land use changes indicated in Table 2 reinforce the water savings that occurs due to increased water use efficiency at plot scale, and as described below

Table 4

Summer season average meter square and total catchment values for gross primary production (GPP), ecosystem respiration (Reco) and net ecosystem CO₂ exchange (NEE) obtained in the simulations with landscape distribution of ecosystem types as in 1861 and 2002. Also indicated is the total dry biomass and carbon estimated as removed in harvests from intensive and extensive meadows.

	GPP average (g C m^{-2})	GPP total (metric tons C)	Reco average (g C m ⁻²)	NEE average (g C m ⁻²)	NEE total (metric tons C)	Biomass removed (metric tons d.w.)	C removed (metric tons)
1861							
Montane coniferous forest	865	15800	170	-695	-12700		
Subalpine coniferous forest	637	17800	131	-506	-14100		
Very intensive meadow	798	6970	163	-635	-5550	10200	4100
Intensive meadow	615	14700	106	-509	- 12200	24700	9880
Extensive meadow	538	29900	92	-446	-24800	27500	11000
Abandoned meadows	0	0	0	0	0		
Alpine mats	367	6460	78	-289	-5090		
Total					- 74440	62400	24980
2002							
Montane coniferous forest	1000	19900	223	- 783	- 15500		
Subalpine coniferous forest	722	31200	168	-554	-23900		
Very intensive meadow	901	7070	209	-692	-5430	10400	4150
Intensive meadow	768	1910	159	-609	- 1520	2960	1190
Extensive meadow	665	6020	136	-529	-4790	5230	2090
Abandoned meadows	486	10300	122	-364	-7750		
Alpine mats	447	15100	104	- 343	- 11600		
Total					70490	18590	7430

compensate in several ways for increased GPP in 2002 due to higher atmospheric CO₂ concentration. While total water use by forest vegetation increases due to expansion in subalpine regions, total water use by managed grasslands decreases dramatically (loss of intensive and extensive meadows in the valley and on slopes). The influence of vegetation change together with the influence of physiological differences decreases predicted water use (Et) in 2002 to 83% of 1861, while transpiration decreases to 87%. This occurs despite higher LAI in grasslands at mid-season in 2002. It results from expansion of subalpine forest, reduction of intensively used grassland in the valley and on slopes, expansion of the abandoned meadows and alpine grassland mats into areas previously used as extensive meadows at high elevation (Fig. 3), and reduced stomatal conductance with CO₂ increase. Given that summer water use by the vegetation is reduced overall, one would assume that water yield from the valley might have increased over the time studied, but confirming data are lacking.

The results for carbon exchange are given for the 1861 and 2002 Stubai Valley simulations in Table 4 at both point scale (average values) and landscape scale (total values). Also indicated is the simulated total dry biomass and carbon removed in harvests from intensive and extensive meadows. Average GPP increases in 2002 for all vegetation types due to the stimulation of leaf photosynthesis with higher atmospheric CO₂ concentration. Adjusting for ecosystem respiration according to Gill et al. (2002, 2006) as described in the methods, carbon sequestration as NEE over the summer season increases in 2002 by ca. 10 to 20% on a m² basis over all vegetation types due to increased atmospheric CO₂. However, the shift from grassland to subalpine forest and especially more natural grasslands at high elevation compensated for this, reducing landscape level NEE. Overall landscape CO₂ uptake was predicted not to change between 1861 and 2002. Despite constant landscape CO₂ uptake, much greater flow of carbon went to forests during 2002, such that the estimate for harvested biomass removed from grasslands in 2002 is only 30% of 1861

4. Discussion and conclusions

The importance of examining ecosystem processes at different scales has been recognized for decades, especially as a result of research carried out during the International Biological Program (cf. review by Lenz et al., 2001). This recognition provided the impetus for studies during MAB-6 to assess water balances at landscape scale in alpine terrain of the Berchtesgaden National Park. MAB-6 promoted the development of tools for landscape scale assessments as well as those providing potential for examining scenarios of land use change due to shifts in socio-economic driving forces. These challenges have remained with us in the context of IGBP research and the desire to understand Global Change in the context of resulting human needs (Gitay et al., 2001; Millenium Assessment, 2003; Tappeiner et al., 2006).

The PIXGRO model is designed to aid in bridging the gap between ecosystem process studies and resource management in areas with complex terrain. The model provides spatial estimates of ecosystem and landscape gas exchange as related to land use change along elevation gradients for the intensive study site in Stubai Valley. At this location, a high density in information on ecosystem processes exists due to long-term studies that have been supported by continuing project research. Observed data exist for both forests and grasslands along elevation gradients to permit an acceptable parameterization of ecosystem physiology. Even so, the demands of a model such as PIXGRO are large and general information from the literature has been required to complete the model structure. As an example, lack of information on soils required extrapolation from published reports of the Berchtesgaden National Park where terrain is similar. Problems confronted in parameterizing PIXGRO call attention to the importance of establishing more long-term intensive research sites, where data bases are capable of supporting spatial modelling efforts and interdisciplinary assessments. The need for such models can be expected to increase in the future.

A short-coming of the simulations is that the influences of climate shifts between 1861 and 2002, as well as changes in atmospheric CO₂ concentration, have not been considered. The 1861 climate for Stubai Valley is not documented, but we can assume that the average summer for this time period was cooler and with a shorter growing season. Warming has increased in recent decades, leading to an increase in mean temperature during June to August on the nearby summit of Mt. Patscherkofel of ca. 1.6 °C since 1965 (Bahn and Körner, 2003). With a cooler climate in 1861, the described decrease in water use by vegetation in 2002 is probably overestimated. Although actual NEE and biomass production during 1861 may also have been lower than predicted, land use change in Stubai Valley in any case compensates for the influence of increasing CO₂ concentration. While the situation is even more complex than described by the current version of the model, applying a constant meteorology emphasizes the interactive effects of land use change and CO₂ concentration that we encounter when we move to larger scales. Although biomass production and export of carbon from the valley ecosystems may have been lower in 1861 than indicated in Table 4, the differences shown with respect to 2002 are so large that an important impact in this sense must be included, when considering the consequences of the documented land use change.

Two points must be made with respect to the summaries given in Tables 3 and 4. First, the GPP, NEE and Reco values cannot be compared to results that are reported in general for coniferous forest and grasslands in ongoing eddy covariance studies over annual cycles. The summer season NEE values given in Table 4 are similar to those summarized across sites and over annual cycles for many conifer stands by Owen et al. (2007; their Tables 3 and 7), but more negative than reported for grasslands. In both cases, GPP and Reco in the Stubai Valley would continue over the remainder of the year resulting in much higher GPP and Reco totals, probably in the case of grasslands predominantly influencing Reco and making NEE less negative. The PIXGRO model and supporting data base are not yet sophisticated enough to support an annual carbon balance assessment. While the contributions from redistribution of forests in the landscape to changes in landscape CO₂ exchange and water use depend on shifts in physiological regulation in relation to climate, the reasons for change in flux rates among grassland types relates to nutrient limitations of the photosynthetic process (Bahn et al., 1999), cold temperature effects, and/or the increased occurrence in the abandoned and natural plant communities of slow growing species (Li et al., 2008). Feedbacks via the nitrogen cycle on flux rates have been implicitly included into PIXGRO in the parameterization steps described with respect to Fig. 9.

Secondly, changes in water use by the vegetation as described in Table 3 could mean that water yield from the valley should increase. A 10 to 15% change in water volume is significant, for example in terms of power generation downstream or for other uses. On the other hand, water balance of the catchment depends on many other factors, such as climate trends and water release from the glaciers to the Ruetz River which drains Stubai Valley. In this regard, it is interesting to note that bare rock surface increased by 22.6 km² between 1861 and 2002, while long-term snowcover disappeared over 9.2 km² (Table 2). Such long-term change in factors influencing catchment hydrology could either mask or override the changes in water use by vegetation. Measurements of discharge by the Ruetz River have only been recorded for ca. 25 years, during which time the estimated ratio of precipitation to discharge has remained relatively constant. On the other hand, altered vegetation water balance on particular slopes or where local water is drawn off for other uses could easily be influenced by the 10+% changes in water availability and would remain quite important for the local population.

Although the PIXGRO model is basically a spatial summarization of hypothesized response and spatial interactions are not included, the results that were obtained could not be visualized clearly without the simulations. The complexity of response to multiple environmental variables, variation in land use, and time dependent changes in LAI leads to the necessity for a PIXGRO-like model. A further question is whether the results from CO₂ studies have been correctly applied within the context of model assumptions, but this can only be resolved as further information on the response of C3 grasslands and coniferous forests to atmospheric CO₂ is obtained. Lack of knowledge of whether long-term adjustments in forest structure and function have occurred along with change in atmospheric CO₂ concentration, e.g., modification of average stand level LAI, change in average stomatal apertures or stomatal frequencies, or regulation of leaf carboxylation capacity (Wang et al., submitted for publication), additionally contribute to the uncertainty of model results. Spatial validation of the model has not been carried out. Especially the spatialization of human activities, e.g. management such as fertilization and harvest of the grasslands, are difficult to validate. It may be possible in the future to accomplish spatial validation of PIXGRO and improve the simulation of management practices via the application of remote sensing and remotesensing based models (Xiao et al., 2004, 2005).

Trends in water use as well as carbon sequestration in mountain regions are important points that require clarification in global change science due to far-reaching implications in resource planning and with respect to socioeconomic stability. Due to the existence of long-term historical information on land use as well as a strong tradition in ecological research, the European Alps may be viewed as a region that can provide us with new paradigms focusing on the linkages between ecology, ecosystem services, socioeconomics and cultural practices (Tappeiner et al., 2006). Based on 43 natural habitat, socioeconomic and agroeconomic indicators examined across the entire alpine region, eight types of structured alpine landscapes were defined in the project SUSTALP (Tappeiner et al., 2003). While it would require the parameterization of controls on water and carbon fluxes for new landscape elements, the PIXGRO model provides an analysis tool that permits comparison of such regions in terms of carbon and water balances. Although the certainties related to output will depend, as in the present case, on quality of supporting spatial data, translation of existing data bases into the form provided by the "PIXGRO tool box" can be carried out with efficiency, i.e., a more generalized view of different management schemes and their relation to natural resources may be accomplished. Similarly, the consequences of future development in alpine regions, viewed from the standpoint of 'future landscapes' generated via 1) transition matrix modelling, 2) stakeholder consultations, or 3) agroeconomic modelling (Tappeiner et al., 2006), can be evaluated in terms of potential future carbon and water balances with the PIXGRO model.

The IGBP Project BAHC (Biospheric aspects of the hydrological cycle, BAHC, 1993) was initiated to examine "how terrestrial ecosystems and their components affect the water cycle, freshwater resources and the partitioning of energy on earth" (Kabat et al., 2004). It evolved further to emphasize "the nature of interactions among the physical, biological, and social dimensions of the land-based water cycle". In the context of this latter focus, along with the conclusion that human disturbance and land cover change make the prediction of climate change effects uncertain, it was proposed that vulnerability assessments provide an extremely important means for assessing risk, for defining critical thresholds and for considering resistance of natural systems to change and reliability of those systems in providing needed water resources (Pielke et al., 2004; Bravo de Guenni et al., 2004).

While stability in water resources is clearly an issue, equal attention should be given to GPP as a key variable determining useful products and ecosystem services that may be at risk. In the BAHC synthesis, an important contribution is that of Krysanova et al. (2004), who examined hydrological relationships at different scales but simultaneously evaluated the associated nitrogen cycle as it influences crop production as well as water quality. Vulnerability in their example for the Elbe Basin must be considered not only in terms of water resources, but also in terms of water quality, the costs of production and production yields. It is in this same sense that important variables related to vulnerability in mountain regions can be described with PIXGRO. While water resources are critical, simultaneous evaluation of GPP quantifies the biosphere feedback on water balance and determines biomass products. We visualize that further development of PIXGRO will allow us to evaluate the scenarios of future development described above as well as to compare such scenarios in different mountain regions. Going beyond the current descriptions of gas exchange, GPP provides an index to examine influences on crop yields, relate estimated carbon gain to forestry production patterns, and relate vegetation water uses to catchment water balances, and thus aid in assessments of vulnerability in mountain regions.

Acknowledgements

We thank Dr. Michael Vogel, Helmut Franz, Dr. Volkmar Konnert, and staff members of the Berchtesgaden National Park for their support and help with logistics in the field, and access to data archives of the national park. Prof. Christian Bernhofer and Prof. Michal Marek provided unpublished eddy covariance data for spruce forests at the Tharandt and Bily Kriz sites, respectively. The simulation modelling and field studies were supported by the EU projects CARBOMONT and IP CarboEurope, and the BMBF project GLOWA-Danube coordinated by the Institute of Geography, Univ. of Munich. We thank Rob Jackson (Duke University) and Richard Gill (Washington State University) for information exchange on the response of grasslands to shifts in atmospheric CO₂ exchange and their sharing of unpublished data. We also express our appreciation to technical help and students of the University of Innsbruck who have contributed over the long-term in building data bases that support spatial studies of ecosystem processes. Several anonymous reviewers provided numerous insightful comments that have helped us greatly with the improvement of the manuscript.

This paper is dedicated to Dr. Alfred Becker in appreciation of his long-term interests and contributions to BAHC, to mountain ecohydrology, and to assessments of coupled water, carbon and nitrogen balances at catchment scales.

References

- Adiku, S.G.K., Reichstein, M., Lohila, A., Dinh, N.Q., Aurela, M., Laurila, T., Lueers, J., Tenhunen, J.D., 2006. PIXGRO: a model for simulating the ecosystem CO₂ exchange and growth of spring Barley. Ecol. Model. 190, 260–276.
- Anderson, L.J., Maherali, H., Johnson, H.B., Polley, H.W., Jackson, R.B., 2001. Gas exchange and photosynthetic acclimation over subambient to elevated CO₂ in a C-3 and C-4 grassland. Glob. Chang. Biol. 7, 693–707.
- BAHC, 1993. Biospheric aspects of the hydrological cycle. The Operational Plan. Stockholm, IGBP.
- Bahn, M., Körner, C.H., 2003. Recent increases in summit flora caused by warming in the Alps. In: Nagy, L., Grabherr, G., Körner, C.H., Thompson, D.B.A. (Eds.), Alpine Biodiversity in Europe. Ecological Studies, vol. 167. Springer, pp. 437–442.
- Bahn, M., Wohlfahrt, G., Haubner, E., Horak, I., Michaeler, W., Rottmar, K., Tappeiner, U., Cernusca, A., 1999. Leaf photosynthesis, nitrogen contents and specific leaf area of 30 grassland species in differently managed mountain ecosystems in the Eastern Alps. In: Cernusca, A., Tappeiner, U., Bayfield, N. (Eds.), Land-use Changes in European Mountain Ecosystems. ECOMONT– Concept and Results. Blackwell Wissenschaft, Berlin, pp. 247–255.
- Ball, J.T., Woodrow, I.E., Berry, J.A., 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggins, I. (Ed.), Progress in Photosynthesis Research. Proceedings of the VII International Photosynthesis Congress, vol. IV.5, pp. 221–224.
- Bernhofer, C., Aubinet, M., Clement, R., Grelle, A., Grünwald, T., Ibrom, A., Jarvis, P., Rebmann, C., Schulze, E.-D., Tenhunen, J.D., 2003. In: Valentini, R. (Ed.), Spruce Forests (Norway and Sitka Spruce, Including Douglas Fir): Carbon and Water Fluxes and Balances, Ecological and Ecophysiological Determinants. Fluxes of Carbon, Water and Energy of European Forests, Ecol. Studies, vol. 163. Springer-Verlag, Heidelberg, pp. 99–123.
- Bobeva, A., 2003. Quantifying the distribution of forest functional types and forest Leaf Area Index in the Alps. Doctoral Thesis, University of Bayreuth, Bayreuth, Germany, available on line URN: urn:nbn:de:bvb:703-opus-678; URL: http://opus.ub.unibayreuth.de/volltexte/2003/67/.

- Bravo de Guenni, L., Schulze, R.E., Pielke Sr., R.A., Hutchinson, M.F., 2004. The vulnerability approach. In: Kabat, P., Claussen, M., Dirmeyer, P.A., et al. (Eds.), Vegetation, Water, Humans and the Climate. Springer-Verlag, Berlin, pp. 499–501.
- Cernusca, A., Tappeiner, U., Bayfield, N., 1999. Land-use change in European Mountain ecosystems. ECOMONT – Concept and Results. Blackwell Wiss.-Ver., Berlin.
- Charles-Edwards, D.A., Doley, D., Rimmington, G.M., 1986. Modelling Plant Growth and Development. Academic Press, Sydney, Australia.
- Erdmann, K.H., Nauber, J., 1995. Der deutsche Beitrag zum UNESCO-Programm "Der Mensch und die Biosphäre". MAB, Bonn.
- Falge, E., Tenhunen, J., Aubinet, M., Bernhofer, C., Clement, R., Granier, A., Kowalski, A., Moors, E., Pilegaard, K., Rannik, Ü., Rebmann, C., 2003. A model-based study of carbon fluxes at ten European forest sites. In: Valentini, R. (Ed.), Fluxes of Carbon, Water and Energy of European Forests, Ecol. Studies, vol. 163. Springer-Verlag, Heidelberg, pp. 151–177.
- Farquhar, G.D., von Caemmerer, S., 1982. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), Modeling Photosynthetic Response to Environmental Conditions. Encyclopedia of Plant Physiology, New Series, vol. 12b. Springer Verlag, Berlin, Germany, pp. 550–587.
- Fryer, J.H., Ledig, F.T., 1972. Microevolution of the photosynthetic temperature optimum in relation to the elevational complex gradient. Can. J. Bot. 50, 1231–1235.
- Gill, R.A., Polley, H.W., Johnson, H.B., Anderson, LJ., Maherali, H., Jackson, R.B., 2002. Nonlinear grassland responses to past and future atmospheric CO₂. Nature 417, 279–282.
- Gill, R.A., Polley, H.W., Johnson, H.B., Jackson, R.B., 2006. Progressive nitrogen limitation limits carbon sequestration in a grassland exposed to past and future atmospheric CO₂. Ecology 87, 41–52.
- Gitay, H., Brown, S., Easterling, W., et al., 2001. Ecosystems and their goods and services. In: McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J., White, K.S. (Eds.), Climate change 2001: Impacts, Adaptation, and Vulnerability. Cambridge Univ Press, Cambridge, pp. 235–342.
- Granier, A., 1985. A new method of sap flow measurement in tree stems. Ann. Sci. For. 42, 193–200.
- Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol. 3, 309–319.
- Haber, W., Grossman, W.D., Kerner, H., Kunz, A., Richter, U., Schaller, J., Sittard, M., Spandau, L., 1983. Ökosystemforschung Berchtesgaden. Durchführung des MAB-Projektes "Der Einfluß des Menschen aus Hochgebirgsökosysteme". Ziele, Fragestellungen und Methoden. MAB-Mitteilungen des Deutschen Nationalkommitees, Band 16, 137 Seiten.
- Harley, P.C., Tenhunen, J.D., 1991. Modeling the photosynthetic response of C3 leaves to environmental factors. In: Boote, K.J. (Ed.), Modeling Crop Photosynthesis – From Biochemistry to Canopy. Proceedings of American Society of Agronomy Symposium. ASA, Madison, Wisconsin, pp. 17–39.
- IGBP, 1997. Predicting Global Change Impacts on Mountain Hydrology and Ecology: Integrated Catchment Hydrology/Altitudinal Gradient Studies. IGBP Report 43, Stockholm, Sweden.
- Jones, J.W., 1991. Crop growth, development and production modeling. Proc Symposium, Automated Agriculture for the Future. Am Soc Agric Eng, 1–17 December, Chicago, Illinois, pp. 447–457.
- Kabat, P., Claussen, M., Dirmeyer, P.A., et al. (Eds.), 2004. Vegetation, Water, Humans and the Climate. Springer-Verlag, Berlin.
- Köppel, J., 1995. Der Beitrag der Vegetation zum Wasserhaushalt, Forschungsbericht 029, Berchtesgaden National Park, Berchtesgaden, Germany.
- Körner, C., 2003. Alpine Plant Life. Springer-Verlag, Heidelberg.
- Körner, C., Asshoff, R., Bignucolo, O., Hättenschwiler, S., Keel, S.G., Pelaez-Riedl, S., Pepin, S., Siegwolf, R.T.W., Zotz, G., 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO₂. Science 309, 1360–1362.
- Kolcun, O., 2005. Water use of forests along elevation gradients in the Berchtesgaden National Park. Doctoral Thesis, University of Bayreuth, Bayreuth, Germany, URN: urn: nbn:de:bvb:703-opus-2037; URL: http://opus.ub.uni-bayreuth.de/volltexte/2006/ 203/.
- Krysanova, V., Becker, A., Wechsung, F., 2004. Integrated ecohydrological analysis of a temperate developed region: the Elbe River Basin in Central Europe. In: Kabat, P., Claussen, M., Dirmeyer, P.A., et al. (Eds.), Vegetation, Water, Humans and the Climate. Springer-Verlag, Berlin, pp. 429–439.
- Larcher, W., 2003. Physiological Plant Ecology, 4th Edition. Springer-Verlag, Berlin.
- Lenz, R., Haber, W., Tenhunen, J.D., 2001. In: Tenhunen, J., Lenz, R., Hantschel, R. (Eds.), A Historical Perspective on the Development of Ecosystem and Landscape Research in Germany. Ecosystem Approaches to Landscape Management in Central Europe, Ecological Studies, vol. 142. Springer Verlag, Heidelberg, pp. 17–35.

- Li, Y.-L., Tenhunen, J., Owen, K., Schmitt, M., Bahn, M., Otieno, D., Schmidt, M., Gruenwald, T.H., Hussain, M.Z., Mirzae, H., Bernhofer, C.H., 2008. Patterns in CO₂ gas exchange capacity of grassland ecosystems in the Alps. Agriculture and Forest Meteorology. 148, 51–68.
- Lohila, A., Aurela, M., Tuovinen, J.-P., Laurila, T., 2004. Annual CO₂ exchange of a peat field growing spring barley or perennial forage grass. J. Geophys. Res. 109, D18116. doi:10.1029/2004JD004715.
- Maherali, H., Reid, C.D., Polley, H.W., Johnson, H.B., Jackson, R.B., 2002. Stomatal acclimation over a subambient to elevated CO₂ gradient in a C₃/C₄ grassland. Plant Cell Environ. 25, 557–566.
- Millenium Assessment, 2003. Ecosystems and Human Well-being. Island Press, Washington, p. 245.
- Mountain Agenda, 1998. Mountains of the world. Water Towers for the 21st Century. Paul Haupt AG, Berne, Switzerland.
- Owen, K.E., Tenhunen, J., Reichstein, M., Wang, Q., Falge, E., Geyer, R., Xiao, X., Stoy, P., Ammann, C.H., Arain, A., Aubinet, M., Aurela, M., Bernhofer, C.H., Chojnicki, B.H., Granier, A., Gruenwald, T.H., Hadley, J., Heinesch, B., Hollinger, D., Knohl, A., Kutsch, W., Lohila, A., Meyers, T., Moors, E., Moureaux, C.H., Pilegaard, K., Saigusa, N., Verma, S., Vesala, T., Vogel, C.H., 2007. Comparison of seasonal changes in CO₂ exchange capacity of ecosystems distributed along a north–south European transect under non-waterstressed conditions. Global Change Biology. 13, 734–760.
- Pielke Sr., R.A., Petschel-Held, G., Kabat, P., et al., 2004. Predictability and uncertainty. In: Kabat, P., Claussen, M., Dirmeyer, P.A., et al. (Eds.), Vegetation, Water, Humans and the Climate. Springer-Verlag, Berlin, pp. 485–490.
- Pisek, A., Winkler, E., 1958. Assimilationsvermögen und Respiration der Fichte (*Picea excelsa* LINK) in verschiedener Höhenlage und der Zirbe (*Pinus cembra* L.) an der alpinen Waldgrenze. Planta 53, 532–550.
- Reichstein, M. 2001 Drought effects on carbon and water exchange in three Mediterranean ecosystems. Doctoral Thesis, University of Bayreuth, Bayreuth, Germany.
- Reichstein, M., Tenhunen, J., Roupsard, O., Ourcival, J.-M., Rambal, S., Miglietta, F., Peressotti, A., Pecchiari, M., Tirone, G., Valentini, R., 2003. Inverse modeling of seasonal drought effects on canopy CO₂/H₂O exchange in three Mediterranean Ecosystems. Journal of Geophysical Research 108(D23), 4726.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., et al., 2006. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. Glob. Chang. Biol. 11, 1424–1439.
- Tappeiner, U., Tappeiner, G., Hilbert, A., Mattanovich, E. (Eds.), 2003. The EU Agricultural Policy and the Environment, Evaluation of the Alpine Region. Blackwell Verlag, Berlin.
- Tappeiner, U., Tasser, E., Leitinger, G., Tappeiner, G., 2006. Landnutzung in den Alpen: historische Entwicklung und zukünftige Szenarien. In: Psenner, R., Lackner, R. (Eds.), Die Alpen im Jahr 2020. Alpine Space – Man and Environment, vol. 1. University Press, Innsbruck, pp. 23–39.
- Tobias, K., 1991. Konzeptionelle Grundlagen zur angewandten Oekosystemforschung. Beiträge zur Umweltgestaltung: A, Band, vol. 128. Erich Schmidt, Berlin.
- Tranquillini, W., 1979. Physiological Ecology of the Alpine Timberline. Ecological Studies, vol. 31. Springer-Verlag, Heidelberg.
- Wang, Q., Tenhunen, J., Falge, E., Bernhofer, C., Granier, A., Vesala, T., 2003. Simulation and scaling of temporal variation in gross primary production for coniferous and deciduous temperate forests. Glob. Chang. Biol. 10, 37–51.
- Wang, Q., Tenhunen, J., Schmidt, M., Otieno, D., Kolcun, O., Droesler, M., 2005. Diffuse PAR irradiance under clear skies in complex alpine terrain. Agric. For. Meteorol. 128, 1–15.
- Wang, Q., Tenhunen, J., Schmidt, M., Kolcun, O., Droesler, M., 2006. A model to estimate global radiation in complex terrain. Bound. Layer Meteorol. 119, 409–429.
- Wang, Q., Iio, A., Tenhunen, J., Kakubari, Y., submitted for publication. Annual and seasonal variation in photosynthetic capacity of *Fagus crenata* along elevation gradients in the Naeba Mountains, Japan. Oecologia.
- Wohlfahrt, G., Anfang, Ch., Bahn, M., Haslwanter, A., Newesely, Ch., Schmitt, M., Drösler, M., Pfadenhauer, J., Cernusca, A., 2005. Quantifying nighttime ecosystem respiration of a meadow using eddy covariance, chambers and modelling. Agric. For. Meteorol. 128, 141–162.
- Xiao, X., Hollinger, D., Aber, J., Goltz, M., Davidson, E.A., Zhang, Q., Moore III, B., 2004. Satellite-based modeling of gross primary production in an evergreen needleleaf forest. Remote Sens. Environ. 89, 519–534.
- Xiao, X., Zhang, Q., Hollinger, D., Aber, J., Moore III, B., 2005. Modeling gross primary production of an evergreen needleleaf forest using MODIS and climate data. Ecol. Appl. 15, 954–969.