



Dynamics of forage production in pasture-woodlands of the Swiss Jura Mountains under projected climate change scenarios

K. Gavazov, A. Peringer, A. Buttler, F. Gillet, T. Spiegelberger

► To cite this version:

K. Gavazov, A. Peringer, A. Buttler, F. Gillet, T. Spiegelberger. Dynamics of forage production in pasture-woodlands of the Swiss Jura Mountains under projected climate change scenarios. *Ecology and Society*, 2013, 18 (1), 13 p. 10.5751/ES-04974-180138 . hal-00808888

HAL Id: hal-00808888

<https://hal.science/hal-00808888v1>

Submitted on 8 Apr 2013

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Dynamics of forage production in pasture-woodlands of the Swiss Jura Mountains under projected climate change scenarios

Konstantin Gavazov^{1, 2*}, Alexander Peringer^{1, 3}, Alexandre Buttler^{1, 2, 4}, François Gillet^{1, 4}, Thomas Spiegelberger^{1, 5}

¹ Ecole Polytechnique Fédérale de Lausanne EPFL, School of Architecture, Civil and Environmental Engineering ENAC, Laboratory of ecological systems ECOS, Station 2, 1015 Lausanne, Switzerland

² Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Site Lausanne, Station 2, 1015 Lausanne, Switzerland.

³ University of Stuttgart, Institute for Landscape Planning ILPOE, Keplerstrasse 11, 70174 Stuttgart, Germany

⁴University of Franche-Comté – CNRS, UMR 6249 Chrono-environnement, 16 route de Gray, F-25030 Besançon Cedex, France

⁵ Irstea, UR EMGR Mountain Ecosystems, 2 rue Papeterie, BP 76, F-38402 Saint-Martin d'Hères, France

*Corresponding author: konstantin.gavazov@epfl.ch

ABSTRACT

Silvopastoral systems of the Swiss Jura Mountains serve as a traditional source of forage and timber in the subalpine vegetation belt, but their vulnerability to land-use and climate change puts their future sustainability at stake. In this paper we couple experimental and modelling approaches to assess the impacts of climate change on the pasture-woodland landscape. We draw conclusions on the resistance potential of wooded pastures with different management intensities by sampling along a canopy-cover gradient. This gradient spans from unwooded pastures associated with intensive farming, to densely wooded pastures associated with extensive farming. Transplanted mesocosms of these ecosystems placed at warmer and drier conditions provided experimental evidence that climate change reduced herbaceous biomass production in unwooded pastures, but had no effect in sparsely wooded pastures, and even stimulated productivity in densely wooded pastures. Through modelling these results with a spatially explicit model of wooded pastures (WoodPaM) modified for the current application, results were extrapolated to the local landscape under two regionalised IPCC scenarios for climate change. This led to the suggestion that within the Jura pasture-woodlands, forage production in the near future (2000-2050 AD) would be affected disproportionately throughout the landscape. A stable forage supply in hot, dry years would be provided only by extensive and moderate farming, which allows the development of an insulating tree cover within grazed pastures. We conclude that such structural landscape diversity would grant wood-pastures with a buffering potential in the face of climate change in the forthcoming decades.

KEYWORDS

Pasture; Woodland; Silvopastoral system; Subalpine; Grassland; Ecotone; Aboveground biomass; Drought; Transplantation

INTRODUCTION

History and importance of pasture-woodlands

Pasture-woodlands are a traditional man-made landscape in European mountains (Etienne 1996) and cover a major part of the Swiss Jura Mountains. They consist of a mosaic of open grassland, closed forest, and semi-forested pastureland with scattered or clumped trees and owe their shape to a long history of multifunctional land use, mainly pasturing and forestry (Buttler et al. 2009). Wood-pastures are true ecotones between closed forests and open grassland and thus more than just a simple interface between those two vegetation types. In such silvopastoral ecosystems, grasslands and woodlands are intimately associated in space and time as the result of a balance between counteracting ecological processes (Gillet et al. 2002, Gillet 2008). Forest encroachment and its suppression by browsing of livestock and extensive pasture management leads to a spatio-temporal heterogeneity of the landscape, defined by disturbance regimes, microclimate, and topography, and provides favourable conditions for high biodiversity (Gillet et al. 1999, Dufour et al. 2006).

At present, pasture-woodlands vary substantially in the amount and quality of ecosystem services they provide. Economically important factors such as forage supply are maintained higher through intensively managed treeless pastures than through extensive wood-pastures with free grazing livestock. This is important for local farmers who, from a socio-economic view, are the main users of wooded pastures and, as such, may deliberately shape the landscape into an unwooded one. Apart from farmin, in some regions revenues generated from forestry activities may be substantial (Gillet and Gallandat 1996). The significance of this landscape for the tourist economy has also been acknowledged, though it remains difficult to measure (Miéville-Ott and Barbezat 2005).

The coexistence of pastureland and woodland in a single and diverse silvopastoral ecosystem is not easy to preserve and calls for integrated management schemes (Barbezat and Boquet 2008). Both intensification and extensification of the current land use may lead to a breakdown of this precarious association, resulting in a segregation of woodland and grassland (Buttler et al. 2009). Even though anthropogenic land use change has been considered a major threat for mountain ecosystems worldwide (Körner et al. 2006), little is known about its interaction with climate change in the future.

Climate change in the European mountains

Global warming and associated environmental changes are predicted to have a strong impact on mountain ecosystems this century (IPCC 2007). The observed trend in Swiss mountains during the 20th century for a 1.5 K rise in mean annual air temperature (Beniston et al. 1997) is paralleled by increased instances of extreme summer temperature maxima and prolonged droughts (Schär et al. 2004, Beniston 2009). Throughout the current century these tendencies are predicted to become more pronounced and northern hemisphere temperate mountains will experience the most intensive temperature rise with a rate of warming typically two-to-three times higher (range +2.8 K to +5.3 K) than that recorded over the 20th century (Nogues-Bravo et al. 2007). Alongside, predicted hot spells and a 30 % diminishing precipitation will intensify the dry periods in Central Europe (Beniston et al. 2007, CH2011). These will bring about changes in summer soil moisture

availability, plant phenology and growing season length, which would ultimately have repercussions on ecosystem distribution and function (Parry 2000, FOEN/FSO 2011).

Response of plant communities to climate change

Episodic extreme climate events, such as summer heat waves, have strong and distinct impacts at the landscape scale (Ciais et al. 2005, Reichstein et al. 2007, Teuling et al. 2010). A mechanistic understanding of primary ecological processes occurring in a heterogeneous landscape such as pasture-woodlands is therefore essential for an efficient management. To date, a wealth of literature, encompassing various experimental methodologies, exists about the effects of warmer and drier climate on pristine cold-adapted vegetation. Transplantation experiments along natural climatic gradients, offer a powerful method for testing hypotheses about how species and communities are affected by future climatic changes. Although there are relatively few published studies using this technique, some successful attempts have been carried out in contrasting terrestrial environments: in peatlands (Wieder and Yavitt 1994, Breeuwer et al. 2010), in boreal forests (Hobbie and Chapin 1998), in montane meadows (Bruehlheide 2003), in subalpine grasslands (Sebastia 2007), and in alpine vegetation (Scheepens et al. 2010). The results from those, however, outline idiosyncratic patterns for plant community responses to environmental change. Concerning plant aboveground biomass, recent studies have reported an increase in annual herbaceous biomass production with warmer and drier climate (Bruehlheide 2003, Sebastia 2007). Others (Harte and Shaw 1995, Zhang and Welker 1996), to the contrary, have observed no cumulative change in aboveground biomass. Drought alone has been found to exert a negative effect on plant biomass (Johnson et al. 2011). At the level of plant community composition, these studies fail to give a holistic picture on shifts in diversity resulting from a climate manipulation. Either graminoids or forbs have been shown to successfully dominate after a climatic perturbation. Opportunistic plants may be granted competitive advantage through advanced phenological development (Dunne et al. 2003, Körner 2003, Inouye 2008), or through utilization of newly available nutrient resources (Bowman et al. 2006, Soudzilovskaia et al. 2007). Others may benefit from their inherent tolerance to specific environmental stress (Buchner and Neuner 2003, Brock and Galen 2005). Overall, more fertile early-successional grassland communities have been shown as more responsive to climate warming and drought, compared to late successional ones, typically found in areas of low intensity management (Grime et al. 2000). Drought resistance and recovery potential of plant communities have also been attributed to high species richness (van Ruijven and Berendse 2010), whereas grazing of highland pastures has been shown to both promote herbaceous richness and decrease evapotranspiration loss and thus water consumption (Körner et al. 2006). In comparison to grasslands, forests exhibit a more conservative water use and hence cope better with long-lasting heat and drought stress (Teuling et al. 2010).

In light of these findings, and given the heterogeneous landscape structure and high biodiversity of pasture-woodlands, we suspect that the productivity of such a mosaic of forest and extensively grazed diverse mountain grassland communities could be robust to the effects of heat and drought.

Upscaling from experimental plots to landscape level

Inspired by the work of Dunne et al. (2004), which demonstrates the challenging but beneficial task of extrapolating experimental results on ecosystem response to climate change from the scale of plots to that of landscapes, in this study we couple an experimental with a modelling approach. We believe that such combinations of observational, manipulative and modelling techniques are highly adapted to assess ecosystem vulnerability or resilience to environmental change (Spiegelberger et al. 2012).

To this aim, we established a transplantation experiment along an altitudinal gradient, to derive the response of plant communities of open grassland, semi-wooded pastures and grazed forests to climate manipulation (warming of up to +4 K). We built the results on biomass production into a dynamic simulation model of wood-pasture ecosystems, in order to assess the impact of drought events on forage provision for livestock at landscape level and in the proximate timeframe of climate change projections (until 2050 AD).

Hypotheses

We hypothesised that (1) herbaceous aboveground biomass (AGB) production in characteristic plant communities from wood-pastures would be more stable under climate change than in those from treeless grasslands. Based on this hypothesis at plot level, we predicted (2) that at landscape scale forage production in wood-pastures would be more stable during projected heat wave periods, than that in intensively-managed unwooded pastures. At last, (3) we put forward the hypothesis that wooded pastures represent a more robust land use form than conventional treeless pastures considering future climate change impacts.

METHODS

Study area and design of the warming experiment

The Combe des Amburnex in the Swiss Jura Mountains is a characteristic subalpine area of pasture-woodlands, situated within the boundaries of the Park Jurasien Vaudois. The climate is predominantly oceanic with a mean annual rainfall of *ca.* 1750 mm at 1350 m a.s.l. (including more than 450 mm snow precipitation) and a mean annual temperature of 4.5 °C. The ground is generally covered with snow from November to May.

In August 2009 three wooded pastures of similar area lying along the Combe des Amburnex at 1350 m were chosen according to their tree canopy cover resulting from different intensity of land use. These were, in increasing order of management intensity – a densely wooded pasture, a sparsely wooded pasture and an unwooded pasture. The pastures were situated within a 1 km distance from each other, measured each about 2 ha, and shared the same geomorphology, microtopography and exposition. Within each of the three pasture types, fifteen plots were randomly selected to represent the characteristic herbaceous vegetation of the respective area. To allow for a transplantation of soil turfs, plots were severed into 12 separate 20 cm × 20 cm and 30 cm deep soil cores and assembled back into rectangular PVC boxes of 60 × 80 cm² size and of 30 cm height. Chunks of intersected tree roots (diameter > 1 cm) were removed from the soil cores and the remaining gaps were filled in

with adjacent soil from the same horizon. The resulting 45 mesocosms were left in place to recover from the excavation until the end of the vegetation season and then transported to their receptor sites in October 2009. In total, three transplantation sites were established along an altitudinal transect: Combe des Amburnex (1350 m a.s.l., N 46°54', E 6°23'), Saint-George (1010 m a.s.l., N 46°52', E 6°26'), and Arboretum d'Aubonne (570 m a.s.l., N 46°51', E 6°37'). The first site at 1350 m a.s.l. served as a control site with unchanged climate, and the other two were chosen to represent a combination of annual temperature increase of +2 K and a precipitation decrease of -20 % at 1010 m a.s.l., and of +4 K and -40 % at 570 m a.s.l., respectively. These preliminary approximations were derived from interpolated data from nearby weather stations. At each site fifteen mesocosms, representing five replicates of each pasture type and all originating from the Combe des Amburnex, were transplanted following a completely randomised design. The boxes were dug down to surface level into previously prepared trenches thus preventing lateral heat exchange with the atmosphere. Mesocosms with turfs from sparsely wooded pastures and densely wooded pastures were shaded using two types of UV resistant nylon mesh, which reduced PAR by 40% and 80% respectively, simulating field-measured light conditions in the corresponding habitats during the 2009 growing season (*unpublished data*). The mesh fabric was suspended on wooden frames 50 cm above the ground surface and did not intercept rain precipitation. Those remained in the field only during the snow free period of the year, as to avoid interference with snowpack. As a means of keeping the grazing pressure on the plots and to avoid a confounding effect of "abandonment" and accumulation of standing litter, plots were clipped close to ground level at the end of the vegetation season.

Herbaceous biomass was harvested at the end of July 2010 during the first year following turf transplantation, and served as an estimate of the annual AGB production. At each plot a fixed area of 35 cm by 35 cm was cut down to *ca.* 1 cm above the soil surface, determined to species level, dried at 70 °C for 48 h and weighed.

Climate parameters were monitored continuously throughout the experiment by means of one automated weather station (Sensor Scope Sàrl, Switzerland) per experimental site measuring at a one minute interval air temperature and humidity 2 m above the ground surface, as well as rain precipitation. Decagon Devices Em50 data-loggers coupled to Decagon ECH₂O sensor probes recorded soil temperature and volumetric water content at top soil horizon (0 to -3 cm) every minute and data were averaged over one hour intervals. Data presented here are given for the months of the 2010 growing season – April, May, June, July, August, and September (AMJJAS).

Statistical analysis of experimental data

The experimental design allows for the explanation of annual variation of herbaceous biomass during the first year after transplantation by four factors: two categorical ones - initial pasture type and climate of the transplantation site; and two continuous physical ones – soil temperature and soil moisture. Each of the two edaphic variables was averaged per plot over the growing season (between respective soil thaw and day of harvest), thus integrating the microclimate conditions experienced by the plants. An ANCOVA model was fit through the raw data, testing the significance of single factors and their two-way interactions.

In order to extrapolate from experimental plot data, obtained under a distinct set of environmental conditions, to continuous site gradients in real landscapes, we built a linear regression model

predicting the seasonal AGB production from the two continuous variables tree cover percentage and degree of temperature change. The experimental shading of the plots was related to tree cover as follows: 0 % shading (light extinction under the canopy) for unwooded pasture with 0 % tree cover, 40 % shading for sparsely wooded pasture with 50 % tree cover, and 80 % shading for densely wooded pasture with 100 % tree cover. Temperature increase (ΔT) was calculated as the difference between local plant growing season temperature and that at the control site at 1350 m a.s.l. during the experimental year 2010. The parameter estimates for those factors retained in the optimal model fit were implemented into the landscape model of wooded pastures WoodPaM.

All statistical analyses were performed using R version 2.13.1. (R Development Core Team 2012).

Spatially-explicit simulation model of wood-pasture ecosystems WoodPaM

The dynamic simulation model of wooded pastures WoodPaM was developed by Gillet et al. (2002) and Gillet (2008) to investigate the successional dynamics of wooded pastures in the Swiss Jura Mountains. WoodPaM is a spatially explicit ecosystem model. As such, it is able to simulate the emergence of a semi-open landscape structure from selective grazing of large herbivores (cattle) by explicitly considering the foodchain from primary productivity to forage consumption by livestock. During simulations, selective foraging of cattle causes local impacts on vegetation (i.e., grazing, browsing, dunging, and trampling). Those, in turn, and together with geomorphologic and climatic conditions, promote or hinder forest development, and by this means drive the development of the landscape structure.

In WoodPaM, a pasture is represented by an arrangement of quadratic, 25 m wide, grid cells (as in Figure 1). In each cell the vegetation is represented by a herb, a shrub, and a tree submodel. Succession in the herb layer is driven by the intensity of grazing and dunging, as well as by tree cover. As such, it is categorised in the following four vegetation types – eutrophic pasture, oligotrophic pasture, fallow, and understory, which differ in pastoral value (PV) (see Table 1). A first estimate of yearly forage production P in a grid cell is computed based on a new regression model (in comparison to Gillet (2008)), which relates empirical data on productivity from the same set of vegetation surveys from the Jura Mountains and the Alps as used in Gillet (2008) to the pastoral value PV and the length of the vegetation period $vegdays$, with:

P = yearly forage production ($t\ DM\ ha^{-1}\ a^{-1}$)

PV = average pastoral value of the herb layer in the grid cell, weighted by the relative cover of vegetation types

$vegdays$ = length of the vegetation period (days)

fpm = maximal production ($20\ t\ DM\ ha^{-1}\ a^{-1}$)

fpi = “initial” production for $PV = 0$ ($8.5\ t\ DM\ ha^{-1}\ a^{-1}$)

ra = altitude effect on the growth coefficient ($2.152\ 10^{-5}$)

rm = maximal growth coefficient for $A = 0$ (0.05)

During simulations, the first estimate of yearly forage production is calculated from the current pastoral value of the vegetation types of each grid cell and the average length of the vegetation period during the last 50 simulation years. By this means, we take into account that the productivity of grassland plant communities increases slowly following the general trend of temperature rise (see

Figure 2), rather than spontaneously in single warm years. In the second case, a drought effect has to be expected, which we address separately (see next paragraph).

As a further innovation in comparison to former versions of WoodPaM (see Gillet 2008, Peringer et al. *this issue*), we modify the first estimate of forage production by applying a multiplier D for the drought effect of high average temperatures in the vegetation period during hot years. This modifier is calculated from the regression model of AGB response to transplantation along the climate warming gradient (see section “Statistical analysis of experimental data” and “Effects of increased temperature on aboveground biomass production at plot level”). No modifier is applied in cooler years, because the transplantation experiment did not deliver data for climate cooling. The temperature anomaly ΔT is the difference between the average temperature of the current vegetation period to the long-term mean temperature of the vegetation periods during years 1961 to 2010 (the experiment took place in year 2010, thus plant communities are adapted to recent past climate). As the regression function also expresses the dependency of productivity on tree cover (low forage production of understory in comparison to grassland), the pastoral value of understory is set equal to the value of grassland (see Table 1). The combined impact of drought and tree cover is computed according to Equation 1:

<eqn1>

Thus, the final yearly forage production in each cell, taking into account the slow prolongation of the vegetation period and yearly positive anomalies in the average temperature of the vegetation period, is computed as the product of P and D .

This model modification assumes that (1) the productivity of mountain grassland communities slowly increases with the increasing length of the vegetation period experienced during the last 50 years (community adaptation), however (2) their productivity in extraordinary hot years is consistently reduced by drought. We set the current climate (see Figure 2) as a baseline for the estimation of the drought impact, because we do not expect the development of new (drought resistant) genotypes, especially not, because grasslands are dominated by perennial species and species immigration is slow.

Consequently, simulated forage production per grid cell is a function of the successional state of the herb layer (pastoral value of vegetation types), the average length of the vegetation period during the last 50 years, and a drought impact in single hot years. Local grazing impacts at grid cell level depend on selective habitat use of cattle. In turn, the attractiveness of grid cells for cattle grazing depends on their forage provision and local site characteristics (i.e., steepness of terrain, rock outcrops). By this means, the feedback loop between grazing impacts and vegetation succession is closed, from which the spatio-temporal distribution of productivity of herb layer vegetation types emerges during simulations.

The ratio of consumed forage and forage production in a grid cell is expressed as local utilization rate (LUR) and based on a daily forage consumption of 18 kg DM per livestock unit. The same ratio calculated at pasture level is termed global utilization rate (GUR).

For a further and detailed description of the model structure and the implementation of herb layer and tree layer dynamics, as well as that of rules for selective grazing, refer to Gillet (2008). Recent model refinements beyond this model description are given in Peringer et al. (*this issue*).

Design of simulations

We simulate forage production under observed and projected climate in three separate wooded pastures in the region of Bullet, Switzerland, which lie in the same landscape of the Swiss Jura Mountains as the experimental site, *ca.* 40 km NE along the mountain crest. These pastures are adjacent (Figure 1), hence share identical climate, but differ in grazing intensity and consequently in their vegetation structure. *Les Planets Ouest* (1200 m a.s.l., N 46°83', E 6°55') is an intensively used commonage with 46 LU (livestock units) on 25.6 ha, resulting in 1.79 LU/ha for 170 days/year (see also Chételat et al. *this issue*). It is practically treeless, and for the purpose of this study it is referred to as Intensive Wooded Pasture (IWP). *Les Planets Milieu Est* (1200 m a.s.l., N 46°84', E 6°55') is mostly open grassland but features some sparsely wooded pasture far in the Northwest. It has a moderate stocking density with 22 LU on 14.1 ha, resulting in 1.56 LU/ha for 135 days/year, and from here-on is referred to as Moderate Wooded Pasture (MWP). *Les Cluds Sud* (1200 m a.s.l., N 46°84', E 6°56') is a mosaic pasture with several patches of woodland and is extensively grazed with 23 LU on 23.3 ha, resulting in 0.99 LU/ha for 153 days/year. It is referred to as Extensive Wooded Pasture (EWP). Although ongoing socio-economic developments will likely lead to reduced stocking of wooded-pastures (Huber et al. *this issue-a*), for the purpose of this study, we simulate constant stocking densities.

Time series of temperature and precipitation are derived from the regionalisation of observed climate in the period 1950-2000 AD and two climate change scenarios of the IPCC-SRES report (2000) for the period 2000-2100 AD, as provided by the Climatic Research Unit CRU of the University of East Anglia, Norwich, UK and the Tyndall Centre for Climate Change Research (regionalization by Schmatz *personal communication*). We select the moderate scenario B2 with +4 K warming and the extreme scenario A1FI with +8 K warming, assuming that a realistic future development will lie within the range between the two scenarios. The corresponding yearly mean temperatures are displayed in Figure 2, together with the yearly mean temperatures of the vegetation period. The latter drive drought impact during simulations, whereas the average temperature of the last 50 years drives productivity increase. We initialized the model from aerial photographs taken in 2000 AD and applied a 50-years spin-up period 1950-2000 AD. Simulations run from 2000 on for a period of 50 years.

RESULTS

Effects of increased temperature on aboveground biomass production at plot level

Transplantation downslope exposed the plant communities in the experimental plots to an (expected) increase in ambient air temperature and reduced precipitation during the vegetation period (Table 1). Following this treatment, soil temperature generally increased, while soil moisture decreased (Table 1). Along the gradient in simulated tree cover, at each site soil temperature decreased almost linearly with approximately 1 K for each level of canopy shading (0 %, 40 %, and

80 %). Shading prevented also soil water evaporation at lower altitudes compared to the control site. In the case of densely wooded pastures, soils kept up to 70 % of their moisture content at 570 m a.s.l. and 96 % at 1010 m a.s.l.

Results from the ANCOVA model indicated that AGB production along the transplantation gradient was significantly affected by pasture type ($P_{2,25} < 0.001$), and its interaction with the altitude of the transplantation site ($P_{4,25} < 0.001$). Significant effect exerted also soil temperature ($P_{1,25} = 0.016$) and soil moisture ($P_{1,25} = 0.008$). AGB quantity decreased significantly along the land-use intensity gradient in the order unwooded > sparsely wooded > densely wooded pastures (Figure 2). These differences were most evident at the control site at 1350 m a.s.l., but were weakened at warmer climate where AGB production was stimulated in densely wooded pastures, reduced in unwooded pastures, and remained unchanged in sparsely wooded pastures (see Figure 2, and the statistically significant interaction between pasture type and altitude). The transplantation altitude alone had no consistent effect on AGB across the pasture types.

Fitting a linear regression model through the biomass data allowed us to estimate the influence of landuse and climate parameters on pasture productivity. The resulting model ($R^2 = 0.85$, $P_{3,41} < 0.001$) is given in Equation 2:

<eqn2>

It expresses the production of herbaceous biomass *AGB* as a function of tree cover percentage *TreeCover*, air temperature anomaly ΔT and their interaction. All parameter estimates, including the model's intercept were highly significant ($P_{1,41} < 0.001$) and were hence implemented into the WoodPaM model in the form of a factor applied to the first estimate of forage production in the grassland-forest mosaic (see section "Spatially-explicit simulation model of wood-pasture ecosystems WoodPaM").

Effects of temperature anomalies on forage production at landscape level

Simulated time series of global forage utilization rates (GUR) followed distinct trajectories according to the management intensity within each of the studied pastures (Figure 4). Most obvious was the trivial effect of a higher utilization rate with higher stocking density, which led to well-separated curves for each pasture. The spin-up period ended around year 1980 and realistic utilization rates were simulated for extensive (EWP, ~70 %), moderate (MWP, ~80 %) and intense pastures (IWP, ~100 %). An utilization rate of 100 % means an optimal stocking density in an economic sense, because all available forage is consumed. An utilization rate below 100 % indicates undergrazed patches, which are typical in extensively grazed pastures, and provide niches where shrubs and woods can develop and form the specific landscape mosaic of pasture-woodlands.

From year 2000 onwards, utilization rates did not decrease, as one would expect from the increase in productivity following the prologation of the vegetation period with climate change (see Figure 2). The rapid temperature rise and subsequent increase in simulated drought due to an increasing number of years with hot summers compensated for this effect. In the course of time, the utilization rates of IWP and MWP started to fluctuate with increasing amplitude and peaks far above the threshold of 100 %. To the contrary, the utilization rate of EWP remained always below 100 % and

fluctuations were far smaller. For the drastic warming scenario A1FI (+8K) such effects were even more pronounced, especially in the projected heatwave in simulation years 2042-2047.

Overall, for current stocking densities, simulations of extensive pastures showed a continuous provision of sufficient forage, while in intense pastures scarcity of forage was indicated. The stable forage provision in EWP (i.e., low amplitude of projected GUR in Figure 4) might appear trivial due to intrinsically low stocking densities in this pasture. Nevertheless the stimulated AGB production in its forested landscape patches did provide a quantitative buffering capacity against heatwaves. Such a contribution of landscape heterogeneity to ecosystem process resilience is exemplified (Table 3) though the comparison of a pair of simulated years with hot (2021) and ambient (2022) temperatures from the simulation continuum of IPCC-SRES climate change scenario B2 (Figure 2). We chose two consecutive years in order to compare a quasi identical landscape structure. Within the treeless IWP in the hot year 2021, forage production decreased with drought causing an increase of 12.5 % in GUR (Table 3 and Figure 5). Similar drought impacts on forage production were also recognisable within the grasslands of MWP and EWP (Figure 5), however, the utilization rate in EWP, which is a true forest-grassland mosaic, increased only with 6.7% in GUR (Table 3). An additional mathematical correction for the potential bias of extensive pastures being less prone to overshooting GUR levels in response to forage scarcity was implemented by dividing GUR values for a given year by the longterm average GUR. As seen in Table 3, the corrected differences in GUR values between the two years remained higher in IWP and MWP (11.9 and 12.4, respectively) compared to those in EWP (9.5), which indicated the simulated buffering potential of wood-pastures.

DISCUSSION

Distinct effects of climate change on herbaceous production across land-cover types

Our experimental study was novel for directly comparing climate change impacts on several neighbouring grasslands experiencing different intensities of management, which were manifested by a gradient of forest canopy cover and herbaceous species composition. The results unequivocally displayed the decline in herbaceous productivity in open pastures in contrast to a stable and even increasing one in forested pastures. This pattern became apparent after only one year of experimental treatment, which emphasises the importance of stochastic heat waves for the functioning of pasture-woodland ecosystems. As a result of the transplantation treatment, open pastures experienced disproportionately stronger drought effects than the two wood-pasture types and this was driven mainly by decreased soil moisture availability. Even though our simplistic design for shading of the mesocosms did certainly not encompass all the microclimate effects of a real tree canopy (i.e., ambient humidity, wind interception, canopy leachate and litter deposition, or underground competition for resources), we believe our results on herbaceous production are robust due to the appropriate use of control plots and the overall short time span of the treatment, which prevented accumulation of confounding carry-over effects.

One of the most prominent factors driving the reduction in AGB was the decrease in soil moisture availability during the plant growing season. Whereas soil temperature increased linearly with warmer climate for all pasture types, we found that soil humidity was mainly affected in the

unwooded pasture plots paralleled by a decrease in standing plant AGB. Moreover most of this AGB had already senesced at peak growing season due to drought (NDVI measurements, *unpublished data*). This phenomenon arose from an intensified evapotranspiration in open-canopy plots in comparison to the shaded ones, where the mesh covers have adequately served their “forest-like” purpose in limiting energy exchange with the atmosphere during the hot summer months (see Teuling et al. 2010).

An alternative explanation could be that intensive farming (Körner et al. 2006) coupled to high fertilization levels and impeded successional development (Grime et al. 2000) played itself a role in rendering intensively managed open pastures more vulnerable to climate change. One could speculate that those grassland communities, composed of fast-growing species with access to high nutrient availability, are more responsive to environmental change. This scenario, however, was not explicitly tested in our experimental design (no fertilisation manipulations) and remains only hypothetical.

Landscape patterns of forage provision under climate change

Our approach to implement experimental results into a process-based simulation model of wooded pastures merits more than a simple extrapolation across spatial scales (from plot to landscape levels). Since biomass production of grasslands forms represents the base of WoodPaM simulations, climate change impacts on primary production mechanistically determine forage availability for cattle, which in turn shapes landscape structure via selective grazing behaviour (Kohler et al. 2006). Regardless of the limitations of our experimental design, which did not account for plausible interaction between precipitation and temperature, we do not expect a qualitative bias in our interpretations. Our confidence comes from the locally observed and predicted strong negative correlation between these two climatic factors, hence we included only temperature in our predictive model for AGB production. Even though we based our choice of transplantation gradient on both current weather observations and climate predictions, we could not account for ecosystem responses to future warm and wet, or cold and dry plant growing seasons.

While other studies of climate-change impacts on wooded pastures rely mainly on the climate sensitivity of tree species (Peringer et al. *this issue*), ours focused on the functioning of grasslands. The design of simulations encompassed a much shorter timeframe from 2000 to 2050 AD – a period short enough to detect climatic stress while assuming no plant species adaptation (development of drought adapted ecotypes), or significant community change through immigration. Even though this assumption may appear unrealistic for the last decades of simulation, we considered three reasons for it: (1) there is no simple way to implement evolutionary and dispersal processes for grassland species in the model; (2) species shift from lowland following climate change is probably very slow in this area, due to forest barriers to the dispersal of herbaceous species; (3) phenotypic plasticity and genetic polymorphism of established plant populations is likely to allow yet some adaptation to drought stress due to the long history (ecological continuity) of these mountain pastures. Furthermore, this period is too short to produce any substantial shift in the tree layer and thus the landscape structure; see Peringer et al. (*this issue*) for long term dynamics of climate change. Nevertheless, one should bear in mind that, in the long run, impacts of climate change on grassland productivity could feedback on landscape structure due to adaptive grazing behaviour of cattle (Smit et al. 2007, Vandenberghe et al. 2007, Vandenberghe et al. 2009). In hot years, depleted

forage resources in open pastures would provoke cattle grazing in the forest understory, where drought impacts were found to be smaller and forage would still be available. Forest regeneration would be hence put at stake and landscape structural dynamics could be expected to shift towards a more open landscape. Such a development would counteract projected forest encroachment and canopy thickening (Peringer et al. *this issue*) rendering a stable forage provision in the far future.

Our simulations showed that in extensive grazing systems it was not only the generally lower stocking density, but also the resulting grassland-forest mosaic, which contributed to the robust provision of forage. The observed stable AGB production in sparsely wooded pastures, and increasing production in densely wooded pastures in the face of warming and drought, were in sharp contrast with the decreased AGB in unwooded pastures. Consequently, the apparent advantage in terms of productivity of unwooded pasture diminished with drought and wooded pastures became a forage source of similar importance. In sight of the relatively large area sparsely and densely wooded pastures cover in extensively stocked pastures, such formerly unproductive patches showed a clear potential to compensate the breakdown of productivity within open grasslands.

Given that mosaic emergence is a process over centuries (Gillet 2008, Peringer et al. *this issue*), such kind of resilience of the system is a precious good, because it is rapidly destroyed but slowly reestablished. Chételat et al. (*this issue*) have shown that landscape transformations of such great magnitude could result, for example, from higher wood and food demands (e.g. during wartime) and from natural events (storms, droughts, bark beetle outbursts). Similar conclusions about the beneficial role of tree canopy on understory microclimate during drought has been found for agroforestry systems (Powell and Bork 2006). Across the landscape, spatial variation itself stimulates ecosystem resilience and resistance to drought. Godfree et al. (2011) show that naturally occurring extreme climatic events such as drought can be mitigated through the protective role of heterogeneous environments. This concept is shared by Foley et al. (2005) who advocate the maintenance of a diverse portfolio of ecosystem services by a single ecosystem, such that sustainable land use strategies could be implemented for both short- and long-term needs. Here we show that in the case of subalpine wooded pastures this can be accomplished through the preservation of the mosaic landscape. It is, nevertheless, acknowledged that decisions about the future of cultural landscapes (i.e. wood-pastures) come from stakeholders rather than scientists, and that such a stability requires both maintenance of historically established agricultural practices (Küster 2004) and adaptive management, including change in policies (Huber et al. *this issue-b*). Either courses of intensification or abandonment would place the ecosystem's stability at stake and disrupt the delivery of its prime ecosystems services.

CONCLUSION

In summary, different grassland types within the pasture-woodland landscape of the Swiss Jura Mountains were shown to exhibit a strictly non-uniform response to climate change in terms of herbaceous forage provision. The mosaic patchiness of the landscape would be a valuable asset in the face of climate warming and its inherent diversity may hold the key to sustainable land use management. Presented were empirical and modelling evidence, that wood-pastures may provide forage for livestock in a robust way by buffering impacts of climate change for the next decades.

We believe that this property of the landscape should hence be credited in order to avoid any future landscape segregation and associated economic and cultural impacts.

LITERATURE CITED

- Barbezat, V. and J. F. Boquet. 2008 Gestion intégrée des paysages sylvo-pastoraux de l'Arc jurassien – Manuel (Hankbook). Conférence TransJurassienne. La Chaux-de-Fonds, Besançon, 160 p et 1 CD-ROM.
- Beniston, M. 2009. Decadal-scale changes in the tails of probability distribution functions of climate variables in Switzerland. *International Journal of Climatology* **29**:1362-1368.
- Beniston, M., H. F. Diaz, and R. S. Bradley. 1997. Climatic change at high elevation sites: An overview. *Climatic Change* **36**:233-251.
- Beniston, M., D. B. Stephenson, O. B. Christensen, C. A. T. Ferro, C. Frei, S. Goyette, K. Halsnaes, T. Holt, K. Jylha, B. Koffi, J. Palutikof, R. Scholl, T. Semmler, and K. Woth. 2007. Future extreme events in European climate: an exploration of regional climate model projections. *Climatic Change* **81**:71-95.
- Bowman, W. D., J. R. Gartner, K. Holland, and M. Wiedermann. 2006. Nitrogen critical loads for alpine vegetation and terrestrial ecosystem response: Are we there yet? *Ecological Applications* **16**:1183-1193.
- Breeuwer, A., M. Heijmans, B. J. M. Robroek, and F. Berendse. 2010. Field Simulation of Global Change: Transplanting Northern Bog Mesocosms Southward. *Ecosystems* **13**:712-726.
- Brock, M. T. and C. Galen. 2005. Drought tolerance in the alpine dandelion, *Taraxacum ceratophorum* (Asteraceae), its exotic congener *T. officinale*, and interspecific hybrids under natural and experimental conditions. *American Journal of Botany* **92**:1311-1321.
- Bruehlheide, H. 2003. Translocation of a montane meadow to simulate the potential impact of climate change. *Applied Vegetation Science* **6**:23-34.
- Buchner, O. and G. Neuner. 2003. Variability of heat tolerance in alpine plant species measured at different altitudes. *Arctic Antarctic and Alpine Research* **35**:411-420.
- Buttler, A., F. Kohler, and F. Gillet. 2009. The Swiss Mountain Wooded Pastures: Patterns and Processes. Pages 377-396 in A. Rigueiro-Rodrigues, J. McAdam, and M. R. Mosquera-Losada, editors. *Agroforestry in Europe, Current Status and Future Prospects*. Springer Netherlands.
- CH2011. 2011. Swiss Climate Change Scenarios CH2011. published by C2SM, MeteoSwiss, ETH, NCCR Climate, and OcCC, Zurich, Switzerland.
- Chételat, J., M. Kalbermatten, K. Lannas, T. Spiegelberger, J. B. Wettstein, F. Gillet, A. Peringer, and A. Buttler. *this issue*. A contextual analysis of observed land-use and vegetation changes applied to two wooded pastures in the Swiss Jura Mountains. Submitted to *Ecology and Society*.
- Ciais, P., M. Reichstein, N. Viovy, A. Granier, J. Ogee, V. Allard, M. Aubinet, N. Buchmann, C. Bernhofer, A. Carrara, F. Chevallier, N. De Noblet, A. D. Friend, P. Friedlingstein, T. Grunwald, B. Heinesch, P. Keronen, A. Knohl, G. Krinner, D. Loustau, G. Manca, G. Matteucci, F. Miglietta, J. M. Ourcival, D. Papale, K. Pilegaard, S. Rambal, G. Seufert, J. F. Soussana, M. J. Sanz, E. D. Schulze, T. Vesala, and R. Valentini. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* **437**:529-533.

- Dufour, A., F. Gadallah, H. H. Wagner, A. Guisan, and A. Buttler. 2006. Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. *Ecography* **29**:573-584.
- Dunne, J. A., J. Harte, and K. J. Taylor. 2003. Subalpine meadow flowering phenology responses to climate change: Integrating experimental and gradient methods. *Ecological Monographs* **73**:69-86.
- Dunne, J. A., S. R. Saleska, M. L. Fischer, and J. Harte. 2004. Integrating experimental and gradient methods in ecological climate change research. *Ecology* **85**:904-916.
- Etienne, M., editor. 1996. *Western European Silvopastoral Systems*. INRA Editions, Paris, France.
- FOEN/FSO. 2011. *Environment Switzerland 2011*. Bern and Neuchâtel, Switzerland.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. *Science* **309**:570-574.
- Gillet, F. 2008. Modelling vegetation dynamics in heterogeneous pasture-woodland landscapes. *Ecological Modelling* **217**:1-18.
- Gillet, F., O. Besson, and J.-M. Gobat. 2002. PATUMOD: a compartment model of vegetation dynamics in wooded pastures. *Ecological Modelling* **147**:267-290.
- Gillet, F. and J. D. Gallandat. 1996. Wooded pastures of the Jura mountains. Pages 37–53 in M. Etienne, editor. *Western European Silvopastoral Systems*. INRA Editions, Paris, France.
- Gillet, F., B. Murisier, A. Buttler, J.-D. Gallandat, and J.-M. Gobat. 1999. Influence of tree cover on the diversity of herbaceous communities in subalpine wooded pastures. *Applied Vegetation Science* **2**:47-54.
- Godfree, R., B. Lepschi, A. Reside, T. Bolger, B. Robertson, D. Marshall, and M. Carnegie. 2011. Multiscale topographic heterogeneity increases resilience and resistance of a dominant grassland species to extreme drought and climate change. *Global Change Biology* **17**:943-958.
- Grime, J. P., V. K. Brown, K. Thompson, G. J. Masters, S. H. Hillier, I. P. Clarke, A. P. Askew, D. Corker, and J. P. KIELTY. 2000. The response of two contrasting limestone grasslands to simulated climate change. *Science* **289**:762-765.
- Harte, J. and R. Shaw. 1995. Shifting dominance within montane vegetation community - results of a climate-warming experiment. *Science* **267**:876-880.
- Hobbie, S. E. and F. S. Chapin. 1998. An experimental test of limits to tree establishment in Arctic tundra. *Journal of Ecology* **86**:449-461.
- Huber, R., S. Briner, A. Peringer, S. Lauber, R. Seidl, A. Widmer, F. Gillet, A. Buttler, B. Q. Le, and C. Hirschi. *this issue-a*. Modelling feedback effects between vegetation dynamics, farm structural change and policy development in the pasture woodlands of the Swiss Jura Mountains. *Ecology and Society*.
- Huber, R., H. Bugmann, A. Buttler, and A. Rigling. *this issue-b*. Sustainable land-use practices in European mountain regions under global change: An integrated research concept across scales and disciplines. *Ecology and Society*.
- Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* **89**:353-362.
- IPCC. 2000. *Special Report Emission Scenarios*. Cambridge University Press, Geneva, Switzerland.
- IPCC. 2007. *Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Geneva, Switzerland.

- Johnson, D., J. Vachon, A. J. Britton, and R. C. Helliwell. 2011. Drought alters carbon fluxes in alpine snowbed ecosystems through contrasting impacts on graminoids and forbs. *New Phytologist* **190**:740-749.
- Kohler, F., F. Gillet, S. Reust, H. H. Wagner, F. Gadallah, J. M. Gobat, and A. Buttler. 2006. Spatial and seasonal patterns of cattle habitat use in a mountain wooded pasture. *Landscape Ecology* **21**:281-295.
- Körner, C. 2003. *Alpine plant life: functional plant ecology of high mountain ecosystems*. Springer, Berlin Heidelberg New York.
- Körner, C., G. Nakhutsrishvili, and E. Spehn. 2006. High-elevation land use, biodiversity, and ecosystem functioning. *in* E. Spehn, M. Liberman, and C. Körner, editors. *Land use change and mountain biodiversity*. CRC Press, Boca Raton, FL, USA.
- Küster, H. 2004. Cultural Landscapes. Pages 1-11 *in* M. Dieterich and J. Straaten, editors. *Cultural Landscapes and Land Use*. Springer Netherlands.
- Miéville-Ott, V. and V. Barbezat. 2005. Perception du pâturage boisé: résultats d'un sondage effectué au Communal de la Sagne NE. *Schweizerische Zeitschrift für Forstwesen* **156**:1-12.
- MPI-M. 2006. Climate Data. Max Planck Institute for Meteorology (MPI-M). Hamburg - by order of The Federal Environment Agency, Germany.
- MPI-M. 2009. Climate Data. Max Planck Institute for Meteorology (MPI-M). Hamburg - by order of The German Federal Institute of Hydrology, Germany.
- Nogues-Bravo, D., M. B. Araujo, M. P. Errea, and J. P. Martinez-Rica. 2007. Exposure of global mountain systems to climate warming during the 21st Century. *Global Environmental Change-Human and Policy Dimensions* **17**:420-428.
- Parry, M. L. 2000. Assessment of potential effects and adaptations for climate change in Europe: the Europe ACACIA project. Jackson Environmental Institute, University of East Anglia, Norwich.
- Peringer, A., S. Siehoff, J. Chételat, T. Spiegelberger, A. Buttler, and F. Gillet. *this issue*. Past and future landscape dynamics in wooded pastures of the Jura Mountains under land-use and climate change. Submitted to *Ecology and Society*.
- Powell, G. W. and E. W. Bork. 2006. Aspen canopy removal and root trenching effects on understory vegetation. *Forest Ecology and Management* **230**:79-90.
- R Development Core Team. 2012. R version 2.14.1.
- Reichstein, M., P. Ciais, D. Papale, R. Valentini, S. Running, N. Viovy, W. Cramer, A. Granier, J. OgÉE, V. Allard, M. Aubinet, C. Bernhofer, N. Buchmann, A. Carrara, T. GrÜNwald, M. Heimann, B. Heinesch, A. Knohl, W. Kutsch, D. Loustau, G. Manca, G. Matteucci, F. Miglietta, J. M. Ourcival, K. Pilegaard, J. Pumpanen, S. Rambal, S. Schaphoff, G. Seufert, J. F. Soussana, M. J. Sanz, T. Vesala, and M. Zhao. 2007. Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: a joint flux tower, remote sensing and modelling analysis. *Global Change Biology* **13**:634-651.
- Schär, C., P. L. Vidale, D. Luthi, C. Frei, C. Haberli, M. A. Liniger, and C. Appenzeller. 2004. The role of increasing temperature variability in European summer heatwaves. *Nature* **427**:332-336.
- Scheepens, J. F., E. S. Frei, and J. Stocklin. 2010. Genotypic and environmental variation in specific leaf area in a widespread Alpine plant after transplantation to different altitudes. *Oecologia* **164**:141-150.
- Schmatz, D. *personal communication*. WSL Switzerland, Dept. Ecological process modelling. Land use dynamics.

- Sebastia, M. T. 2007. Plant guilds drive biomass response to global warming and water availability in subalpine grassland. *Journal of Applied Ecology* **44**:158-167.
- Smit, C., C. Vandenberghe, J. den Ouden, and H. Mueller-Schaerer. 2007. Nurse plants, tree saplings and grazing pressure: changes in facilitation along a biotic environmental gradient. *Oecologia* **152**:265-273.
- Soudzilovskaia, N. A., V. G. Onipchenko, J. H. C. Cornelissen, and R. Aerts. 2007. Effects of fertilisation and irrigation on 'foliar afterlife' in alpine tundra. *Journal of Vegetation Science* **18**:755-766.
- Spiegelberger, T., F. Gillet, B. Amiaud, A. Thebault, P. Mariotte, and A. Buttler. 2012. How do plant community ecologists consider the complementarity of observational, experimental and theoretical modelling approaches? *Plant Ecology and Evolution* **145**:4-12.
- Teuling, A. J., S. I. Seneviratne, R. Stockli, M. Reichstein, E. Moors, P. Ciais, S. Luyssaert, B. van den Hurk, C. Ammann, C. Bernhofer, E. Dellwik, D. Gianelle, B. Gielen, T. Grunwald, K. Klumpp, L. Montagnani, C. Moureaux, M. Sottocornola, and G. Wohlfahrt. 2010. Contrasting response of European forest and grassland energy exchange to heatwaves. *Nature Geosci* **3**:722-727.
- van Ruijven, J. and F. Berendse. 2010. Diversity enhances community recovery, but not resistance, after drought. *Journal of Ecology* **98**:81-86.
- Vandenberghe, C., F. Frelechoux, M.-A. Moravie, F. Gadallah, and A. Buttler. 2007. Short-term effects of cattle browsing on tree sapling growth in mountain wooded pastures. *Plant Ecology* **188**:253-264.
- Vandenberghe, C., C. Smit, M. Pohl, A. Buttler, and F. Frelechoux. 2009. Does the strength of facilitation by nurse shrubs depend on grazing resistance of tree saplings? *Basic and Applied Ecology* **10**:427-436.
- Wieder, R. K. and J. B. Yavitt. 1994. Peatlands and Global Climate-Change - Insights from Comparative-Studies of Sites Situated Along a Latitudinal Gradient. *Wetlands* **14**:229-238.
- Zhang, Y. Q. and J. M. Welker. 1996. Tibetan alpine tundra responses to simulated changes in climate: Aboveground biomass and community responses. *Arctic and Alpine Research* **28**:203-209.

Figure 1. Grassland-forest mosaic in year 2000 of the simulated pastures as estimated by aerial photograph interpretation by M. Kalbermatten (see Chételat et al. this issue): The almost treeless intensively grazed pasture *Les Planets Ouest* (IWP), the moderately grazed pasture *Planets Milieu Est* (MWP), and the extensively grazed true mosaic pasture *Les Cluds Sud* (EWP).

Figure 2. Regionalised observed (1950-2000 AD) and simulated (2000-2050 AD) annual (thin solid lines) and vegetation growing season (thick solid lines) temperatures for the two IPCC-SRES scenarios (see text): B2 (dark grey) and A1FI (light grey). The average temperature of the vegetation periods from 1961 to 2010 is presented as a reference threshold (thick dashed black line). The difference between simulated yearly temperatures of vegetation periods and this reference threshold is implemented as a parameter ΔT driving drought stress in simulations. The average temperature of the last 50 years (thin dashed line) is used to simulate the increase of productivity due to the prolongation of the vegetation period.

Figure 3. Change of above-ground biomass (AGB) production in relation to (a) soil moisture, and (b) soil temperature in unwooded pastures (circles), sparsely wooded pastures (squares) and densely wooded pastures (triangles). Altitudes of experimental plots are 570 m a.s.l. (black symbols), 1010 m a.s.l. (grey symbols) and 1350 m a.s.l. (empty symbols).

Figures 4. Global utilization rates (GUR) of produced forage for the three pastures and the two IPCC-SRES climate change scenarios: (a) B2 and (b) A1FI. Pastures are *Les Cluds Sud* - EWP (light grey curve), *Les Planets Milieu Est* – MWP (dark grey curve) and *Les Planets Ouest* IWP (black curve).

Figure 5. Output maps of forage production and local utilization rate (percentage consumed forage) in two arbitrarily chosen years – a hot one (2021) and a cool one (2022), based the moderate climate change scenario B2 with contrasting average temperatures in the vegetation period ($\Delta 1.5$ K). Darker tones indicate higher values of the respective parameters.

Table 1. Vegetation types of the herb layer and simulated environmental factors under which they emerge, as well as their pastoral value, from which a first estimate of biomass production is calculated.

Table 2. Microclimate data overview for the plant growing season (AMJJAS) of 2010. Presented are mean parameter values for each altitude and pasture type.

Table 3. Simulated impact of drought on global utilization rates (GUR) in the three studied wood-pastures. An arbitrarily comparison of a hot year (2021, growing season mean air temperature 11.3 °C) to a normal year (2022, growing season mean air temperature 9.6 °C) under the B2 IPCC-SRES scenario. Long-term (1961-2010) average of the growing season temperature is 9.0°C.

769 Table 1

	Dunging intensity	Dunging intensity	Tree cover	Pastoral value PV ¹
Eutrophic pasture	High	High	Low	40
Oligotrophic pasture	High	Low	Low	20
Fallow	Low	Low	Low	10
Understory	Low	Low	High	40

¹ The pastoral value is based on vegetation surveys (Gillet & Gallandat 1996, Gillet 2002, 2008), except for understory. Here PV is artificially set to the value of eutrophic pasture, because the lower productivity of understory is expressed by a combined influence of drought and tree cover (see text).

770

771 Table 2

Altitude [m a.s.l.]	1350			1010			57	
Air temperature [°C]	10.0			12.3			15	
Air humidity [%]	67.3			77.1			71	
Precipitation [mm]	707.6			599.7			52	
Pasture type ¹	P	WP	F	P	WP	F	P	W
Soil temperature [°C] ²	11.2 ± 0.2	10.4 ± 0.1	9.7 ± 0.1	14.8 ± 0.1	13.3 ± 0.1	12.4 ± 0.1	17.5 ± 0.2	16.2
Soil moisture [%] ³	42.9 ± 2.8	41.3 ± 2.3	33.0 ± 2.7	28.9 ± 1.1	31.8 ± 3.6	31.8 ± 0.5	25.6 ± 0.5	25.7

¹ Pasture type codes, where P refers to unwooded pasture with 0% canopy shading, WP – sparsely wooded pasture with 40% and F – densely wooded pasture with 80% canopy shading.

^{2,3} Reported values for soil temperature and moisture are means and standard errors for five replicate plots.

772

773 Table 3

	GUR of EWP (<i>Les Cluds Sud</i>) [%]	GUR of MWP (<i>Les Planets Milieu Est</i>) [%]	GUR of IWP (<i>Les Planets Ouest</i>) [%]
Simulation year 2021	74.4	89.1	110.1
Simulation year 2022	67.8	78.7	97.6
Δ GUR between years 2021 and 2022	6.7	10.4	12.5
Average GUR in the period 1980-2000	70.0	83.8	104.4
Δ GUR between years 2021 and 2022 corrected ¹ for average GUR	9.5	12.4	11.9

¹ Dividing the simulated GUR by the average GUR corrects for the trivial effect of lower drought impacts in extensive pastures.

774

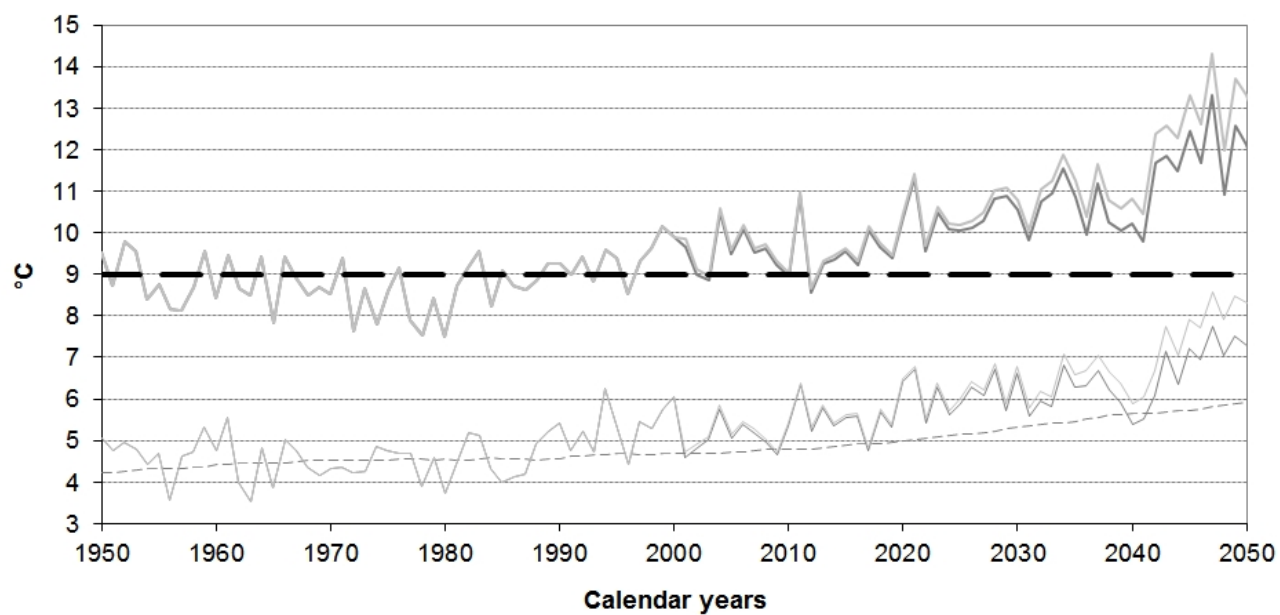
775

776

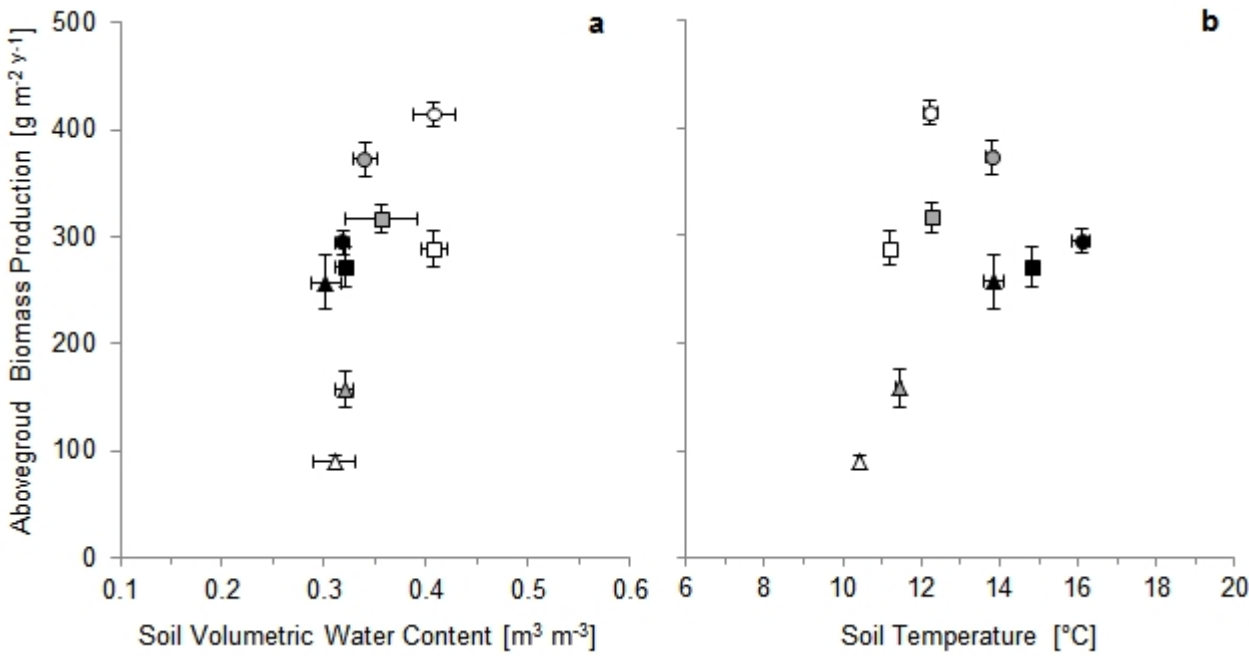
777 Figure 1



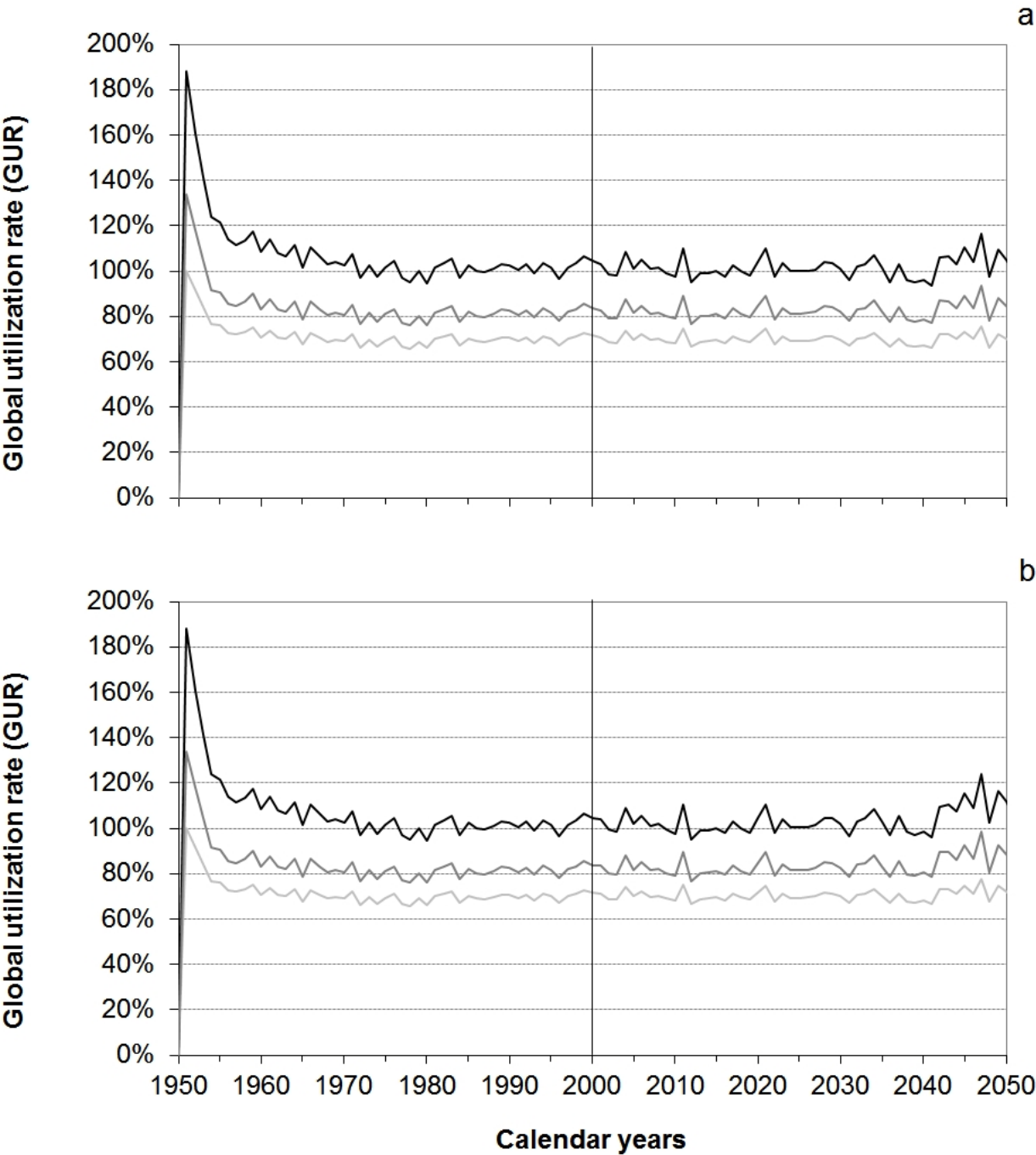
778
779 Figure 2



781 Figure 3



782
783
784



786
787
788

Figure 5

