Subalpine Pasture-Woodlands in a Changing Climate: the Role of Land Use Type in Ecosystem Resistance to Simulated Climate Change

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Table of contents

Summary

Climate change in temperate mountain systems and associated increase in temperature and decrease in precipitation are expected to have strong implications for vegetation productivity, species diversity and carbon turnover in subalpine grasslands. Little is known, however, about the interaction between the effects of climate change and those of local land use management and possible changes in landscape structure.

Pasture woodlands in the Swiss Jura Mountains are a traditional landscape, resulting from a long-lived sustainable use of grasslands and woodlands, and as such provide a suite of important ecosystem services to human society. These range from carbon sequestration and biodiversity preservation, to provision of timber and forage for livestock, and last but not least an aesthetic value, much appreciated by tourism.

In this thesis various aspects of ecosystem functioning have been studied, investigating the combined effects of experimental climate change and land use on structurally different wooded pastures. An altitudinal gradient method has been used to simulate future climate change conditions, by imposing warmer and drier climate on subalpine turfs transplanted at lower elevation. The resulting gradient in mean annual temperature and precipitation – ranging from cold and wet in the subalpine zone, to warm and dry in the colline zone – has allowed for the detection of tipping points and altered states of ecosystem functioning in response to the treatments. The method employed provided also the possibility for a direct comparison of three land use types: unwooded pastures, sparsely wooded pastures, and densely wooded pastures (the result of pasture management intensity), in their response to climate perturbation.

During the four years of experimental work, a series of observations have been made at the plot scale (square metre) in terms of plant performance and biogeochemical cycles, as well as at the landscape scale (hectare) in terms of forage production.

A general threshold level for ecosystem resistance to experimental climate change was detected between the moderate IPCC scenario (+2 K mean annual temperature; -20 % annual precipitation) and the intensive IPCC scenario (+4 K mean annual temperature; -40 % annual precipitation). A concomitant gradient in ecosystem response to climate change was observed across the three land use types. The intensively managed unwooded pasture type was consistently more affected by the experimental treatment and rarely exhibited signs of resistance, especially under the intense climate change scenario. A drastic loss of plant species diversity, reduction of herbaceous biomass, impaired litter decomposition and soil microbial metabolic activity have all contributed to the altered state of ecosystem functioning.

In contrast, the two extensively managed wooded pasture types showed considerable resistance to climate perturbation in terms of both above and belowground ecosystem processes. The reported inter-annual variation in herbaceous diversity and biomass production within these land use types demonstrated their resilience (recovery) potential too. Using a modelling approach for upscaling these results to the heterogeneous landscape of pasture woodlands in the Swiss Jura Mountains, has proven that extensively used wooded pastures could grant sustainable ecosystem services in terms of forage provision for cattle under climate change.

Considering that the two experimental climate change intensities implemented this study are the projected 'best' and 'worst' case scenarios for the coming decades, the reported resistance of wooded pastures to climate change has to be embraced, and sustainable land use set as a goal in high altitude mountain pastures.

Keywords

Climate change; subalpine; grassland; pasture; woodland; transplantation; altitude gradient; temperature; precipitation; snow; plant biomass; litter decomposition; soil respiration; soil microbial communities

Résumé

Le changement climatique dans les milieux montagneux modérés, ainsi que l'augmentation de températures et la réduction des précipitations associées, devraient avoir des conséquences pour la productivité végétale, la biodiversité, et le cycle de carbone des pâturages subalpins. Cependant, on ne sait que très peu sur les interactions entre les effets du changement climatique et ceux dérivant de l'utilisation du sol et des changements de la structure paysagère.

Les pâturages boisés des montagnes du Jura Suisse forment un paysage traditionnel, résultat d'une utilisation durable des pâturages et des bois. Celui-ci fournit à l'humain et la société plusieurs services éco-systémiques importants, à commencer par la capture de carbone, la préservation de la biodiversité et le stockage de bois et de forage, sans oublier sa valeur esthétique apprécié par le tourisme.

Dans cette thèse, plusieurs aspects du fonctionnement éco-systémique ont été étudiés par l'analyse des effets combinés d'un changement climatique expérimental et de l'utilisation du sol sur des pâturages boisés de structure différente. Une méthode de gradient altitudinal a été déployée pour simuler les conditions futures sous changement climatique, en imposant un climat plus chaud et sec à des carottes de sol transplantées à altitude inférieure. Il en résulte un gradient allant de froid et humide dans la zone subalpine, à chaud et sec dans la zone de collines. En réponse aux traitements appliqués, cette méthode a permis de détecter de points de basculement et des changements d'état de l'écosystème, ainsi que de comparer directement trois types de pâturages (ouverts, semi-ouverts, sous forêt) et leur réponse face aux perturbations climatiques.

Pendant quatre années de travail expérimental, plusieurs observations ont été faites à l'échelle du site (m2) concernant la performance de croissance et les cycles générale de la résistance de l'écosystème au changement climatique expérimental se situe entre le scénario IPCC modéré (+2 K température moyenne ; -20 % précipitations annuelles) et le scénario IPCC intense (+4 K température moyenne ; -40 % précipitations annuelles).

Un résultat correspondant a été observé dans les trois types de pâturages ; les pâturages ouverts sous utilisation intense s'est montré plus vulnérable aux traitements expérimentaux, tout particulièrement sous le scénario de changement climatique intense, et montre très peu de signes de résistance. La perte drastique de biodiversité végétale et de biomasse herbacée, ainsi que la réduction de la décomposition de litière et de l'activité microbienne du sol, ont conjointement contribués au changement d'état de l'écosystème. A l'opposé, les deux types pâturages sous gestion durable ont démontré une résistance considérable aux perturbations climatiques, tant au niveau des processus éco-systémiques souterrains que aériens. La variation interannuelle mesurée dans ces types de pâturages, en termes de biodiversité végétale et production de biomasse, apporte également la preuve de leur potentiel de récupération. Modélisant et transférant les résultats à l'échelle du paysage hétérogène des montagnes jurassiennes suisses a montré que ces derniers peuvent sont encore en mesure de fournir les services éco-systémiques en terme de provisions de forage sous conditions de changement climatique.

Sachant que les intensités de changement climatique implémentés dans cette étude correspondent au « best case » et « worst case » scenarios de siècles à venir, la résistance constatée des pâturages boisées doit être prise en considération, ainsi que la gestion durable des sols définie comme objectif dans les paysages montagneux de haute altitude.

Mots-clés

Changement climatique ; subalpine ; pâturage boisée ; transplantation ; gradient d'altitude ; température ; précipitation ; neige ; biomasse herbacée ; décomposition de litière ; respiration du sol ; communautés microbienne

Chapter 1

General introduction

1.1 Pasture woodlands of the Swiss Jura Mountains in transformation (the role of land use change)

Pasture woodlands are semi-natural systems found in places with long history of extensive livestock grazing and forest management (Etienne 1996). They are a dynamic landscape composed of patches with vegetation at different successional stages, which are shaped by the activity of large herbivores. The patterns of cattle's trampling, grazing and dunging are reflected in the landscape structure such that open grasslands are formed within forest stands due to the stimulated growth of pasture vegetation and the impeded forest regeneration (Gillet and Gallandat 1996a). As a consequence, the landscape evolves into a gradient of habitats ranging from open pastures to sparsely and densely wooded pastures, up to grazed forests.

Such landscapes are believed to have covered a large portion of Europe's lowland temperate zone (Vera 2000) and despite that this opinion has remained debatable (Birks 2005; Mitchell 2005; Moore 2005) their current distribution is largely limited to a number of mountain regions which have remained untouched by the pressures of human population density and the associated intense agricultural practices (Gillet and Gallandat 1996b). A typical area of subalpine pasture woodlands is the crest of the Swiss Jura Mountains (Figure 1.1) where within an altitudinal range between 900 and 1400 m a.s.l. seasonal pasturing of cows is practiced (Gillet and Gallandat 1996b). The dominant tree canopy forming species at this altitude is *Picea abies*, though *Fagus sylvatica* and *Acer pseudoplatanus* are also common in the pasture woodlands. The reasons for the success of spruce (*Picea abies*) are manifold but mostly relate to its life strategy regarding seed dispersal, germination rate, and herbivory avoidance (Buttler et al. 2009) and possibly also to the unusually cold oceanic climate of the region with mean annual temperature (MAT) of 4.5 °C and mean annual precipitation (MAP) of 1730 mm from which more than 400 mm fall as snow and stays on the ground for an average of 6 months per year (Source: MeteoSwiss). Studies of the landscape dynamics have demonstrated that the major driver of the landscape formation is the browsing activity of cattle, though foresters sometimes also intervene by taking down old and sick trees (Gillet 2008). Despite the fact that the prevailing form of pasturing is free ranging in which animals are roaming unattended during the entire summer season, there is also a tendency for intensification with implementing grazing rotation systems in which momentary stocking rates as well as fertilisation through urine and dung pats are very high (Gillet and Gallandat 1996b). Such intensification tendencies are detrimental to the pasture woodlands landscape, since they endanger tree regeneration and promote loss in herbaceous biodiversity (Gillet et al. 1999; Buttler et al. 2009).

The high vascular plant diversity in Swiss Jura pasture woodlands with up to 40 species per square meter results from the structural complexity and habitat niches presented by the mosaic mixture of forests and pastures (Dufour et al. 2006). Trees in grasslands may decrease wind speed and evaporation, protect against erosion, improve the water regime, but also decrease light availability, which reduces the quality and the quantity of the herbage, and increase litter accumulation. Having biodiversity preservation as a top goal for this century (Cardinale et al. 2012; Hooper et al. 2012) it is a priority to maintain the pasture-woodlands coexistence. The main threat for that is the separation between grassland and forest, since the recruitment of young trees is difficult in places with intensive grazing and fertilisation, whereas forest encroachment in abandoned pastures prevents grassland regeneration.

Current agricultural policy in Switzerland is not well adapted to meeting the requirements for ecological process understanding and land use management in mountain regions in general (Hirschi and Huber 2012), providing financial support per animal bred in areas rendering agriculture difficult (*i.e.* mountain regions). The reason is that remuneration per capita stimulates land use intensification and ultimately deteriorates landscape structure and the provision of ecosystem services within pasture woodlands (Huber et al. 2012). Pending agricultural reforms in Switzerland should indeed be targeted on remuneration for provided ecosystem goods and services and of landscape preservation through extensive land use (Huber et al. 2013). It has been recognised that land use changes resulting from either management intensification or abandonment is a major threat to mountain pasture ecosystems worldwide (Körner et al. 2006), with strong negative implications for biodiversity (Tasser and Tappeiner 2002; Niedrist et al. 2009) and ecosystem functioning (Theurillat and Guisan 2001). Considering the strong negative implications of biodiversity loss for ecosystem functioning, with a magnitude similar to that of most other anthropogenic impacts (Hooper et al. 2012), it is therefore a priority for ecologists to further investigate the mechanistic drivers of plant community shifts under climate change and its interaction with land use.

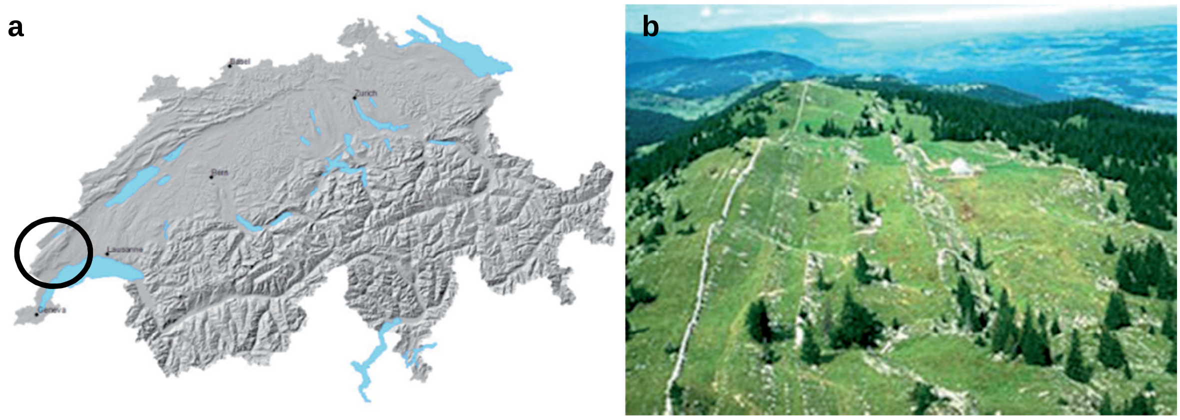

Figure 1.1. Swiss Jura Mountains' a) study site location (in circle) and b) its traditional pasture woodlands landscape (photo Jean-Daniel Gallandat).

1.2 Climate change and its effects on mountain ecosystems

Global warming and associated environmental changes are predicted to have a strong impact on mountain ecosystems this century (Solomon et al. 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 (Schär et al. 2004) and prolonged drought (Beniston 2009). Model simulations predict these tendencies to become even more pronounced regionally. For instance, northern hemisphere temperate mountains are meant to 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 during the growing season will intensify the dry periods in Central Europe (Frei et al. 2006; Beniston et al. 2007). Winter climate in these regions is also undergoing a change with ever decreasing duration and thickness of snow cover as well as an increased rain-to-snow ratio (Beniston 1997; Mote et al. 2005).

There is a rising awareness that the ecological responses to climate change will be strong and with far reaching consequences (Walther et al. 2002; Root et al. 2003). Both episodic extreme climate events, such as summer heat waves (Ciais et al. 2005; Reichstein et al. 2007; Teuling et al. 2010) and winter warm spells (Groffman et al. 2001; Campbell et al. 2005; Edwards et al. 2007; Wipf and Rixen 2010; Bokhorst et al. 2012), and the steady rise in global terrestrial temperatures (Chen et al. 2011; Elmendorf et al. 2012b; Gottfried et al. 2012) have been shown to exert a strong impact on ecosystem functioning and plant community composition. These would also have repercussions on the belowground ecosystem either directly or through its linkages with aboveground processes (Wardle et al. 2004; Bardgett et al. 2013). Since soils represent the earth's largest terrestrial organic carbon sink and this role is maintained though net differences in photosynthetic uptake and respiratory loss (Kutsch et al. 2009) small changes in the rates of the latter can have large impacts on soil carbon sequestration. Indeed, it is recognised that plant litter and soil organic matter decomposition form one of the major carbon fluxes from terrestrial ecosystems exceeding that from burning of fossil fuels (Houghton 2007) and as such can have direct feedback to climate change.

The characteristic temperature limitation of biological processes in cold-adapted mountain ecosystems (Körner 2003) makes them very prone to experience strong impacts from global warming. Both regional precipitation patterns (Engler et al. 2011) and land use intensity (Theurillat and Guisan 2001; de Vries et al. 2012) will interfere with this process presenting even further threats to their sustainable functioning. This calls for an integrative assessment of climate change and land use impacts on mountain ecosystems, a case study of which is presented hereby.

1.3 Outline of the transplantation experiment and the thesis objectives

In order to anticipate the evolution of subalpine wooded pasture ecosystems under future climate and land use changes, this project focused on the interplay between soil, vegetation and climate. It was aimed at providing experimental evidence for chief ecosystem processes, with emphasis on the quality of the ecosystem services provided. The main interest was placed on vegetation turf resistance to climate change along an unwooded – densely wooded pasture gradient (Figure 1.2), where plant productivity, diversity and succession along with rates of carbon cycling and microbial activity provided measures of ecosystem functioning at both plot and landscape level.

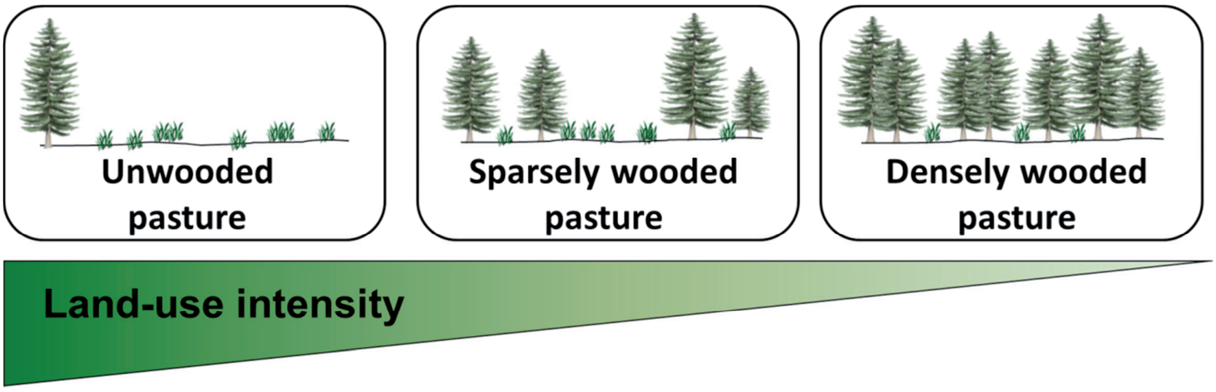

Figure 1.2. Nomenclature of canopy cover classes within pasture woodlands landscape resulting from grazing intensity of cattle.

In order to simulate a year-round warmer and drier climate the natural climate variation along an altitudinal gradient was used as a proxy (see Körner 2007). The aim was to simulate realistic climate change scenarios for the second half of the 21st century predicted by the latest IPCC report (Meehl et al. 2007) and downscaled for Switzerland (CH2011) providing regionalised interpolated projections integrating therein trends for temperature increase and precipitation decrease. By using permanent meteorological stations within the network of the Federal Office of Meteorology and Climatology (MeteoSwiss) we obtained high resolution regional data on the variation of mean annual temperature (MAT) and mean annual precipitation (MAP) in relation to altitude in the Swiss Jura Mountains. A total of 15 stations were selected, ranging from 430m a.s.l. to 1760m a.s.l. lying within less than 50 km apart in the Canton of Vaud, Switzerland. We observed a general increase of +0.5 K in MAT and a decrease of -20 % MAP for each 100 m decrease in altitude along the SE slope of the Swiss Jura Mountains. These relationships served for the selection of the transplantation sites such that in comparison to a control site at 1350 m a.s.l. (Combe des Amburnex, N 46°54', E 6°23') a +2 K MAT and -20 % MAP was achieved at 1010 m a.s.l. (Saint-George, N 46°52', E 6°26'), a +4 K MAT and -40 % MAP at 570 m a.s.l., (Arboretum d'Aubonne, N 46°51', E 6°37'), and a +5 K MAT and -50 % MAP at 395 m a.s.l. (Les Bois Chamblard, N 46°47', E 6°41'). The two stations at 1010 m a.s.l. and 570 m a.s.l. corresponded to the IPCC scenario A1B for a moderate increase in greenhouse gas emissions and to scenario A2 for a high increase in greenhouse gas emissions, respectively. The station at 395 m a.s.l. was chosen to represent an extreme scenario with climate variables lying at the positive tail distribution of model predictions under the A2 scenario.

The control site at Combe des Amburnex lies within the Park Jurasien Vaudois and represents a typical landscape of subalpine pasture-woodlands along the crest of the Swiss Jura Mountains (see Figure 1.1b). The three land use types selected for transplantation (Figure 1.2) were situated within wooded pastures of similar size (circa 2 ha) but different management intensities and tree cover. They were in close proximity to each other (less than 1 km apart) and shared the same geomorphology, microtopography and exposition. Within each of the three pasture types, plots were randomly selected to represent the characteristic herbaceous vegetation of the respective area. These 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 cm^2 size and of 35 cm height, containing a 5 cm layer of gravel on the bottom allowing for the drainage of the mesocosms through a set of pipes. 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. All mesocosms were left in place to recover from the excavation until the end of the vegetation season and then transported to the transplantation sites in October 2009. We assessed the effect of mesocosm construction on the abundance of macroarthropods and earthworms and found no significant difference to the sites of origin. This was important, since previous studies have reported a strong effect of macrodecomposers on soil organic turnover within mesocosms (Seeber et al. 2006).

Following a random selection procedure, at each of the three highest transplantation sites (1350 m, 1010 m, and 570 m a.s.l.) five replicate mesocosms with turfs from unwooded pasture (UW), sparsely wooded pasture (SW) and densely wooded pasture (DW) were allocated. Due to logistical reasons at the lowest site (395 m a.s.l.) only five replicate mesocosms from the UW type were transplanted. All mesocosms were dug down to surface level into previously prepared trenches in the ground thus preventing lateral heat exchange with the atmosphere. Since at each site the mesocosms were placed in a common garden with no light interception mesocosms with turfs from the two wooded pastures (SW and DW) were shaded from direct sun light to simulate the natural light conditions in the corresponding habitats. Two types of UV resistant nylon mesh, which intercepted PAR by 40% and 80% but still allowed for rain water to pass through, were installed on wooden frames at 50 cm above the ground surface. These levels of PAR interception were based on field data collected during the 2009 growing season in each of the three land use types. The shade roofs were designed to remain in the field only during the snow free period of the year, as to avoid interference with snow cover establishment. 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. Incoming seed rain from local plants at each transplantation site was limited by frequent mowing of the surrounding vegetation.

Each mesocosm was equipped with a drainage system and was connected to a water tank thus representing a zero potential lysimeter collecting soil solution and precipitation/snowmelt runoff. ECH2O EC-TM sensor probes coupled to Em50 data-loggers (Decagon Devices, Inc., USA) recorded soil temperature and volumetric water content in each mesocosm at the top-soil (0 to -3 cm) every minute and data were averaged over one hour intervals. Climate parameters at each transplantation site were monitored continuously throughout the experiment by means of automated weather stations (Sensor Scope Sàrl, Switzerland), measuring rain precipitation (non-heated tipping bucket gauges) and air temperature and humidity 2 m above the ground surface at one minute intervals.

A baseline analysis of the vegetation in the mesocosms (Figure 1.3) revealed that the unwooded pasture vegetation is of a rich grassland type, has a higher above ground biomass (AGB) than its wooded pastures counterparts and is characterised by a higher abundance of graminoids. Both wooded pasture types, in contrast, have a higher abundance of forbs. Sparsely wooded pasture vegetation has a characteristic dense moss layer (dominated by *Rhytidiadelphus triquetrus*), whereas densely wooded pasture vegetation is of a forest understory type with patches of bare ground, accumulated litter and occasional ligneous species. The vegetation of three land use types shared a similar vascular plant diversity of *ca*. 30 species m^{-2}.

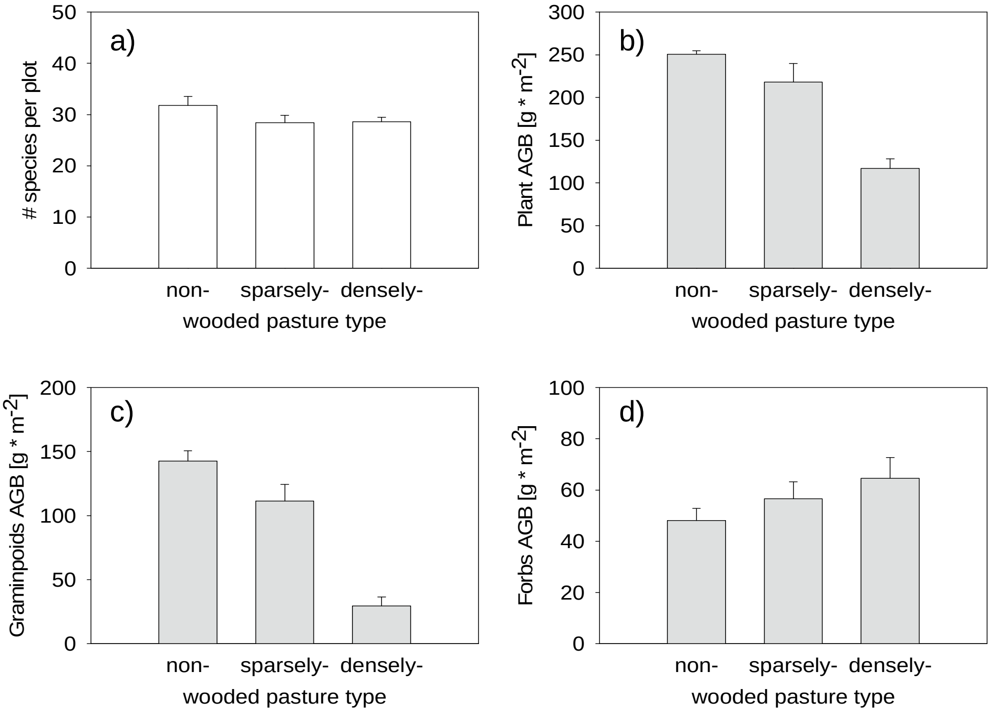

Figure 1.3 Vegetation analyses from the 2010 growing season (*i.e.* the first year following the transplantation experiment at the control site at 1350 m a.s.l. Presented are a) vascular plant richness, b) aboveground plant biomass (AGB), and AGB separated in two plant growth forms: c) graminoids and d) forbs

Chapter 2

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

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

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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. We coupled experimental and modelling approaches to assess the impact of climate change on the pasture-woodland landscape. We drew conclusions on the resistance potential of wooded pastures with different management intensities by sampling along a canopy cover gradient. This gradient spanned 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 regionalized Intergovernmental Panel on Climate Change 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

Aboveground biomass; drought; ecotone; grassland; pasture; silvopastoral system; subalpine; transplantation; woodland

2.1 Introduction

2.1.1 History and importance of pasture-woodlands

Pasture-woodlands are a traditional human-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 are 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 socioeconomic view, are the main users of wooded pastures, and as such, may deliberately shape the landscape into an unwooded one. Apart from farming, in some regions, revenues generated from forestry activities may be substantial (Gillet and Gallandat 1996b). 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 to be a major threat for mountain ecosystems worldwide (Körner et al. 2006), little is known about its interaction with climate change in the future.

2.1.2 Climate change in the European mountains

Global warming and associated environmental changes are predicted to have a strong impact on high-altitude ecosystems this century (Solomon et al. 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 during the growing season 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).

2.1.3 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 efficient management. Currently, there is a wealth of literature, encompassing various experimental methodologies, 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 relatively few published studies have used this technique, some successful attempts at contrasting terrestrial environments have been carried out: in peatlands (Wieder and Yavitt 1994; Breeuwer et al. 2010), in boreal forests (Hobbie and Chapin 1998), in montane meadows (Bruelheide 2003), in subalpine grasslands (Sebastia 2007), and in alpine vegetation (Scheepens et al. 2010). The results from those studies, however, outline idiosyncratic patterns of 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 (Bruelheide 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 of 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). Other plants may benefit from their inherent tolerance of specific environmental stress (Buchner and Neuner 2003; Brock and Galen 2005). Overall, more fertile early successional grassland communities have been shown to be 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; Mariotte et al. 2013), whereas grazing of highland pastures has been shown to both promote herbaceous richness and reduce evapotranspiration loss and thus water consumption (Körner et al. 2006). In comparison to grasslands, forests exhibit 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.

2.1.4 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 coupled an experimental with a modelling approach. We believe that such combinations of observational, manipulative, and modelling techniques are highly adapted to assessing 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 the landscape level and in the proximate time frame of climate change projections (until 2050 AD).

2.1.5 Hypotheses

We hypothesized 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 landscape-scale forage production in wood-pastures would be more stable during projected heat wave periods than 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.

2.2 Methods

2.2.1 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 meters above sea level (m a.s.l.), including more than 450 mm of 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 a.s.l. were chosen according to their tree canopy cover, which resulted 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 1 km of each other, each measured about 2 ha, and all shared the same geomorphology, microtopography, and aspect. Within each of the three pasture types, 15 plots were randomly selected to represent the characteristic herbaceous vegetation of the respective area. To allow for a transplantation of soil turfs, plots were divided into 12 separate 20 cm × 20 cm and 30-cm deep soil cores and were assembled back into rectangular PVC boxes of 60 cm × 80 cm and 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 until the end of the vegetation season to recover from the excavation, and then were 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., 46°54' N, 6°23' E), Saint-George (1010 m a.s.l., 46°52' N, 6°26' E), and Arboretum d'Aubonne (570 m a.s.l., 46°51' N, 6°37' E). The first site at 1350 m a.s.l. served as a control site with unchanged climate. The site at 1010 m a.s.l. was chosen to represent a combination of annual temperature increase of +2 K and a precipitation decrease of -20%. The site at 570 m a.s.l. represented a combination of annual temperature increase of +4 K and a precipitation decrease of -40%. These preliminary approximations were derived from interpolated data from nearby weather stations. At each site, 15 mesocosms, thus representing five replicates of each pasture type and all originating from the Combe des Amburnex, were transplanted following a completely randomized 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 photosynthetic active radiation by 40% and 80%, respectively, thus 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 in order to avoid interference with the snowpack. As a means of keeping the grazing pressure on the plots and avoiding a confounding effect of "abandonment" and accumulation of standing litter, plots were clipped close to ground level at the end of the vegetation growing season.

Herbaceous biomass was harvested at the end of July 2010 during the first year after turf transplantation, and served as an estimate of annual AGB production. At each plot, the vegetation within a fixed area of 35 cm × 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, which measured at a one-minute interval air temperature and humidity 2 m above the ground surface, as well as rain precipitation. ECH$_2$O EC-TM sensor probes coupled to Em50 data-loggers (Decagon Devices, Inc., USA) recorded soil temperature and volumetric water content at topsoil 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.

2.2.2 Statistical analysis of experimental data

The experimental design allowed for the explanation of annual variation in herbaceous biomass during the first year after transplantation by four factors: two categorical ones – initial pasture type and altitude 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 to test the significance of single factors and their two-way interactions. Assumptions of normality and homoscedasticity of the residuals were verified visually using diagnostic plots.

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 to predict the seasonal AGB production from the two continuous variables – tree cover percentage and degrees 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 change 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 incorporated into the landscape model of wooded pastures WoodPAM.

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

2.2.3 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 due to selective grazing of large herbivores (cattle) by explicitly considering the food chain from primary productivity to forage consumption by livestock. During simulations, selective foraging by 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.

Table 2.1. 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.

	Grazing 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).

In WoodPaM, a pasture is represented by an arrangement of quadratic, 25-m wide, grid cells (Figure 2.1). In each cell the vegetation is represented by an 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, the herbaceous vegetation is categorized in the following four vegetation types—eutrophic pasture, oligotrophic pasture, fallow, and understory, which differ in pastoral value (PV) (Table 2.1).

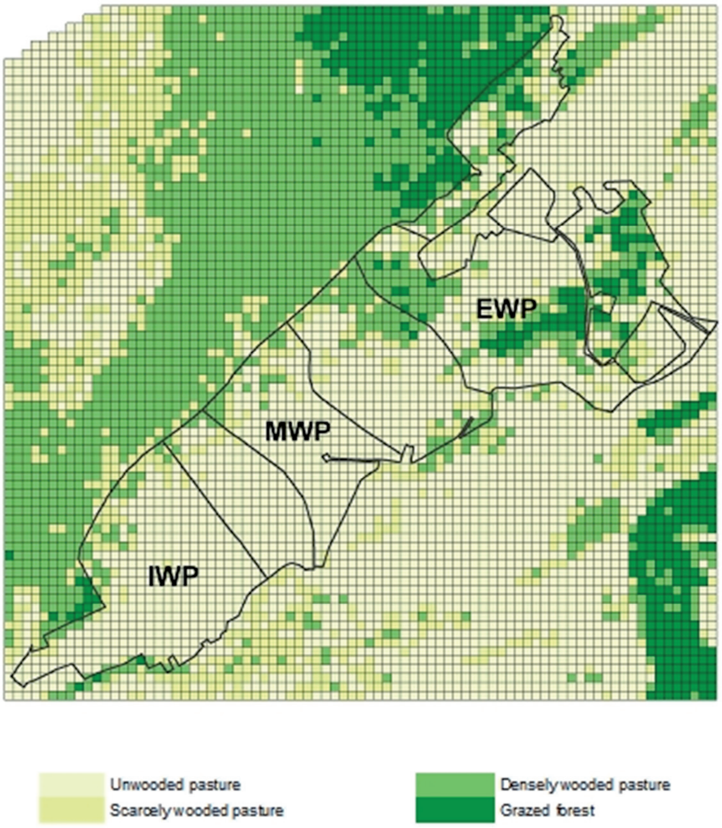

Figure 2.1. Grassland-forest mosaic in year 2000 of the simulated pastures as estimated by aerial photograph interpretation (see Chételat et al. 2013): The almost treeless intensively grazed pasture Les Planets Ouest (IWP), the moderately grazed pasture Planets Milieu Est (MWP), and the extensively grazed true mosaic pasture Les Cluds Sud (EWP).

A first estimate of yearly forage production “P” in a grid cell is computed based on a new regression model (in comparison to Gillet), 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 growing period “vegdays”, with:

P = yearly forage production ($t\ DM \cdot ha^{-1} \cdot a^{-1}$)
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 growing period (days)
fpm = maximal production ($20\ t\ DM \cdot ha^{-1} \cdot a^{-1}$)
fpi = “initial” production for PV = 0 ($8.5\ t\ DM \cdot ha^{-1} \cdot a^{-1}$)
ra = altitude effect on the growth coefficient ($2.152 \cdot 10^{-5}$)
rm = maximal growth coefficient for A = 0 (0.05)

During simulations, the first estimate of yearly forage production was calculated from the current pastoral value of the vegetation types in each grid cell and the average length of the vegetation growing period during the last 50 simulation years. By this means, we took into account that the productivity of grassland plant communities increases slowly following the general trend of temperature rise (Figure 2.2) rather than spontaneously in single warm years. In the second case, a drought effect has to be expected, which we addressed separately.

As a further innovation in comparison to former versions of WoodPaM (see Gillet 2008; Peringer et al. 2013), we modified the first estimate of forage production by applying a multiplier “D” for the drought effect of high average temperatures in the vegetation growing period during hot years. This modifier was calculated from the regression model of AGB response to transplantation along the climate warming gradient (see sections 2.2.2 and 2.3.1). No modifier was 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 growing period and the long-term mean temperature of the vegetation growing periods during years 1961–2010 (the experiment took place in year 2010, thus plant communities are adapted to recent past climate). Because 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 was set equal to the value of grassland (Table 2.1). The combined impact of drought and tree cover was computed according to Equation 2.1:

$$D = (55.670 - 3.291\,\Delta T - 0.456\,TreeCover + 0.070\,TreeCover\,\Delta T) / 55.670, \text{ for } \Delta T > 0 \tag{2.1}$$

$$D = 1, \text{ for } \Delta T \leq 0$$

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

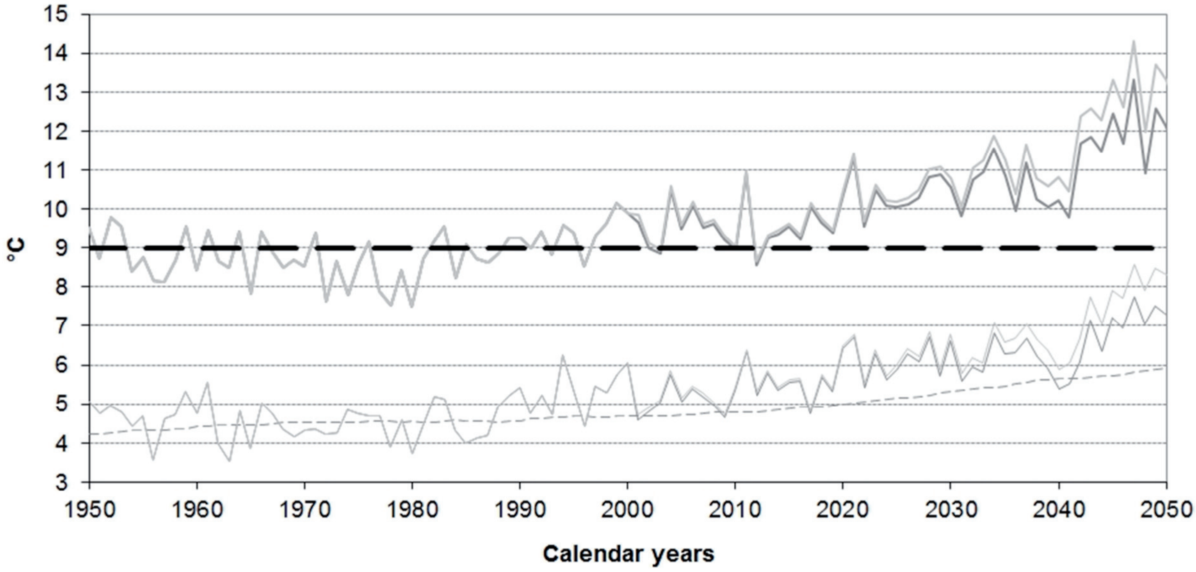

Figure 2.2. Regionalised observed (1950-2000 AD) and simulated (2000-2050 AD) annual (thin solid lines) and vegetation growing season (thick solid lines) temperatures for the two IPCC-SRES scenarios (see text): B2 (dark grey) and A1FI (light grey). The average temperature of the vegetation periods from 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.

This model modification assumed that (1) the productivity of mountain grassland communities slowly increases with the increasing length of the vegetation growing period experienced during the last 50 years (community adaptation); however, (2) their productivity in extraordinarily hot years is consistently reduced by drought. We set the current climate (Figure 2.2) as a baseline for the estimation of the drought impact because we did not expect the development of new (drought resistant) genotypes, especially 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 growing 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 was expressed as local utilization rate (LUR) and was based on a daily forage consumption of 18 kg DM per livestock unit. The same ratio calculated at pasture level was termed global utilization rate (GUR).

For a further detailed description of the model structure and the implementation of herb layer and tree layer dynamics, as well as rules for selective grazing, refer to Gillet (2008). Recent model refinements beyond this model description are given in Peringer et al. (2013).

2.2.4 Design of simulations

We simulated forage production under observed and projected climate in three separate wooded pastures in the region of Bullet, Switzerland. The pastures are located 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 to one other (Figure 2.1); hence, they share identical climate but differ in grazing intensity and consequently vegetation structure. Les Planets Ouest (1200 m a.s.l., 46°83' N, 6°55' E) is an intensively used commonage with 46 livestock units (LU) on 25.6 ha, resulting in 1.79 LU/ha for 170 days/year (see also Chételat et al. 2013). This pasture is practically treeless, and for the purpose of this study, is referred to as Intensive Wooded Pasture (IWP). Les Planets Milieu Est (1200 m a.s.l., 46°84' N, 6°55' E) is mostly open grassland but features some sparsely wooded pasture far in the northwest. It has a moderate stocking density of 22 LU on 14.1 ha, resulting in 1.56 LU/ha for 135 days/year, and is referred to as Moderate Wooded Pasture (MWP). Les Cluds Sud (1200 m a.s.l., 46°84' N, 6°56' E) 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 socioeconomic developments will likely lead to reduced stocking of wooded-pastures (Huber et al. 2013), for the purpose of this study, we simulated constant stocking densities.

Time series of temperature and precipitation were derived from the regionalization of observed climate in the period 1950–2000 AD and two climate change scenarios from the Intergovernmental Panel on Climate Change Special Report Emissions Scenarios (IPCC-SRES 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 D. Schmatz, WSL-Switzerland, personal communication). We selected the moderate scenario B2 with +2 K warming and the extreme scenario A1FI with +4 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 2.2, together with the yearly mean temperatures of the vegetation growing 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-year spin-up period: 1950–2000 AD. Simulations run from 2000 on for a period of 50 years.

2.3 Results

2.3.1 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 2.2). Following this treatment, soil temperature generally increased, while soil moisture decreased (Table 2.2). 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 2.3). 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 2.3, and the statistically significant interaction between pasture type and altitude). The transplantation altitude alone had no consistent effect on AGB across the pasture types.

Table 2.2. Microclimate data overview for the plant growing season (AMJJAS) of 2010. Presented are mean parameter values for each altitude and pasture type.

Altitude [m a.s.l.]	1350			1010			570		
Air temperature [°C]	10.0			12.3			15.1		
Air humidity [%]	67.3			77.1			71.7		
Precipitation [mm]	707.6			599.7			524.6		
Pasture type [1]	P	WP	F	P	WP	F	P	WP	F
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 ± 0.1	15.3 ± 0.2
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 ± 1.1	23.4 ± 1.1

[1] Pasture type codes, where P refers to unwooded pasture with 0% canopy shading, WP – sparsely wooded pasture with 40% canopy shading, 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.

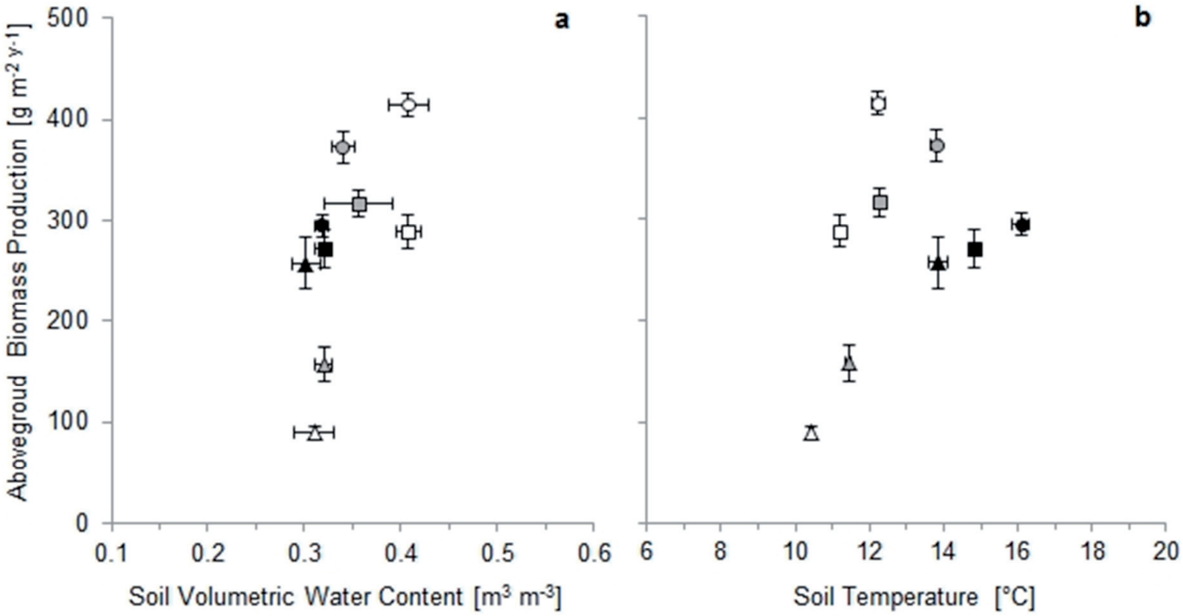

Figure 2.3. Change of above-ground biomass production in relation to (a) soil moisture, and (b) soil temperature in unwooded pastures (circles), sparsely wooded pastures (squares) and densely wooded pastures (triangles). Altitudes of experimental plots are 570 m a.s.l. (black symbols), 1010 m a.s.l. (grey symbols) and 1350 m a.s.l. (empty symbols).

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 2.2:

$$AGB = 55.670 - 3.291\ \Delta T - 0.456\ TreeCover + 0.070\ TreeCover\ \Delta T \qquad (2.2)$$

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 2.2.3).

2.3.2 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 %). A 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.

Figure 2.4. Global utilization rates (GUR) of produced forage for the three pastures and the two IPCC-SRES (2000) 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).

From year 2000 onwards, utilization rates did not decrease, as one would expect from the increase in productivity following the prolongation of the vegetation period with climate change (see Figure 2.2). 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 IWP peak values passed 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 (+4K) such effects were even more pronounced, especially in the projected heat wave 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 2.4) 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 though the comparison of a pair of simulated years with hot (2021) and cool (2022) temperatures from the simulation continuum of IPCC-SRES climate change scenario B2 (Figure 2.2). 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 2.3 and Figure 2.5). Similar drought impacts on forage production were also recognisable within the grasslands of MWP and EWP (Figure 2.5), however, the utilization rate in EWP, which is a true forest-grassland mosaic, increased only with 6.7% in GUR (Table 2.3). 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 long term average GUR. As seen in Table 2.3, 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.

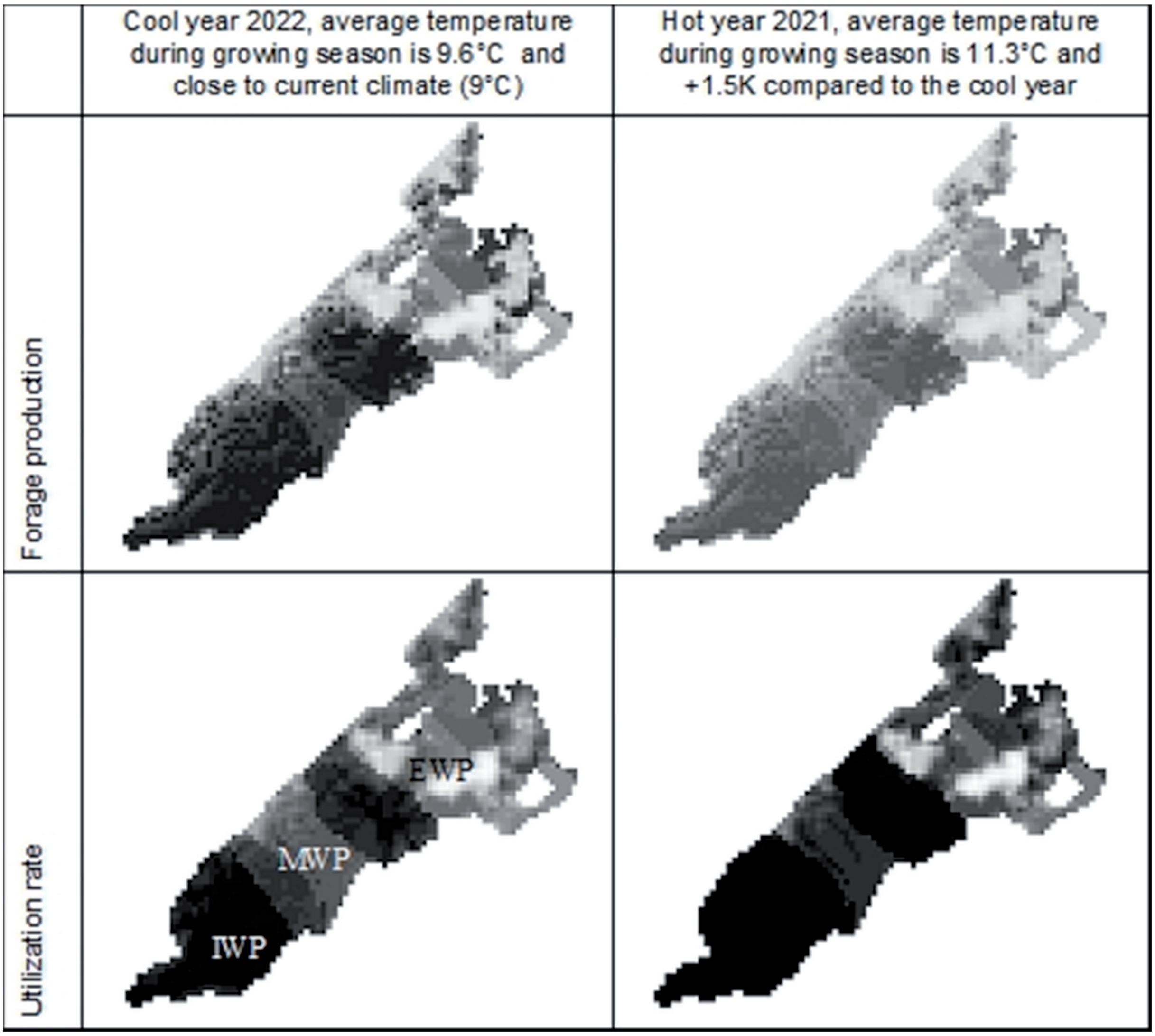

Figure 2.5. Output maps of forage production and local utilization rate (percentage consumed forage) in two arbitrarily chosen years – a hot one (2021) and a cool one (2022), based the moderate climate change scenario B2 with contrasting average temperatures in the vegetation period (Δ 1.5 K). Darker tones indicate higher values of the respective parameters.

Table 2.3. 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.

	GUR of EWP (*Les Cluds Sud*) [%]	GUR of MWP (*Les Planets Milieu Est*) [%]	GUR of IWP (*Les Planets Ouest*) [%]
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.

2.4 Discussion

2.4.1 Distinct effects of climate change on herbaceous production across land-use 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 under warmer climate. 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 shortly after the 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. Moreover, we consider unwooded pastures as intensively managed, but more so in relative terms in comparison to wooded ones, since they are generally subalpine pastures rather than farming fields.

2.4.2 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. 2013), 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. (2013) 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. 2013) 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. 2013), such kind of resilience of the system is a precious good, because it is rapidly destroyed but slowly reestablished. Chételat et al. (2013) 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. 2013). Either courses of intensification or abandonment would place the ecosystem's stability at stake and disrupt the delivery of its prime ecosystems services.

2.5 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.

2.6 Acknowledgements

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Chapter 3

Transplantation of subalpine wood-pasture turfs along a natural climatic gradient reveals lower resistance of unwooded pastures to climate change compared to wooded ones

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Abstract

We used an altitudinal gradient to evaluate the effect of year-round warmer and drier climate on semi-natural subalpine grasslands. Turf mesocosms from three pasture-woodland land use types: unwooded pasture, sparsely-wooded pasture and densely-wooded pasture, spanning a gradient from high to low management intensity, were transplanted downslope testing for their resistance to two intensities of climate change.

We found a strong overall effect of intensive (+4 K scenario) experimental climate change (*i.e.* warming and reduced precipitation) on plant communities' structure and function while moderate (+2 K scenario) climate change did not affect substantially the studied land use types. Under the +4 K scenario the individual land use types were affected differently, with a 60 % decrease of aboveground biomass (AGB) in unwooded pasture turfs, a 40 % decrease in sparsely-wooded pasture turfs, and none in densely-wooded ones. Similarly, unwooded pasture turfs experienced a 30 % species loss, an advanced phenological development (30 days), and a mid-season senescence due to drought stress, while no such effects were recorded for the other land use types.

The observed threshold in the response of subalpine grasslands to warmer and drier climate has important implications for the resistance potential of these ecosystems in the forthcoming decades. The evidence for strongest impacts of climate change on unwooded pastures provides a scope for a sustainable landscape management of pasture-woodlands, with a clear message against landscape segregation and land use intensification.

Key words

Climate change; gradient; land use; mesocosm; NDVI; plant species richness; plant growth form; transplantation; ^{13}C

3.1 Introduction

There is a rising awareness about the current change in climate (Solomon et al. 2007) and about ecological responses to it (Walther et al. 2002; Root et al. 2003). Recent climate impact studies have reported plant community shifts in cold biomes due to the observed global warming (Elmendorf et al. 2012b) and the predicted future warmer climate (Walker et al. 2006; Elmendorf et al. 2012a). Plants have been shown to track changes in temperature by shifting their distributions to either higher altitudes or to higher latitudes (Chen et al. 2011), thus forming new communities with species assemblages adapted to a warmer climate (Gottfried et al. 2012). The general notion from these meta-analyses is that overall plant diversity and richness have not been significantly affected by a warming climate, nevertheless Klein *et al.* (2004) have shown there is potential for rapid community responses depending on land use practices.

Concomitant land use change with either management intensification or abandonment in mountain pastures has been considered a major threat to these ecosystems worldwide (Körner et al. 2006), with strong negative implications to biodiversity (Tasser and Tappeiner 2002; Niedrist et al. 2009). Land use practices can interact with ecosystems' response to climate change (Theurillat and Guisan 2001) by either accelerating it (forest encroachment, grazing overpressure, eutrophication) or counteracting it (traditional practices with low management intensity). Considering the daunting aftermath of biodiversity loss for ecosystem functioning, with a magnitude similar to that of most other anthropogenic impacts (Hooper et al. 2012), it is therefore a priority for ecologists to further investigate the mechanistic drivers of plant community shifts under climate change and its interaction with land use.

Subalpine pasture woodlands, such as those found on the crest of the Swiss Jura mountains, have been a traditional form of land use for millennia (Gillet and Gallandat 1996b), providing equal shares of pastoral land and timber in a patterned landscape where forest encroachment is suppressed by browsing of livestock and extensive pasture management (Buttler et al. 2009). The resulting heterogeneity in the landscape accommodates high floristic diversity (Dufour et al. 2006), which could potentially serve as a buffer to environmental and climate change (Grime et al. 2000; Lavorel 2007). In addition, the more conservative water use efficiency of wooded grasslands compared to unwooded is capable of mitigating heat wave effects on forage production at the landscape scale (Gavazov et al. 2013) and this might also foster ecosystem resistance to climate change effects.

In this study, we present an integrative approach for investigating the response of land use specific vegetation types with subalpine distribution, to both moderate and high levels of climate change, corresponding to the A1B and A2 scenarios outlined by Meehl *et al.* (2007). Our aims were (1) to compare the diversity and biomass responses of plant communities, shaped under contrasting land use history, to different intensities of experimental climate change. To this end we transplanted turfs with vegetation from three land use types, spanning a gradient from open grassland to forest understory, along an altitudinal transect, thus simulating year-round increase in temperature and decrease in precipitation and period of snow cover. This set up allowed us (2) to determine the resistance potential to climate perturbation and the change in species composition and primary production of each land use type. Measures of plant phenology and tissue stable-isotopic signatures were intended (3) to provide a mechanistic explanation of the observed processes leading to changes in community structure and function in response to climate change.

We expected that (1) simulated warmer and drier climate at lower altitude would result in a prolonged vegetation growing season with possible soil moisture limitation at its peak, which (2) would ultimately result in shifts in plant phenology, community composition and ecosystem productivity. We also anticipated (3) these effects to be more strongly expressed in the unwooded pastures due to their intensive land use and the resulting vegetation structure.

3.2 Materials and methods

3.2.1 Site description and design of the experimental climate change

The results presented in this study are from the second year of a climate manipulation study and reflect processes during the entire plant growing season of 2011. Details on the choice of study sites, the pastoral management practices within each land use type and the construction of the mesocosms are described by Gavazov et al. (2013). Briefly, in 2009, 45 mesocosms made of rectangular PVC boxes 60 × 80 cm and 35 cm in height were set up, containing soil monoliths of 30 cm depth and their intact herbaceous vegetation. The depth of these soil cores was sufficient to contain most grassland roots. These turfs originated from Combe des Amburnex (N 46°55’, E 6°24’) – an area of subalpine pasture-woodlands situated along the crest of the Swiss Jura Mountains, circa 1350 m a.s.l. Each mesocosm contained one of the following three land use types: a densely wooded (DW) pasture, a sparsely wooded (SW) pasture, or an unwooded (UW) pasture. The given order reflects a diminishing canopy cover of the dominant tree species *Picea abies* due to an increasing intensity of pasture management, where ecosystem successional stage is kept in-check by cattle grazing pressure. Unwooded pasture vegetation is of a rich grassland type, has a higher productivity than its wooded pastures counterparts and is characterised by higher frequency of graminoids. Both wooded pasture types, in contrast, have a higher frequency of forbs. Sparsely wooded pasture vegetation has a characteristic dense moss layer (dominated by *Rhytidiadelphus triquetrus*), whereas densely wooded pasture vegetation is of a forest understory type with patches of bare ground, accumulated litter and occasional ligneous species. The vegetation of three land use types shares a similar vascular plant diversity of *ca.* 30 species m^{-2}.

In order to create a year-round effect of climate warming and reduced precipitation with respect to the ambient climate at the mountain crest, mesocosms were transplanted to one of the three experimental sites: 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 transplantation control site lying 1.5 km from the coring location, with a mean annual rainfall of *ca.*1750 mm, including more than 450 mm snow precipitation and a mean annual temperature of 4.5 °C. The other two sites 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. (from here on referred to as +2 K scenario), and of +4 K and -40 % at 570 m a.s.l. (referred to as +4 K scenario). These data were spatially interpolated from nearby weather stations (Source MeteoSwiss). The temperature increments were chosen in accordance to the moderate A1B and the intensive A2 climate change scenarios outlined by the latest IPCC report (Meehl et al. 2007) and the predicted concurrent decrease of precipitation for temperate regions

(Frei et al. 2006; CH2011). At each site, fifteen mesocosms (*i.e.* five replicates of each land use type) were transplanted to a common garden 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. In order to limit seed rain of local plants into the plots, the area in immediate proximity to the mesocosms was covered with geotextile and the whole experimental site was mowed fortnightly.

Mesocosms with turfs from sparsely wooded pastures and densely wooded pastures were shaded using two types of UV resistant nylon mesh, which reduced photosynthetically active radiation (PAR) by 40% and 80% respectively, thereby simulating previously recorded light conditions in the corresponding land use types during the 2009 growing season (*unpublished data*). The mesh fabric was suspended on wooden frames 50 cm above the ground surface. Whilst it did not alter rainfall input, it significantly reduced soil moisture evaporation and limited the incoming solar radiation heat flux (Table 3.1). The shades remained in the field only during the snow free period of the year, as to avoid interference with snowpack. As a means of simulating the grazing pressure on the plots and to avoid a confounding effect of "abandonment" and accumulation of standing litter, vegetation was clipped close to ground level at the end of each growing season.

3.2.2 Climate measurements

Climate parameters were monitored continuously throughout the experiment by means of an automated weather station (Sensor Scope Sàrl, Switzerland) in each experimental site, measuring rain precipitation and air temperature and humidity 2 m above the ground surface at one minute intervals. ECH$_2$O EC-TM sensor probes coupled to Em50 data-loggers (Decagon Devices, Inc., USA) recorded soil temperature and volumetric water content in top-soil (0 to -3 cm) every minute and data were averaged over one hour intervals. Data presented are for the six months of the 2011 plant growing season – April through September (AMJJAS).

3.2.3 Vegetation analyses

Herbaceous vegetation was harvested at peak biomass in July 2011 during the second year following the transplantation and served as an estimate of the annual AGB production. At each mesocosm, a permanently-marked area of 35 × 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. Individual species' biomass was allocated to one of the following plant growth forms (PGF): shrub, graminoid, forb or moss.

Plant diversity assessment was carried out on the basis of presence/absence of vascular plant species in the entire mesocosm area. Shannon diversity index was calculated from individual species abundance in terms of biomass within the 35 × 35 cm area.

Plant phenological development was monitored *in situ* throughout the 2011 vegetation season by means of a remote sensing device capturing the normalized difference vegetation index (NDVI) (Pontailler and Soudani 2012). A tripod-held NDVI sensor (Laboratoire Écologie-Systématique-Évolution, CNRS, France) coupled to a CR10X data-logger (Campbell Scientific, Inc., USA) was used during a total of 12 campaigns between 11 April 2011 and 18 October 2011, spanning the time-window between snowmelt and first frost at the control site at 1350 m a.s.l. Pilot work supported such application in grasslands, providing a strong linear relationship (R^2 = 0.97) between AGB and NDVI signal (Landolt 2010).

3.2.4 Isotopic analyses of plant tissue

Drought stress during the plant growing season was investigated by the $\delta^{13}C$ enrichment technique, based on an isotopic discrimination arising from water limitation during photosynthesis (Farquhar et al. 1989). Higher $\delta^{13}C$ values result from a non-preferential fixation of the heavier ^{13}C isotope during a prolonged closure of leaf stomata associated with drought. This process is independent from an altitudinal gradient in $\delta^{13}C$ natural abundance in plants, which results from a decrease in $^{13}CO_2$ discrimination during carboxylation at higher altitude (Körner et al. 1988). To this end, four dominant vascular plant species, represented across all experimental treatments were measured for their carbon stable isotopic composition. These were two graminoids – *Agrostis capillaris* and *Festuca rubra aggr.* and two forbs – *Alchemilla monticola* and *Taraxacum officinale*.

Nitrogen deposition along the transplantation gradient was investigated by determining the nitrogen isotopic composition of a common bryophyte species *Rhytidiadelphus triquetrus* which, due to a lack of root organs, relies on airborne supply of nutrients, and is therefore a sensitive indicator of N input and signature (Harmens et al. 2011). Mean N concentration and $\delta^{15}N$ in the moss tissue were determined for each mesocosm. The first reflected the total level of nitrogen deposition and the second the predominant type of deposition, with higher $\delta^{15}N$ values related to wet and lower ones to dry deposition (Bragazza et al. 2005)

The entire dried (as above) biomass per mesocosm of each species was homogenised, ball mill ground and analysed for isotopic composition using a DELTA V Advantage isotope ratio mass spectrometer (Thermo Scientific, Germany).

3.2.5 Data analysis

All data were analysed according to our completely randomised block design, where block was matched with the transplantation altitude treatment and was treated as a categorical variable (Quinn and Keough 2002). Total and individual PGF biomass, plant species richness and Shannon diversity were analysed using a Type I analysis of variance (ANOVA), with fixed factors *altitude* and *land use*. Significant differences between the levels of each treatment factor and their interactions were examined using pairwise comparisons, where family-wise error rate was controlled using the Bonferroni procedure.

Data on the isotopic composition of plant tissue from the five species mentioned above was analysed using a Type I analysis of variance. A linear mixed effect model was fitted to the data, using the restricted maximum likelihood method (REML) to account for cases where species were not present in each plot (Zuur et al. 2009). The model for all tested plants together included *plant species*, *altitude* and *land use*, as well as all two- and three-way interactions as fixed effects. Based on the results from this overall analysis, we also tested for treatment effects on each plant species individually. Subsequent pairwise comparisons of between treatment factor levels for each species were executed following the Bonferroni method.

A repeated measures linear mixed effects model, using Type I analysis of variance and the REML estimation method, was used to test the evolution of the NDVI signal through the plant growing season. *Altitude*, *land use* and their interaction were treated as between-subject fixed factors, and *sampling date* (categorical variable) and all two- and three-way interactions with date as within-subject fixed factors. Significant differences between levels of the fixed factors were detected using pre-defined linear combinations of contrasts, thus accounting for the model's structure.

Assumptions of normality and homoscedasticity of the residuals in all final models were verified visually using diagnostic plots. For all statistical tests, effects were considered significant at $P < 0.05$. All statistical analyses were performed using R version 2.14.1. (R Development Core Team 2012) and mixed effects models were run using the nlme package (Pinheiro et al. 2012).

3.3 Results

3.3.1 Climate change simulation

During the second year following the transplantation to lower altitudes with warmer and drier climate all mesocosms experienced a tight coupling of soil and air temperatures during the plant growing season with significantly warmer soils at lower altitudes (Table 3.1). In addition, decreasing canopy cover (shading) across the land use types stimulated warmer soil temperatures due to the increase in irradiance. Soil moisture in the mesocosms, however, showed a characteristic patter in its response to the climatic gradient based on the land use type (Table 3.1). Mean seasonal soil moisture values for unwooded pastures decreased significantly under both of the simulated climate change scenarios, whereas in sparsely wooded pastures it decreased only under the +4 K scenario and in densely wooded pastures it remained unchanged.

Table 3.1. Microclimate data overview for the plant growing season (AMJJAS) of 2011. Presented are mean parameter values for each altitude and pasture type.

Altitude (m a.s.l.)	1350			1010			570		
Air temperature (°C)	10.6			13.3			15.9		
Air humidity (%)	74.9			75.8			70.4		
Precipitation (mm)	733.3			624.1			467.4		
Land use type *	UW	SW	DW	UW	SW	DW	UW	SW	DW
Soil temperature (°C) ǂ	12.4 ± 0.1 **a**	11.0 ± 0.2 **b**	10.4 ± 0.1 **ab**	15.6 ± 0.2 **c**	14.3 ± 0.2 **d**	13.2 ± 0.2 **ae**	18.4 ± 0.2 **f**	17.1 ± 0.1 **g**	16.0 ± 0.2 **ch**
Soil moisture (%) §	47.5 ± 4.7 **a**	39.2 ± 2.6 **ab**	30.3 ± 2.2 **bc**	26.3 ± 2.5 **bc**	31.6 ± 5.0 **bc**	25.3 ± 2.3 **bc**	15.9 ± 2.0 **c**	22.2 ± 1.9 **c**	15.8 ± 2.2 **c**

* Land use type codes, where UW refers to unwooded pasture with 0% canopy shading, SW – sparsely wooded pasture with 40% canopy shading, and DW – densely wooded pasture with 80% canopy shading.

ǂ, § Reported values for soil temperature and moisture are means and standard errors for five replicate plots. Different letters indicate significant differences at the P = 0.05 threshold.

3.3.2 Plant diversity

Plant communities transplanted in mesocosms to warmer and drier climate experienced a marked loss in species richness (Figure 3.1a). The number of species decreased with up to 30 % ($F_{2,36}$ = 15.2, P < 0.001), with a significant effect at both transplantation altitudes: 1010 m a.s.l. (P < 0.001) and 570 m a.s.l. (P = 0.011), compared to the control site at 1350 m a.s.l. Species richness among the land use types was equal and did not show a significant interaction with the transplantation treatment. Most prominent losses were observed for graminoid and leguminous species. In contrast to species richness, Shannon diversity index (Figure 3.1b) varied significantly both across altitude ($F_{2,36}$ = 9.2, P < 0.001) and land use ($F_{2,36}$ = 16.0, P < 0.001), with a significant interaction between the two factors ($F_{4,36}$ = 14.7, P < 0.001). This pattern was mainly driven by the significant (P < 0.001) decrease in the Shannon index of unwooded pasture mesocosms transplanted to 570 m a.s.l. (Figure 3.1b). This drastic decline was attributed both to the loss of common species (3.6 Appendix, Table A3.1), and to the reduction in their abundance (3.6 Appendix, Table A3.2). A single graminoid species *Agrostis capillaris*, remained unaffected by the transplantation treatment and thus became dominant in the plant community representing 59 % of the total AGB per mesocosm (compared to 22 % in the control plots).

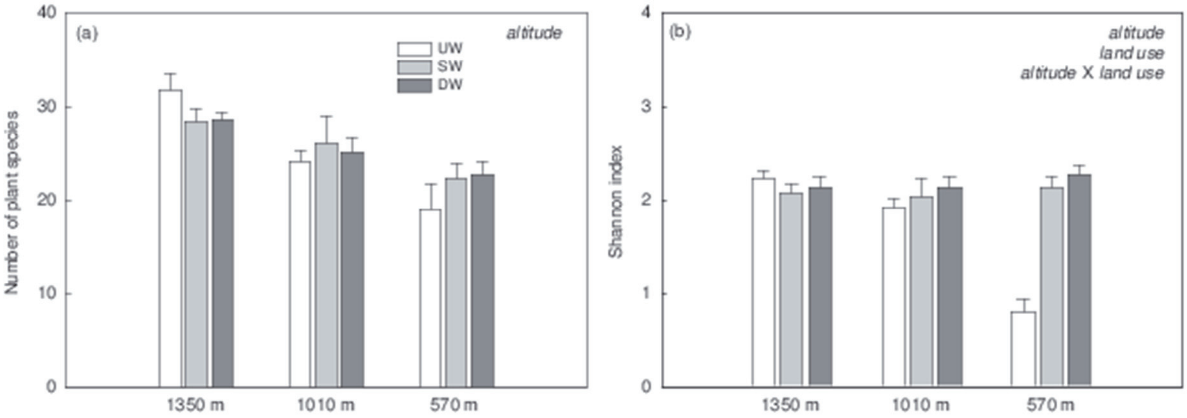

Figure 3.1. Plant species (a) richness and (b) Shannon diversity of the vegetation communities in the three land use types: unwooded pasture (UW), sparsely wooded pasture (SW), and densely wooded pasture (DW). Significant (P < 0.05) factors (in italics) and interactions (marked with X) are shown for each response variable.

3.3.3 Plant biomass

Total herbaceous AGB across all three land use types decreased down to 45 % of that of the control site following the transplantation to warmer and drier climate ($F_{2,36}$ = 29.3, P < 0.001), with a significant effect at the lowest site at 570 m a.s.l. (P < 0.001). Land use exerted a strong effect too ($F_{2,36}$ = 21.0, P < 0.001) and interacted significantly with the transplantation treatment ($F_{4,36}$ = 4.7, P = 0.004). This was manifested by a significant effect of climate change on unwooded pasture (P < 0.001) and on sparsely wooded pasture vegetation (P = 0.012) at the lowest altitude, but not on the densely wooded pasture type (Figure 3.2a).

Different PGFs reacted with different intensities and direction in response to the experimental climate change. Graminoid AGB from all three land use types was strongly negatively affected by the transplantation to lower altitude ($F_{2,36}$ = 18.7, P < 0.001). The response of graminoid AGB to the treatment was vegetation-type dependent, as indicated by a significant interaction term ($F_{4,36}$ = 2.8, P = 0.042), and was strongly expressed at the lowest altitude in the unwooded pasture (P = 0.006) and sparsely wooded pasture (P = 0.005) mesocosms (Figure 3.2b).

Forbs in the three land use types were significantly affected by the altitude of transplantation ($F_{2,36}$ = 10.7, P < 0.001) and altogether, showed an increase in AGB with moderate climate change at 1010 m a.s.l. (P = 0.033). Nevertheless, none of the individual pasture types experienced a significant effect in forb AGB after transplantation to this altitude (Figure 3.2c). To the contrary, the unwooded pasture vegetation at 570 m a.s.l. had a significantly lower (P = 0.005) forb AGB compared to the controls.

The moss AGB, almost exclusively represented by *Rhytidiadelphus triquetrus*, showed a significant reduction following the transplantation to lower altitude ($F_{2,36}$ = 6.2, P < 0.005). Pooled across land use types, this was evident for the site at 1010 m a.s.l. (P = 0.047) and at 570 m a.s.l. (P = 0.004), however, within individual land use types, only unwooded pastures differed significantly (P = 0.002) from the controls (Figure 3.2d).

The fact that ligneous species were only occasionally represented in our mesocosms, and exclusively in those from densely wooded pasture type, did not allow us to build a robust statistical model describing their response to altered climate following the transplantation.

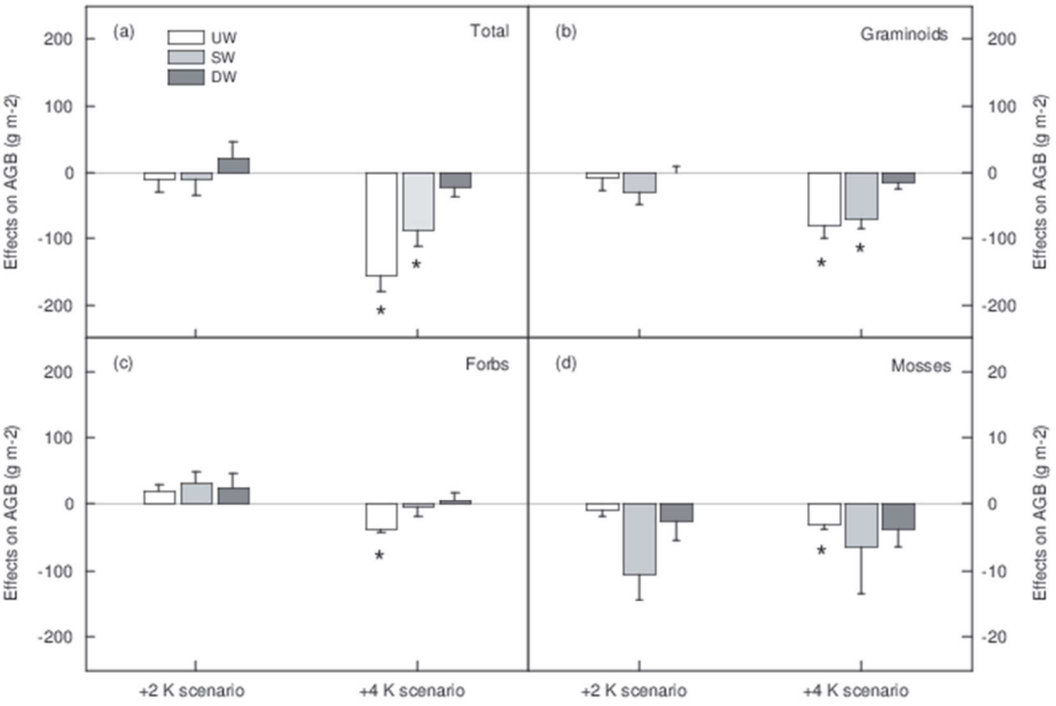

Figure 3.2. Effect of transplantation to warmer and drier climate at 1010 m a.s.l. (+2 K scenario) and 570 m a.s.l. (+4 K scenario) on aboveground biomass (AGB) production. Presented data are for (a) total biomass, and biomass of (b) graminoids, (c) forbs, and (d) mosses (y-axis differently scaled). The three land use types are: unwooded (UW), sparsely wooded (SW), and densely wooded (DW) pastures. Asterisks (*) indicate significant differences (from controls at 1350 m a.s.l.) at the P < 0.05 threshold.

3.3.4 NDVI

The phenological development of herbaceous vegetation in the mesocosms, determined by means of NDVI sensing, showed a marked seasonality (Figure 3.3) with most of the variation in the NDVI signal being explained by the date of sampling ($F_{11,395} = 202.5$, $P < 0.001$). Sampling date was also significant in its two-way interactions with altitude ($F_{22,395} = 80.9$, $P < 0.001$), land use ($F_{22,395} = 15.0$, $P < 0.001$) and their common three-way interaction ($F_{44,395} = 7.9$, $P < 0.001$). This is readily observed on Figure 3.3 where the NDVI signal curves follow different trajectories depending on the land use and the altitude of transplantation. Altitude alone had a strong significant effect on plant phenology ($F_{2,36} = 9.7$, $P < 0.001$) causing an advance of up to 30 days in the development of the vegetation and a mid-season senescence (Figure 3.3). NDVI across land use types differed significantly ($F_{2,36} = 7.6$, $P = 0.002$) and this pattern was significantly influenced in its interaction with altitude ($F_{4,36} = 3.7$, $P = 0.013$). Individual land use types responded differently to the transplantation treatment. Unwooded pasture mesocosms (Figure 3.3a) experienced a significant decrease in NDVI values at 570 m a.s.l. ($t = -3.1$, $P = 0.003$) and a significant increase at 1010 m a.s.l. ($t = 3.4$, $P = 0.002$) in comparison to the controls at 1350 m a.s.l. Those of sparsely wooded pasture type (Figure 3.3b) were not affected significantly, whereas those of densely wooded pasture type (Figure 3.3c) showed a significant increase at 1010 m a.s.l. ($t = 2.1$, $P = 0.038$).

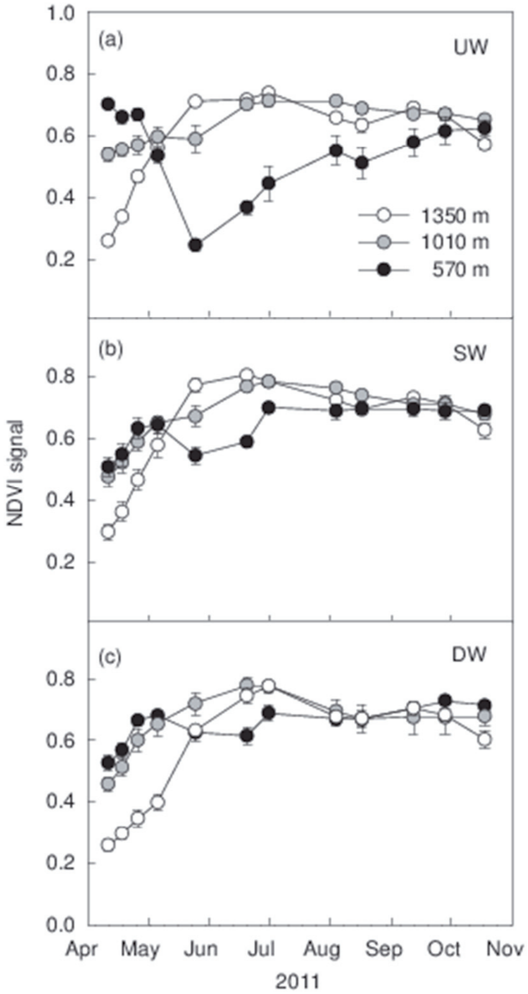

Figure 3.3. Normalized difference vegetation index (NDVI) during the growing season months of 2011 for each of the three pasture types: a) unwooded (UW), b) sparsely wooded (SW), and c) densely wooded (DW) along the altitude transplantation gradient.

3.3.5 Plant isotopic signatures

All of the tested vascular plant species experienced a significant increase in $\delta^{13}C$ ($F_{2,36} = 92.6$, $P < 0.001$) following the transplantation to a lower altitude (Figure 4.4). Inherent differences between species in their $\delta^{13}C$ signatures were present ($F_{3,91} = 184.6$, $P < 0.001$) and those showed significant interactions with land use ($F_{6,91} = 14.9$, $P < 0.001$), altitude ($F_{6,91} = 6.4$, $P < 0.001$) and the combination of land use and altitude ($F_{12,91} = 2.0$, $P = 0.030$). Significant $\delta^{13}C$ enrichment ($P < 0.001$) was observed in all species from mesocosms transplanted to 570 m a.s.l. in comparison to the controls at 1350 m a.s.l. In addition, *Agrostis capillaris* (Figure 4.4a) showed a significant $\delta^{13}C$ enrichment ($P = 0.011$) also at 1010 m a.s.l. compared to the control.

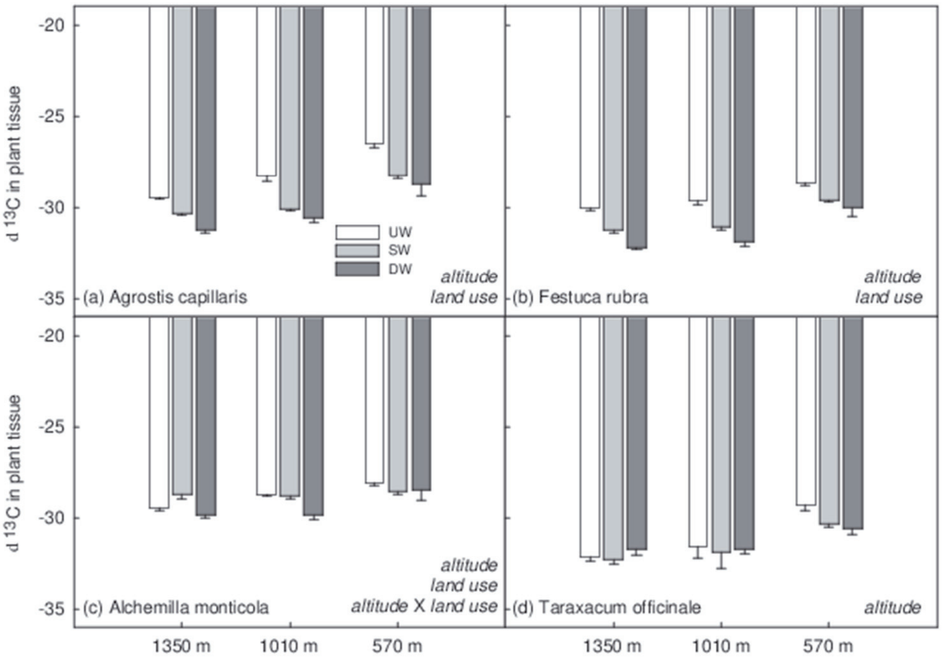

Figure 3.4. Carbon isotopic signatures of the four most common vascular plant species sampled from each of the three studied land use types: unwooded pasture (UW), sparsely wooded pasture (SW), and densely wooded pasture (DW). Higher $\delta^{13}C$ values within a given species are an indication of water limitation during the vegetation season. Significant ($P < 0.05$) factors (in italics) and interactions (marked with X) are shown for each species tested

Table 3.2. Concentration of N and $\delta^{15}N$ of green moss tissue from the species *Rhytidiadelphus triquestrus* collected from the transplanted mesocosms in July 2011. Presented are mean parameter values* for each altitude.

Altitude (m a.s.l.)	1350	1010	570
N content (%)	1.80 ± 0.10 **a**	1.72 ± 0.09 **a**	1.98 ± 0.14 **a**
$\delta^{15}N$	-5.77 ± 0.27 **a**	-8.14 ± 0.21 **b**	-8.34 ± 0.27 **b**

* Reported values are means and standard errors for up to 15 replicates. Different letters indicate significant differences at the P = 0.05 threshold.

Nitrogen concentration in the green tissue of the moss *Rhytidiadelphus triquetrus* did not exhibit any significant differences among the three altitudes of transplantation (Table 3.2), leading to the conclusion that quantities of aerial nitrogen deposition were similar at the three altitudes.

The $\delta^{15}N$ signature, however, was significantly affected by altitude ($F_{2,36} = 33.0$, $P < 0.001$), being more depleted in ^{15}N at lower elevation in comparison to the control site , thus indicating that the predominant type of N deposition is dry deposition.

3.4 Discussion

Vegetation responses to the transplantation along an altitudinal gradient, simulating a warmer climate and reduced precipitation, were driven to a large extent by the magnitude of the treatment. Significant deviations from control conditions in plant aboveground biomass, phenology, richness and diversity were observed primarily for the communities exposed to the intensive climate change treatment (+4 K scenario), with little to no effect of the moderate climate change treatment (+2 K scenario). The direction of these responses, however, was overall the same, indicating a threshold (see Beier et al. 2012) in the physiological tolerances of plants to simulated climate change. Another major finding from this experimental manipulation was that across land use types, intensively-used unwooded pastures were consistently more responsive to climate change than their counterparts from extensively used wooded pastures of either sparsely or densely wooded type.

3.4.1 Plant community attributes

The observed rapid decrease in species richness and diversity in response to climate change is comparable to experimental findings in other mountain grassland ecosystems (Klein et al. 2004; Sebastia et al. 2008). We found a reduction in total number of vascular plant species with warmer and drier climate for all three studied land use types, with stronger effect size at stronger treatment intensity. The decrease in Shannon diversity, however, was only expressed in the unwooded pasture vegetation, reflecting a combined loss in species richness, reduction in individual species abundance and increased dominance of a single graminoid species – *Agrostis capillaris*. Both total biomass and biomass of individual plant growth forms decreased substantially following the transplantation to lower altitudes. The strong increase in mean annual temperature and reduction in precipitation (+4 K scenario) halved the aboveground biomass in unwooded pasture mesocosms, which were associated with the strongest deficiency in soil moisture content during the plant growing season and experienced the most-pronounced enrichment in plant tissue $\delta^{13}C$, a legacy of drought stress. These experimental findings corroborate modelling evidence (see Engler et al. 2011) for a strong dependence of mountain plant performance and floristic composition on the severity of drought episodes during projected climate warming this century.

3.4.2 Plant growth forms

Regarding PGFs, we expected that plants with different morphologies and life strategies will respond differently under changing environmental conditions (Lavorel 2007). Indeed, we observed that the graminoid PGF was more strongly affected by the simulated warmer and drier climate, than either forbs or bryophytes, a finding that goes in line with previous work in plant communities from subalpine grasslands (Sebastia 2007; Gilgen and Buchmann 2009), and from an alpine snowbed (Johnson et al. 2011). Graminoids experienced a consistent decrease in biomass in both unwooded and sparsely wooded pastures, and contributed substantially to the overall decrease in the total aboveground biomass in these land use types. We believe that inherent differences in the morphology, growth and ecophysiology between graminoids and forbs could have driven the dichotomous response of these growth forms. First, it has been shown that in cold adapted biomes forbs exhibit a capability for belowground resource storage and leaf bud preformation which could grant them a competitive advantage over graminoids under climatic perturbation (Wookey et al. 2009). Both large tap roots and rhizomes of the mountain forbs at our pasture-woodlands field site seem more beneficial under prolonged periods without precipitation, as compared to near-surface fine roots of the graminoids. Second, preliminary results from our transplantation experiment (Hildbrand and Wohlgemuth 2013) suggest a shortened leaf lifespan and intensified production of leaf cohorts in forbs during the growing season, which indicates their means for regrowth following extended periods without precipitation. Third, forbs from a range of subalpine grasslands have been reported to exhibit a better water use efficiency than graminoids due to a tighter regulation of stomatal conductance (Signarbieux and Feller 2012). Indirect evidence for the latter could be found in the carbon isotopic ratio of green plan tissues collected from the mesocosms: whereas forbs did not show a consistent response to climate manipulation according to land use of origin, graminoids were consistently more enriched in $\delta^{13}C$ in more open canopy pastures and at higher intensity of climate change. We interpret this as a capacity of subalpine forbs to minimise water loss under unfavourable dry conditions. All these mechanisms point to the advantageous growth form of forbs under warmer and drier subalpine climate, demonstrating furthermore the usefulness of such PGF classification (see Dorrepaal 2007) for predicting ecosystem responses to climate change.

3.4.3 Plant phenology

Plant phenological development was controlled to a large extent by the magnitude of the simulated climate change. At the onset of the growing season, mesocosms exposed to the +4 K scenario were considerably 'greener' than the controls at the top of the gradient. This result confirmed our expectations that shorter snow cover duration and warmer soils in spring will advance plant phenological development; corroborating findings from annual variations in winter climate (Inouye 2008) and experimental snow manipulations (Wipf and Rixen 2010). Subsequent soil moisture limitation due to the absence of spring snow melt and a pronounced reduction in growing season precipitation, however, exposed these turfs to drought stress, reflected by a premature senescence of the vegetation. This was particularly evident in the unwooded pastures which were subjected to the direct effects of sun irradiation and wind.

3.4.4 Land use

The land use types chosen in this study have been shaped through a history of different pasture management intensities and the reason why the vegetation from unwooded pastures was significantly more affected by the warmer and drier climate than that from both wooded pasture types could be manifold. Above we have explored the hypothesis for a differential response of PGFs, hence considering the higher frequency of forbs in wooded pastures and their conservative water use, this may contribute to the observed land use pattern. We believe however that other factors are also playing a role and their individual effects are hard to tease apart. First, in accordance to our results, highly productive early-successional grassland communities have been shown to be more responsive to climate warming and drought, compared to late successional ones, typically found in areas of low intensity management (Grime et al. 2000). Second, drought resistance and recovery potential of plant communities has been also attributed to species richness (van Ruijven and Berendse 2010), where an important role is played by subordinate plant species (Mariotte et al. 2013). Our results do not support such a hypothesis since unwooded pastures hosted some of the richest communities with over 30 vascular plant species within a single mesocosm (0.5 m^{-2} of surface). Third, at the landscape scale, forests and wooded pastures, in contrast to grasslands, exhibit a more conservative water use through a limited evaporation and hence cope better with long-lasting heat and drought stress (Teuling et al. 2010; Gavazov et al. 2013). Moreover, once soil moisture reserves in grassland landscapes are depleted by increased evapotranspiration in response to high atmospheric temperatures, drought creates a positive feedback thus increasing soil temperatures even further (Seneviratne et al. 2006). The linearity between soil and air temperature observed in our data does not suggest such a feedback loop, however evapotranspiration was probably higher from unwooded pasture mesocosms considering that they exhibited a disproportional decrease in soil moisture compared to the other two wooded land use types. This interaction of climate warming and land use in terms of soil moisture status was furthermore confirmed by the fact that within species, $\delta^{13}C$ enrichment was significantly higher in non-shaded plots for three of the four tested species.

3.4.5 Experimental considerations

The experimental design employed in this study allowed for the direct comparison of the vegetation response of three distinct land use types to two levels of climate change with warmer and drier climate (+2 K and +4 K scenarios). We are nevertheless knowledgeable that the simulated climate scenarios are spatially limited to temperate mountain systems which, in contrast to high latitude systems, are due to experience a decrease in summer precipitation. Furthermore, some statistical limitations arise from the absence of true spatial replication per altitude, due to the single transect chosen, and thus limit our generalisations to the selected elevations of the transplantation sites and their respective climate, instead of interpolating our findings over the entire gradient. The lack of a treatment effect on the tissue nitrogen concentration on the ubiquitous moss species *Rhytidiadelphus triquetrus*, in addition to the mapped information (FOEN 2009) for comparable loads of nitrogen deposition along the slopes of Jura Mountains, gave us grounds to eliminate a potential confounding factor related to N emissions along the gradient. Additionally, informal comparisons of control plots with neighbouring intact grasslands (*unpublished data*) suggested that there was no effect of turf transplantation on the vegetation composition after two years of treatment, similarly to other findings in the literature (MacGillivray et al. 1995; Sebastia et al. 2008). We did not detect any incoming species in the plots at lower altitudes over the two experimental years.

In conclusion, our findings provide unequivocal evidence that the studied temperate subalpine pastures have a resistance potential at moderate levels of climate change (+2 K scenario) in terms of productivity and plant diversity. The observed negative impact of the high level of climate change (+4 K scenario) was strongest in the intensively managed unwooded pasture system and only minimal in the extensively used sparsely and densely wooded pastures. This experimental evidence provides a scope for a sustainable landscape management, where traditional land use in pasture woodlands can hold the key to mitigating future negative effects of climate change.

3.5 Acknowledgements

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3.6 Appendix

Table A3.1. Number of replicate mesocosms (n=5) in which a given species occurred during the second year after transplantation.

Altitude	1350 m			1010 m			570 m		
Land Use *	UW	SW	DW	UW	SW	DW	UW	SW	DW
FORBS:									
Achillea millefolium	2	0	0	2	0	0	0	0	0
Ajuga reptans	0	5	5	0	5	5	0	3	5
Alchemilla conjuncta	0	0	1	0	2	1	0	0	1
Alchemilla monticola	5	5	5	5	5	5	5	5	4
Bellis perennis	2	1	0	1	2	0	1	3	1
Caltha palustris	1	0	1	1	0	0	0	0	0
Campanula rhomboidalis	1	0	3	0	0	1	0	0	1
Campanula rotundifolia	0	0	3	0	0	2	0	1	0
Cardamine pratensis	5	5	2	5	5	4	1	2	3
Carum carvi	5	3	1	3	0	0	2	1	1
Cerastium fontanum ssp. vulgare	4	3	3	2	1	1	1	3	1
Chaerophyllum temulum	0	0	0	0	0	1	0	0	0
Cirsium acaule	0	0	0	0	1	0	0	1	0
Crepis biennis	0	1	2	0	0	1	2	1	0
Crepis mollis	1	0	0	0	1	0	0	0	0
Crocus albiflorus	5	5	5	5	5	5	5	5	5
Cruciata laevipes	0	1	0	1	1	0	0	0	0
Epilobium montanum	0	0	0	0	0	2	0	0	0
Galium pumilum	0	0	3	0	0	1	0	0	3
Geranium sylvaticum	1	1	4	1	1	2	0	1	2
Geum rivale	3	0	0	0	0	2	2	1	0
Hieracium lactucella	1	2	3	1	3	2	2	5	3
Hieracium murorum	0	0	5	1	2	5	0	0	5
Hieracium pilosella	0	0	0	0	0	0	0	1	0
Homogyne alpina	0	1	1	0	1	2	0	0	2
Hypericum maculatum spp. maculatum	0	5	0	3	2	1	1	2	1
Leontodon automnalis	0	4	2	0	0	1	0	1	0
Leontodon hispidus ssp. hispidus	1	5	5	0	3	4	1	4	0
Leucanthemum vulgare	5	0	0	0	0	1	3	0	1
Lotus corniculatus	0	1	1	1	3	0	2	3	2
Lysimachia nemorum	0	3	0	0	1	0	0	1	0
Melampyrum sylvaticum	0	0	0	1	0	0	0	0	1
Oxalis acetosella	0	0	5	0	1	5	0	0	4
Phyteuma spicatum	0	0	0	0	1	1	0	0	0
Plantago atrata	1	0	0	0	0	0	1	1	0
Plantago lanceolata	0	0	0	0	1	0	0	2	3
Plantago media	2	0	2	2	2	0	2	0	0
Polygala vulgaris ssp. vulgaris	0	0	0	0	2	0	0	0	0
Polygonum bistorta	3	0	0	0	1	0	0	0	0
Potentilla aurea	0	0	0	0	1	0	0	0	0
Potentilla erecta	1	5	2	1	2	1	1	5	2
Primula elatior	5	5	5	0	4	5	0	2	4
Prunella vulgaris	5	5	3	2	3	3	3	5	1
Ranunculus acris ssp. friesianus	5	5	5	5	5	4	5	5	4

Rhinanthus minor	0	0	0	1	0	0	0	0	0
Rumex acetosa	1	1	0	5	2	0	1	0	0
Rumex alpestris	0	0	0	1	0	0	1	0	0
Sanguisorba minor ssp. minor	0	0	0	0	0	1	0	0	0
Saxifraga rotundifolia	2	1	1	0	0	0	0	0	0
Silene flos-cuculi	0	0	0	0	0	0	0	1	0
Silene nutans ssp. nutans	0	0	1	0	0	0	0	0	0
Stellaria graminea	0	0	0	0	0	0	0	1	0
Taraxacum officinale	5	5	5	4	4	5	4	3	5
Thymus pulegioides	0	0	2	0	2	0	0	0	2
Trifolium pratense ssp. pratense	5	3	0	5	3	1	3	3	0
Trifolium repens	5	5	1	5	5	0	1	1	0
Trollius europaeus	5	2	1	2	0	0	0	0	0
Veratrum album ssp. lobelianum	5	0	0	2	1	0	0	0	0
Veronica chamaedrys	3	5	5	5	4	5	4	3	5
Veronica officinalis	0	4	5	0	1	4	0	3	5
Veronica serpyllifolia ssp. serpyllifolia	5	5	1	5	1	1	3	2	1
Viola reichenbachiana	0	0	4	0	2	5	0	0	3
GRAMINOIDS:									
Agrostis capillaris	5	5	5	5	5	5	5	5	5
Anthoxanthum odoratum	5	4	1	2	3	1	3	1	0
Briza media	1	0	0	0	0	0	0	1	0
Carex caryophyllea	4	1	0	1	1	0	0	0	0
Carex flacca	4	0	1	1	2	2	2	0	0
Carex leporina	4	0	0	0	3	0	2	3	0
Carex pallescens	0	2	0	1	4	2	0	1	1
Carex sylvatica	0	3	0	1	1	2	1	0	2
Cynosurus cristatus	5	2	0	4	0	0	3	0	0
Dactylis glomerata	3	1	0	3	1	1	3	0	1
Deschampsia cespitosa	3	1	0	0	0	0	0	1	0
Festuca pratensis	5	2	2	5	0	0	5	0	0
Festuca rubra aggr.	5	5	5	5	5	5	5	5	5
Juncus effusus	0	0	0	1	0	0	0	0	0
Luzula campestris	3	1	5	0	2	4	1	3	5
Nardus stricta	0	1	1	0	2	0	0	5	0
Phleum pratense	0	0	0	1	0	0	1	0	0
Poa chaixii	5	5	3	4	3	1	2	1	2
Poa pratensis	0	1	0	2	0	0	0	0	0
Poa trivialis ssp. trivialis	1	0	2	0	0	0	0	0	0
WOODY:									
Abies alba	0	0	0	1	0	1	0	0	1
Fragaria vesca	0	0	3	0	0	1	0	0	2
Picea abies	1	1	0	0	1	1	0	0	0
Rosa corymbifera	0	0	1	0	0	0	0	0	0
Rubus idaeus	0	0	4	0	0	3	0	0	1
Sorbus aucuparia	0	0	2	0	0	1	0	0	3
MOSS:									
Rhytidiadelphus triquetrus	5	5	5	5	5	5	5	5	5

* Land use type codes, where UW refers to unwooded pasture with 0% canopy shading, SW – sparsely wooded pasture with 40% canopy shading, and DW – densely wooded pasture with 80% canopy shading.

Table A3.2. Average AGB (g m-2) per treatment clipped from a 35 x 35 cm subplot in each transplanted mesocosm in July 2011.

Altitude	1350 m			1010 m			570 m		
Land Use *	UW	SW	DW	UW	SW	DW	UW	SW	DW
FORBS:									
Achillea millefolium	6.33	0.01		4.92					0.26
Ajuga reptans		2.09	2.13		3.71	3.17		6.68	6.92
Alchemilla conjuncta			0.31		12.65	1.22			3.36
Alchemilla monticola	11.96	23.41	0.69	21.23	34.79	7.61	4.05	15.17	5.08
Bellis perennis					0.08				
Caltha palustris	0.09			0.30					
Campanula rhomboidalis	0.48		3.43						3.26
Campanula rotundifolia			2.03			0.46		1.53	
Cardamine pratensis	1.18	2.40	0.86	0.87	1.25	0.98	0.06	1.14	2.63
Carum carvi	1.80			1.27					
Cerastium fontanum ssp. vulgare	0.26	0.21	0.47	0.67			0.41		
Chaerophyllum temulum									
Cirsium acaule								1.66	
Crepis biennis							3.64		
Crepis mollis					20.49				
Crocus albiflorus									
Cruciata laevipes		3.38		13.96	1.30				
Epilobium montanum						1.88			
Galium pumilum			6.77			0.94			1.56
Geranium sylvaticum			5.08			11.63			2.39
Geum rivale	1.45					41.14	0.68		
Hieracium lactucella	1.98	0.20	1.05	0.82	1.44			4.08	0.47
Hieracium murorum		2.05	4.05	1.13	2.36	5.84			10.46
Hieracium pilosella								0.96	
Homogyne alpina		0.34	4.98		1.24	1.64			0.91
Hypericum maculatum spp. mac.	2.68	4.09		2.33	7.39	1.29		2.03	
Leontodon automnalis		4.77	2.80		1.26	1.00	4.07	9.74	
Leontodon hispidus ssp. hispidus		1.81	6.75	0.35	24.24	1.31		9.33	7.88
Leucanthemum vulgare	4.11						6.27		4.99
Lotus corniculatus		1.76		0.28	0.53			0.01	
Lysimachia nemorum		0.06			30.53			0.38	
Melampyrum sylvaticum				2.91					2.14
Oxalis acetosella			2.78		0.04	4.64			2.49
Phyteuma spicatum									
Plantago atrata									
Plantago lanceolata								2.45	15.51
Plantago media	0.16				3.28		12.24		
Polygala vulgaris ssp. vulgaris					1.20			0.24	
Polygonum bistorta	3.41				0.76				
Potentilla aurea		1.35	0.02					8.51	
Potentilla erecta	0.02	1.57	1.18	0.64	5.27			1.05	0.29
Primula elatior	0.53	2.28	20.66		1.55	8.44		0.82	6.68
Prunella vulgaris	4.20	1.92		9.55	0.71	0.46		2.04	
Ranunculus acris ssp. friesianus	15.43	8.51	2.83	19.99	4.52	4.26	0.34	2.88	2.14
Rhinanthus minor									
Rumex acetosa				0.83	0.19				

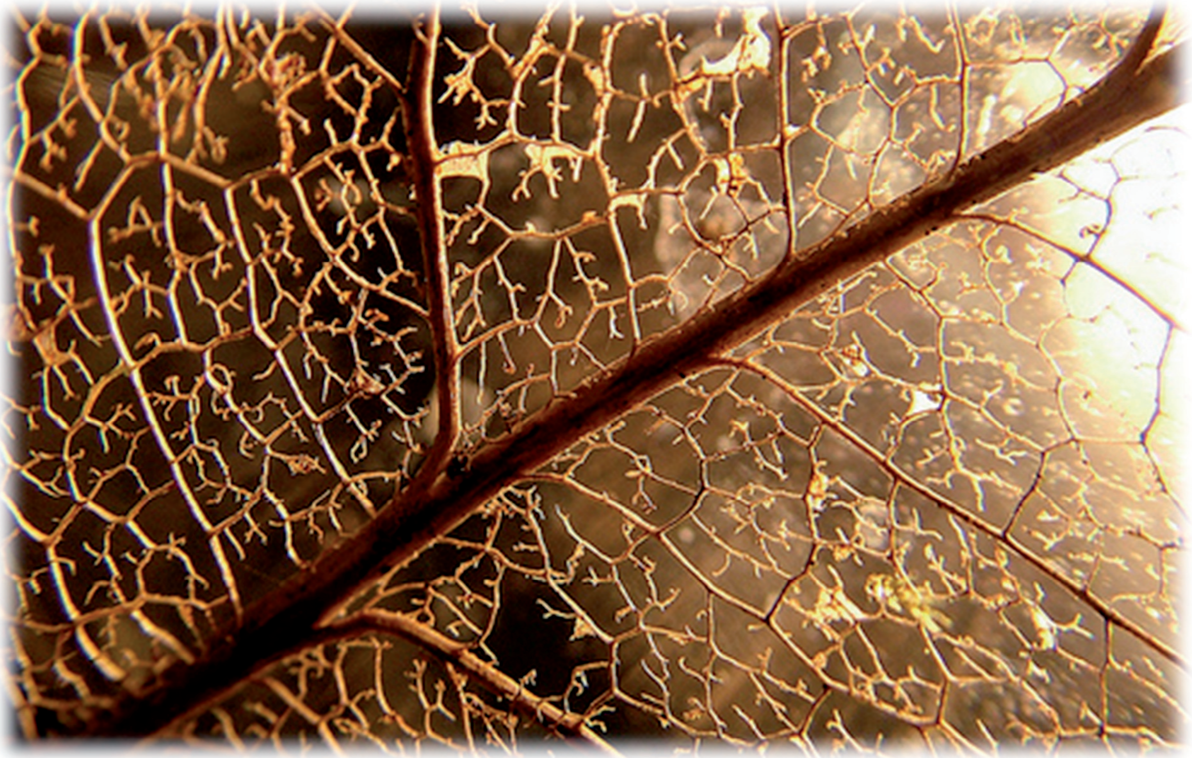
Rumex alpestris	1.43	1.40		0.29			2.29		
Sanguisorba minor ssp. minor									
Saxifraga rotundifolia			11.92						
Silene flos-cuculi								0.80	
Silene nutans ssp. nutans									
Stellaria graminea								0.11	
Taraxacum officinale	1.19	1.71	12.50	0.66	8.26	3.08	1.16	4.67	11.46
Thymus pulegioides			0.24						4.17
Trifolium pratense ssp. pratense	1.40	0.74		2.14	2.22			0.20	
Trifolium repens	0.82	1.50		0.31	0.09			0.03	
Trollius europaeus	1.83		0.74	1.07					
Veratrum album ssp. lobelianum	0.20			4.73	7.67				
Veronica chamaedrys	0.36	3.45	2.84	10.59	11.48	25.14	0.22	2.12	9.29
Veronica officinalis		0.65	6.15		0.30	4.90		2.06	2.23
Veronica serpyllifolia ssp. serpyllifolia	1.35	0.39		3.34	0.23	0.37		0.08	
Viola reichenbachiana			0.30		0.04	0.49			0.69
GRAMINOIDS:									
Agrostis capillaris	54.69	76.33	22.76	87.12	48.90	9.32	57.62	29.50	7.86
Anthoxanthum odoratum	11.91	6.45	0.58	3.63	2.55	43.76	0.48		
Briza media								0.23	
Carex caryophyllea	11.34				24.57				
Carex flacca					1.04				
Carex leporina	7.82				0.51		1.08	2.17	
Carex pallescens		1.56		2.38	2.52	10.69		14.53	
Carex sylvatica	10.20	2.65		0.16	2.63	0.06		0.74	0.43
Cynosurus cristatus	6.02	1.99		4.52			2.00		
Dactylis glomerata	0.63	7.59		11.15					
Deschampsia cespitosa	0.74	1.10						0.12	
Festuca pratensis	45.81	1.47		11.45			1.98		
Festuca rubra aggr.	11.60	20.39	5.56	20.72	19.18	7.32	1.43	5.20	5.45
Juncus effusus				2.33					
Luzula campestris	1.14	1.66	1.02		2.94			2.20	0.82
Nardus stricta					12.00			2.25	
Phleum pratense				8.78					
Poa chaixii	3.75	2.97	1.36	0.50	0.13		0.60	0.26	0.12
Poa pratensis		1.04							
Poa trivialis ssp. trivialis	1.97		0.76						
WOODY:									
Abies alba						0.57			
Fragaria vesca			0.62			0.15			
Picea abies	0.09	0.05			0.06	0.48			
Rosa corymbifera			1.75						
Rubus idaeus			0.23			8.24			0.67
Sorbus aucuparia			20.57			11.43			0.91
MOSS:									
Rhytidiadelphus triquetrus	3.09	17.21	4.60	2.27	6.66	2.02	0.05	10.73	0.88

* Land use type codes, where UW refers to unwooded pasture with 0% canopy shading, SW – sparsely wooded pasture with 40% canopy shading, and DW – densely wooded pasture with 80% canopy shading.

Chapter 4

Effects of experimental climate change on the decomposition of *Fagus sylvatica* leaf litter along an altitudinal gradient in contrasting land use types

Gavazov, K., R. Mills, T. Spiegelberger, J. Lenglet and A. Buttler



Gavazov, K., R. Mills, T. Spiegelberger, J. Lenglet and A. Buttler (*in review*). "Effects of experimental climate change on the decomposition of *Fagus sylvatica* leaf litter along an altitudinal gradient in contrasting land use types." Soil Biology & Biochemistry.

Abstract

Climate change can affect the process of carbon cycling and leaf litter decomposition in multiple ways, both directly and indirectly, though the strength and direction of this relationship is often context dependent. In this experiment we have used a standard litter type – senescent leaves of European beech Fagus sylvatica – and followed the dynamics of its decomposition along a climatic gradient over a period of 2.5 years. To control the edaphic conditions we used transplanted intact-turf mesocosms with three structurally different (unwooded or wooded) land use types from within a subalpine pasture-woodlands landscape. Our results from a gradient spanning 1000 altitudinal meters with a change from a cold and wet to a warm and dry climate indicate a strong moisture constraint on the decomposition of Fagus sylvatica but no clear soil temperature effect. The different land use types further influenced the decomposition process as mass loss from litter bags incubated in mesocosms with turfs from shaded woody pastures was entirely decoupled from the climatic conditions. This is also reflected in the lack of response to the climate treatment by the functional composition of microbial communities (fungal/bacterial ratio) on the litter within those mesocosms. Furthermore, both the abundance and composition of the microbial communities have been strongly influenced by the quality of the remaining litter and by the seasonal and climate-driven biogeochemical processes in the transplanted turfs. We believe that our findings bring substantial evidence for the controlling role of soil moisture on litter decomposition as well as for the indirect effects of climate through changes in the decomposer community. These results present plausible feedback mechanisms to beech encroachment into subalpine pastures driven by climate and land use change, which are worth exploring under future scenarios.

Keywords

Beech; climate warming; C/N ratio; decay rate; fungal/bacterial ratio; Jura Mountains; K value; litter bag; mass remaining; pasture woodlands; PLFA; transplantation

4.1. Introduction

Litter and soil organic matter decomposition represent one of the major carbon fluxes from terrestrial ecosystems (Houghton 2007). Environmental conditions directly affect the rates of litter decomposition (Swift et al. 1979; Chapin et al. 2002) such that in cold environments, such as mountain regions, ecosystems contain most of their carbon in the soil organic matter due to physiological constraints on the decomposer community (Körner 2003). In such cold biomes, temperature exerts a hierarchical control on litter decomposition, however, soil moisture modulates its direct positive effect and often causes contrasting directions of the response based on regional precipitation and evapotranspiration regimes (Aerts 2006). In milder climate, litter quality is much more important for the rate of decomposition, especially during the initial stage of mass loss when labile substances are released (Couteaux et al. 1995), but also during the subsequent degradation of recalcitrant material by filtering the composition of microbial communities (Bray et al. 2012). This demonstrates how climate can also have indirect effects on decomposition mediated by a change in vegetation or in its litter quality (Cornelissen et al. 2007; Cornwell et al. 2008), but also by vegetation's feedback on soil microclimate (Körner 2003; Körner 2012). Concomitant climate-driven changes in the soil microbial communities also affect the carbon cycle (Bardgett et al. 2013) and litter decomposition in particular (Allison et al. 2013), thus exerting another indirect climate effect.

In a changing climate (Solomon et al. 2007), where mountain systems are said to experience a disproportionately higher increase in temperature (Nogues-Bravo et al. 2007), the coupling between atmospheric and soil climatic conditions (Seneviratne et al. 2006) can induce positive climate change feedbacks with far reaching implications for future terrestrial carbon cycling and litter decomposition. Reports on the confounding effect of soil moisture in climate warming experiments on litter decomposition come from a range of studies in both high latitude (Robinson 2002) and high altitude (Gavazov 2010) regions. These studies suggest a link to a documented strong moisture limitation of underlying metabolic processes in the soil (Steinweg et al. 2012). Considering hence soil moisture's essential role for C turnover, and that it can both contribute to, and be driven by changing temperature (Mueller and Seneviratne 2012), it is important to assess the impact of these environmental parameters on litter decomposition in concert.

Altitudinal gradient studies represent a natural approach to evaluate the impact of climatic parameters on ecological processes (Körner 2007). In particular, transplantation studies along climatic gradients present great potential for integrating ecosystem-scale climate change manipulations with natural environmental variation along substantial temporal and spatial scales (Beier et al. 2012). They grant the possibility of mapping the response of an ecological process to a large range of variation in a given environmental parameter of interest (*i.e.* temperature, precipitation, etc.), while controlling for the effect of others (*i.e.* substrate, edaphic factors), establishing a causal relationship through a statistical regression approach (Cottingham et al. 2005). Detecting non-linearity in the response variable could also point to potential thresholds (Smith 2011) and tipping points (Lenton 2011) in the ecosystem behaviour arising from extreme climatic conditions.

In this study we present data on decomposition rates of a common substrate – senesced leaf litter of European beech *Fagus sylvatica* – along an altitudinal gradient of approximately 1000 metres spanning from the subalpine (wet and cold) to the colline (dry and warm) vegetation zones in the Swiss Jura Mountains (Figure 4.1a). In order to standardise the edaphic conditions along the gradient, the litter was incubated on the surface of transplanted turf mesocosms originating from three different land use types (Table 4.1) lying within a mosaic of pasture woodlands with different canopy cover, represented here by a shading treatment. Alongside mass loss and chemical composition of the decaying litter, we monitored the temporal dynamics of the decomposer microbial community. Based on the climatic gradient used, we hypothesised that beech litter decomposition rates will be most rapid within an optimum climatic range at mid-altitude and experience a soil moisture limitation at lower altitude and a temperature limitation at higher altitude (Figure 4.1b). Distinct trajectories were expected for the three land use types, such that at the top of the gradient unwooded pastures, characterised by rich grassland communities, would provide better conditions for litter decomposition in terms of warmer microclimate and a microbial community adapted to a faster soil organic matter cycle. However, at the bottom of the gradient, the pattern will be reversed since wooded pastures will experience less soil moisture limitation due to their canopy shading.

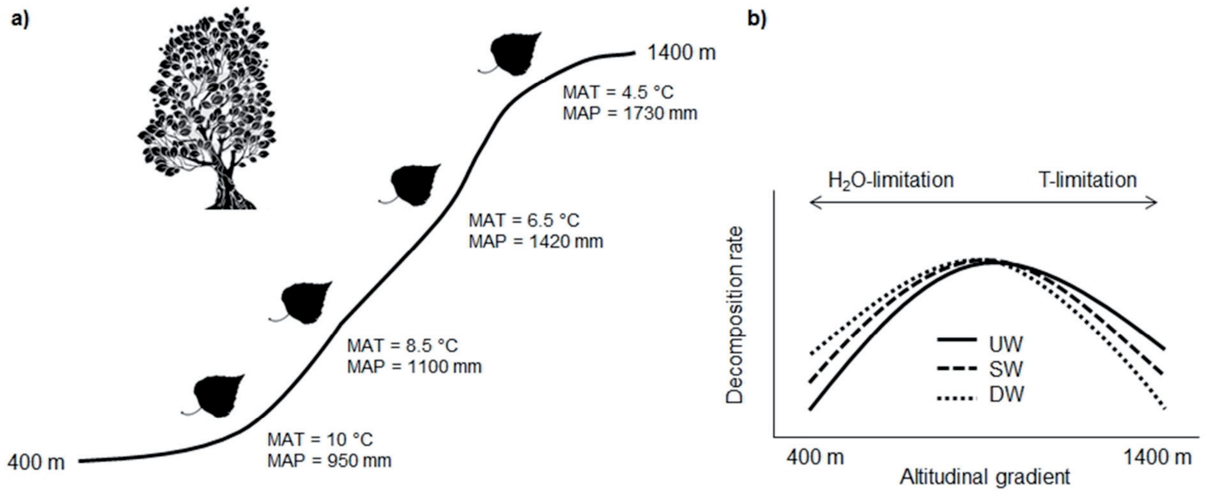


Figure 4.1. a) Schematic representation of the altitudinal gradient used in this study and the corresponding climate experienced by litter bags with *Fagus sylvatica* leaves incubated on the surface of transplanted mesocosms. b) A conceptual chart demonstrating the hypothetical controlling role of soil moisture and soil temperature on the litter decomposition process in each of the three studied land use types: unwooded pasture (UW), sparsely wooded pasture (SW) and densely wooded pasture (DW).

4.2. Material and methods

4.2.1 Experimental design and litter bag preparation

The study was conducted within an existing turf-transplantation experiment at four distinct altitudes simulating effects of climate change on pasture woodlands in the Swiss Jura Mountains (see Gavazov et al. 2013). We used this gradient as a proxy for different *in situ* climatic conditions as represented in Figure 4.1a. Briefly, at each given altitude: 1350 m a.s.l. (Combe des Amburnex, N 46°54’, E 6°23’), 1010 m a.s.l. (Saint-George, N 46°52’, E 6°26’), 570 m a.s.l., (Arboretum d’Aubonne, N 46°51’, E 6°37’), and 395 m a.s.l. (Les Bois Chamblard, N 46°47’, E

6°41’), a common garden was set up with individual mesocosms made of rectangular PVC boxes 60 x 80 cm and 35 cm in height. The intact turf monoliths for each mesocosm were translocated from the donor site at Combe des Amburnex (N 46°55’, E 6°24’) – a mosaic area of subalpine pasture-woodlands situated along the crest of the Swiss Jura Mountains, at *circa* 1350 m a.s.l. The landscape is dominated by Norway spruce *Picea abies* and beech *Fagus sylvatica* interspersed by large clearings for cattle pastures, where more intensive land use management and grazing pressure keeps ecosystem succession in check. Fifteen mesocosms were transplanted at each of the elevations: 1350 m, 1010 m, and 570 m a.s.l. with five replicates coming from one of the following three land use types representing a gradient of land use intensity, respectively grazing activities: a densely wooded pasture (DW) with 80 % light interception by the canopy and a typical understory of woody plants and forbs, a sparsely wooded pasture (SW) with 40 % light interception and a rich community of mountain forbs and feather mosses, and an unwooded pasture (UW) without light interception and a subalpine grassland community. The respective canopy shading in the common gardens was simulated by meshed roofs suspended over wooden frames at 50 cm above the respective mesocosms. Due to logistical limitations, only five mesocosms of an unwooded pasture type were transplanted to 395 m a.s.l. Details of edaphic characteristics for each land use type are given in Table 4.1.

Table 4.1. Biogeochemical characteristics of the topsoil layer (0 to -10 cm) at the control site at 1350 m a.s.l.

Land use type [1]	UW	SW	DW
Bulk density (g/cm3)	0.57 ± 0.01	0.54 ± 0.04	0.55 ± 0.02
pH in H_2O	5.88 ± 0.06	5.47 ± 0.15	5.85 ± 0.08
SOM (g/g dry soil)	0.20 ± 0.01	0.18 ± 0.01	0.20 ± 0.01
C/N ratio	15.90 ± 0.57	18.83 ± 0.62	20.25 ± 0.42
Soil PLFA fungal/bacterial ratio	0.200	0.217	0.350

[1] Land use type codes, where UW refers to unwooded pasture with 0% canopy shading, SW – sparsely wooded pasture with 40% canopy shading, and DW – densely wooded pasture with 80% canopy shading.

Each mesocosm was equipped with a set of ECH_2O EC-TM sensor probes coupled to Em50 data-loggers (Decagon Devices, Inc., USA) recording soil temperature and volumetric water content in top-soil (0 to -3 cm) every minute and averaging data over one hour intervals. In addition, at each experimental site an automated weather station (Sensor Scope Sàrl, Switzerland) measured rain precipitation and air temperature and humidity 2 m above the ground surface at one minute intervals.

The decomposition rate along the gradient was evaluated using the litter bag technique (Crossley and Hoglund 1962) and a standard leaf litter of European beech *Fagus sylvatica*. Beech is a common deciduous tree species in European forests and its distribution in Swiss mountains ranges between 400 and 1400 m a.s.l. (Weber et al. 2010). We used naturally senesced and shed leaves which were intercepted with meshes suspended at about one metre above the forest floor within a homogeneous, mature beech stand situated at 580 m a.s.l. in the Arboretum National d’Aubonne N 46°51’, E 6°37’. Leaves were collected in October 2009 without bias towards size, shape or colour, and petioles were considered part of the leaf. Following air drying at 20°C until constant weight was reached, approximately 1.5 g litter was enclosed in UV resistant polypropylene litterbags (10 x 10 cm) of 5 mm mesh size, and the mass of each bag was recorded. A double layer mesh was used for the bottom of the bags to limit the loss of fragmented litter, but still allowing for the access of macroarthropodes and earthworms (Cornelissen 1996). Subsamples were taken for establishing the initial chemical (carbon and nitrogen) composition and the gravimetric water content of the litter.

Litter bags were incubated on top of the soil after parting the extant vegetation and fixed in place by means of small plastic pegs, one in each corner of the bag. Five individual litter bags were placed in each plot in November 2009 and then collected sequentially in spring 2010, autumn 2010, spring 2011, autumn 2011, and spring 2012. In order to reflect the difference in winter season length at each altitude, spring sampling took place shortly after snowmelt and the flowering of *Crocus albiflorus* in the mesocosms. Both autumn samplings took place in early October with the onset of vegetation senescence.

4.2.2 Litter mass-loss, chemical and PLFA analyses

Collected litterbag samples were brushed of adherent soil and subsequently lyophilised in a freeze drier (CHRIST Beta 2-8 LD plus, Germany) and weighed to determine their dry weight. Litter decomposition was expressed as percentage of initial dry mass-loss over time. A subsample of coarsely fragmented litter was taken for phospholipid fatty acid (PLFA) analysis and the rest of the sample was ground in a ball mill (Retsch MM200, Germany) for estimation of carbon and nitrogen content in an elemental analyser (Carlo Erba CNS-O 1108, Italy).

Total microbial biomass, fungal, and bacterial biomass were determined using PLFA biomarkers. The analysis followed the protocol of White et al. (1979) with modifications as in Andersen et al. (2010). In brief, lipids from 300 ± 1 mg of lyophilised litter were dissolved in a 1:2:0.8 solution of chloroform, methanol and potassium phosphate buffer and shaken for 2 h. Equal volumes of chloroform and buffer were then added and the two phases were left to separate overnight. The chloroform phase was reduced by N_2 evaporation and the lipids were then split into neutral, glyco- and phospholipids with silica solid phase extraction cartridges by eluting sequentially with chloroform, acetone, and methanol. The phospholipids were then trans-esterified in fatty acid methyl esters (FAMEs), evaporated under oxygen-free N_2, and re-suspended in 1 ml hexane containing 100 µl of methyl nonadecanoate (19:0) (Sigma-Aldrich, Switzerland) as an internal standard. FAMEs were subsequently identified by retention time in a gas chromatograph (Varian Inc. CP3800, USA) with reference to commercial standards including bacterial and fungal acid methyl esters (Supelco, USA).

We used PLFAs i15:0, a15:0, 15:0, i16:0, 16:1ω7c, i17:0, cy17:0, 17:0, and cy19 as markers for bacteria; and 18:3ω6 and 18:2ω6c as markers for fungi (Bardgett et al. 1996; Frostegård and Bååth 1996; Wilkinson et al. 2002; Potthoff et al. 2006). Following de Vries et al. (2012), we used the sum of all these biomarkers as an indicator of microbial community size and the ratio between fungal and bacterial biomarkers as an indicator of microbial community structure.

4.2.3 Statistical analysis

Each response variable of interest (daily soil temperature and moisture, remaining litter mass, litter chemistry, amount and composition of microbial PLFA) was tested in a mixed effects model for the effect of *altitude*, with *land use* as a covariable and *sampling date* as a repeated measure.

We used a maximised restricted log-likelihood (REML) procedure (Pinheiro et al. 2012) to account for the unbalanced structure of our dataset, *i.e.* four altitudes in the case of UW land use type, as opposed to three. Upon detection of a significant *land use* effect each of its levels were tested for an *altitude* effect using the same model structure. In addition, linear regression models were employed to establish the effects of atmospheric climate (mean daily values for air temperature, air humidity, and precipitation) on the respective soil microclimate (soil temperature and moisture) within the transplanted mesocosms.

For each mesocosm, mean values of soil temperature and moisture between two sampling dates were used as representative of the microclimate experienced by litter bags during each incubation period. Their effect on the litter mass loss between successive sampling dates was tested in a similar mixed effect model as described above, using them as continuous covariables. Since all sampling dates tightly followed the winter and summer seasons, we tested the effect of sampling date (*i.e.* first winter, first growing season, second winter, second growing season, and third winter) on the sequential litter mass loss, using sampling date as a categorical variable. Similarly, the sampling dates were grouped in two categories – winter and growing season – in order to compare the corresponding mass loss in those two contrasting periods.

Comparison of litter decay rates among the different altitude and land use treatments was done using the decomposition rate constant (K value) from a negative exponential model (Olson 1963). The differences between the individual treatment combinations were tested in an ANOVA model with *altitude* (four levels) and *land use* (three levels) as fixed factors, followed by Tukey's test for honest significant differences.

The variation in litter microbial community composition (fungal/bacterial ratio, fungal PLFA, bacterial PLFA) was constrained in a redundancy analysis (RDA), using litter physicochemical parameters as explanatory variables. The temporal variation during the incubation period was partialled out *a priori* in order to reveal underlying associations between community structure and litter characteristics. Explanatory variables retained in the final model were chosen in a forward selection procedure and tested for their significance using 1000 permutations (Oksanen et al. 2012).

Assumptions of normality and homoscedasticity of the residuals in all linear regression models were verified visually using diagnostic plots and effects were considered significant at $P < 0.05$. All statistical analyses were performed in R 2.15.1 (R Development Core Team 2012), using packages 'nlme' (Pinheiro et al. 2012) and 'vegan' (Oksanen et al. 2012).

4.3. Results

4.3.1 Climatic gradient

Microclimatic conditions in the transplanted mesocosms (Figure 4.2) varied significantly over the 2.5 year decomposition period in relation to *altitude* ($F_{1,44} = 262.2$, $P < 0.001$ for soil temperature; and $F_{1,44} = 30.0$, $P < 0.001$ for soil moisture), and in relation to *land use* ($F_{2,44} = 9.6$, $P < 0.001$ for soil temperature; and $F_{2,44} = 7.0$, $P = 0.002$ for soil moisture). The observed gradient in soil surface temperature in the mesocosms was mainly due to variation in the air temperature along the altitudinal transect (linear regression $R^2 = 0.77$, $P < 0.001$), with the small part of unexplained variation coming from the winter periods when snow covered soils remained decoupled from atmospheric temperature fluctuations. Soil moisture, however, was not directly influenced by any of the measured climatic variables (air temperature, air humidity and precipitation) and showed a significant *altitude* treatment effect only for the unwooded pasture *land use*, but not for the other two wooded pasture types (Figure 4.2).

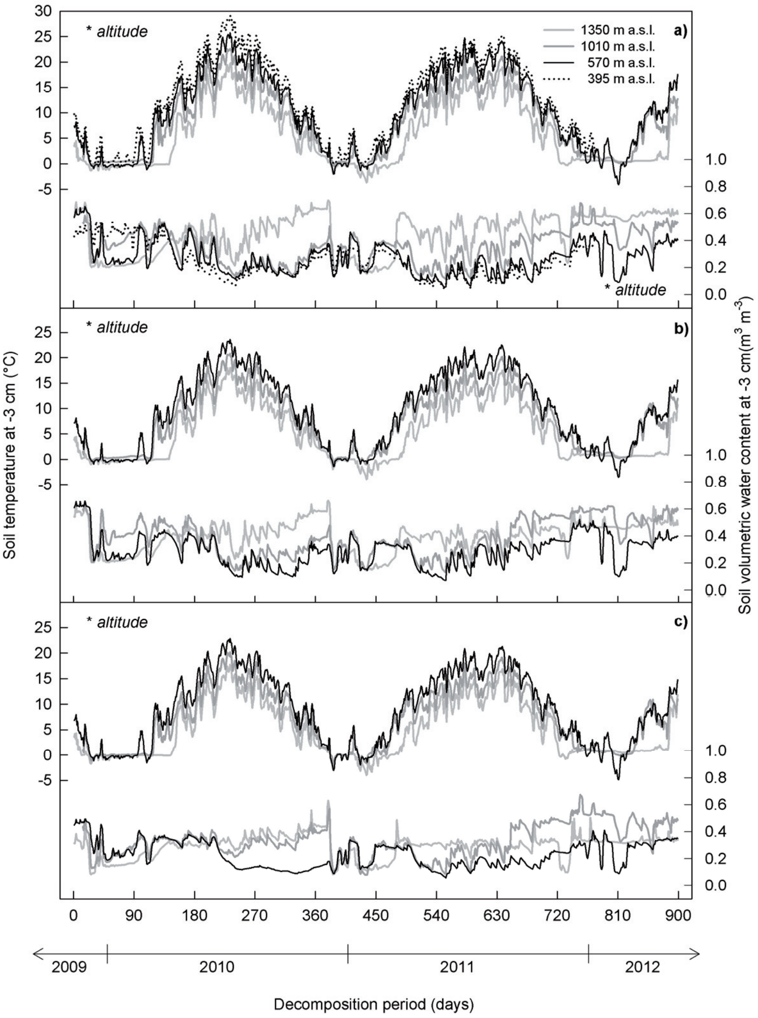


Figure 4.2. Soil microclimate in the transplanted mesocosms with turfs from: a) unwooded pasture, b) sparsely wooded pasture, and c) densely wooded pasture land use type, during the course of the 2.5 year long litter decomposition experiment. Presented are mean daily values for five replicate mesocosms. At the lowest altitude only the unwooded pasture land use was considered. Asterisks indicate significant effects of the specified factors within each of the land use types.

4.3.2 Litter decomposition rates and mass loss

Overall, the remaining mass in the litterbags was significantly affected by the *altitude* treatment ($F_{1,44} = 40.4$, $P < 0.001$) and was significantly less (up to 50 % mass loss after 2.5 years) in the unwooded pasture *land use* ($F_{2,44} = 8.5$, $P < 0.001$). Nevertheless, as seen in Figure 4.3, exclusively the unwooded pastures experienced distinct rates of mass loss with respect to *altitude*, which was reflected by a significant *altitude:land use* interaction ($F_{2,44} = 7.9$, $P = 0.001$). Mean soil moisture between two successive sampling dates had a significant effect on the sequential mass loss of litter ($F_{1,161} = 5.4$, $P = 0.021$), but soil temperature had none. Mass loss was comparable between individual sampling dates and no apparent effect of winter or growing season periods was observed either.

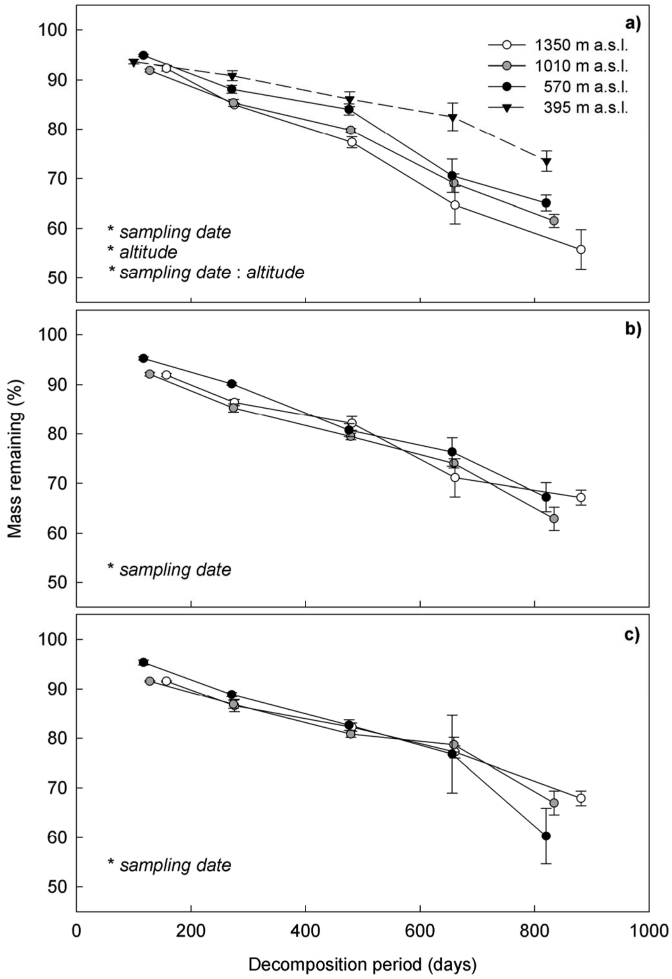


Figure 4.3. Percentage of initial mass remaining in the litter bags at bi-annual sampling intervals, following their incubation in autumn 2009 on the surface of mesocosms from: a) unwooded pasture, b) sparsely wooded pasture, and c) densely wooded pasture land use type. Presented are mean values and standard errors for litterbags from five replicate mesocosms. At the lowest altitude only the unwooded pasture land use was considered. Asterisks indicate significant effects of the specified factors within each of the land use types.

All the estimated decay constants (*K* values) came from significant exponential models with 84 % of the R^2 values within the range 0.8 – 1.0, and no R^2 values below 0.6. The comparison among treatment combinations in terms of *K* values (Table 4.2) revealed that the unwooded pasture plots at 1350 m a.s.l. had the fastest rates of decay, whereas those at 395 m a.s.l. had the slowest. A threshold in the response to climate conditions within this land use was observed between altitudes 570 and 395 m a.s.l. after which the decay rates decreased significantly. Rates of litter decomposition in the other two pasture types were not significantly different.

Table 4.2. Leaf litter decomposition rates (*K* values) [1] of *Fagus sylvatica* along an altitudinal gradient with mesocosms from three land use types.

Land use type [2]		UW	SW	DW
Altitude (m a.s.l.)	1350	0.236 ± 0.024 **a**	0.172 ± 0.012 **bc**	0.156 ± 0.006 **bc**
	1010	0.205 ± 0.007 **ab**	0.189 ± 0.009 **ab**	0.163 ± 0.008 **bc**
	570	0.182 ± 0.013 **ab**	0.166 ± 0.014 **b**	0.151 ± 0.010 **bc**
	395	0.125 ± 0.007 **c**	-	-

[1] Means and standard errors for five replicates. Different letters indicate significant differences between altitudes within the same land use type at the P = 0.05 threshold.

[2] Land use type codes, where UW refers to unwooded pasture with 0% canopy shading, SW – sparsely wooded pasture with 40% canopy shading, and DW – densely wooded pasture with 80% canopy shading.

4.3.3 Litter chemistry

Overall, the initial stoichiometric ratio of carbon and nitrogen (C/N ratio = 71.3) decreased substantially over the course of litter decomposition (*sampling date*: $F_{1,188} = 599.5$, $P < 0.001$), and was largely influenced by the *altitude* of litter bag incubation ($F_{1,44} = 64.0$, $P < 0.001$) and the *land use* ($F_{2,44} = 3.9$, $P = 0.028$). Figure 4.4 shows that litter at lower altitudes had a consistently lower C/N ratio across all three land-use types, however the decrease was most pronounced at the unwooded pasture *land use*. When investigated separately, carbon and nitrogen contents revealed that a pulse increase of +40 % in nitrogen concentration after the first year of incubation and a steady one thereafter (*sampling date*: $F_{1,192} = 5.8$, $P = 0.017$) was responsible for this change (4.5 Appendix, Figure A4.1). This pattern was most expressed at lower *altitude* ($F_{1,44} = 6.8$, $P = 0.012$).

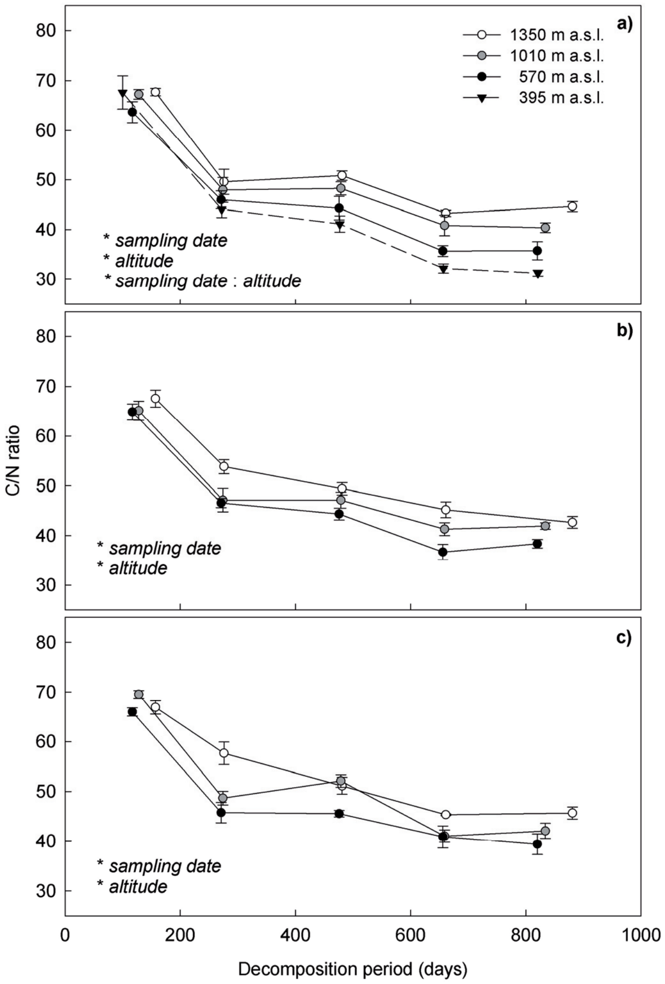


Figure 4.4. Dynamics of leaf litter C/N ratio during the decomposition period in mesocosms with turfs from: a) unwooded pasture, b) sparsely wooded pasture, and c) densely wooded pasture land use type. Presented are mean values and standard errors for five replicate mesocosms. At the lowest altitude only the unwooded pasture land use was considered. Asterisks indicate significant effects of the specified factors within each of the land use types.

4.3.4 Microbial community composition

The microbial communities on decomposing litter, assessed by the sum of the PLFA markers for fungi and bacteria, grew steadily over the course of the experiment (*sampling date*: $F_{1,193} = 180.8$, $P < 0.001$) without a significant *land use* effect (Figure 4.5). Only those litter bags incubated in unwooded pasture mesocosms revealed an *altitude* effect ($F_{1,18} = 7.6$, $P = 0.013$), which, however, varied significantly in its direction over time (*sampling date:altitude* $F_{1,78} = 4.0$, $P = 0.049$) causing either an increase or a decrease in the total amount of PLFAs at a given sampling date.

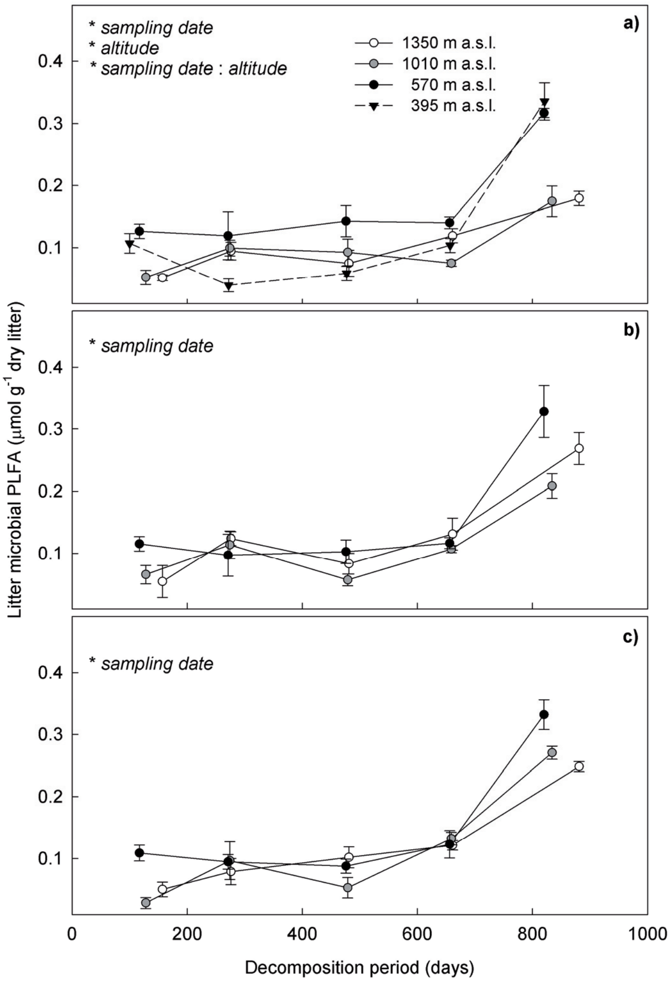


Figure 4.5. Microbial biomass on decomposing litter as represented by PLFA markers. Land use types are: a) unwooded pasture, b) sparsely wooded pasture, and c) densely wooded pasture. Presented are mean values and standard errors for five replicate mesocosms. At the lowest altitude only the unwooded pasture type was considered. Asterisks indicate significant effects of the specified factors within each of the land use types.

A seasonal variation in fungal/bacterial ratio was evident too (Figure 4.6), with a significant overall effect of *sampling date* ($F_{1,193} = 66.9$, $P < 0.001$). The magnitude of the *altitude*:*sampling date* interaction decreased along the unwooded – densely wooded pasture gradient and so did the effect of *altitude per se.* Indeed, as in the case of total microbial PLFA counts, the variation in fungal/bacterial ratio in the litter bags was only influenced by *altitude* within the unwooded pasture mesocosms ($F_{1,18} = 13.2$, $P = 0.002$). Overall, the *altitude* treatment caused a significant increase in bacterial PLFA markers at lower altitude ($F_{1,44} = 17.4$, $P < 0.001$), but did not affect the fungal ones.

Leaf litter chemistry exerted a significant effect ($P < 0.001$) on the composition of microbial communities in the litterbags (Figure 4.7), explaining a total of 20.7 % of the variability in the grouped PLFA dataset. The RDA revealed causal relationships between remaining litter C content and fungal abundance, as well as between fungal/bacterial ratio and C/N ratio. Increasing litter N content had a negative association with fungal abundance. Remaining mass in the litterbags was not a direct indicator of microbial community structure, once the temporal effect of sampling date was removed in the analysis.

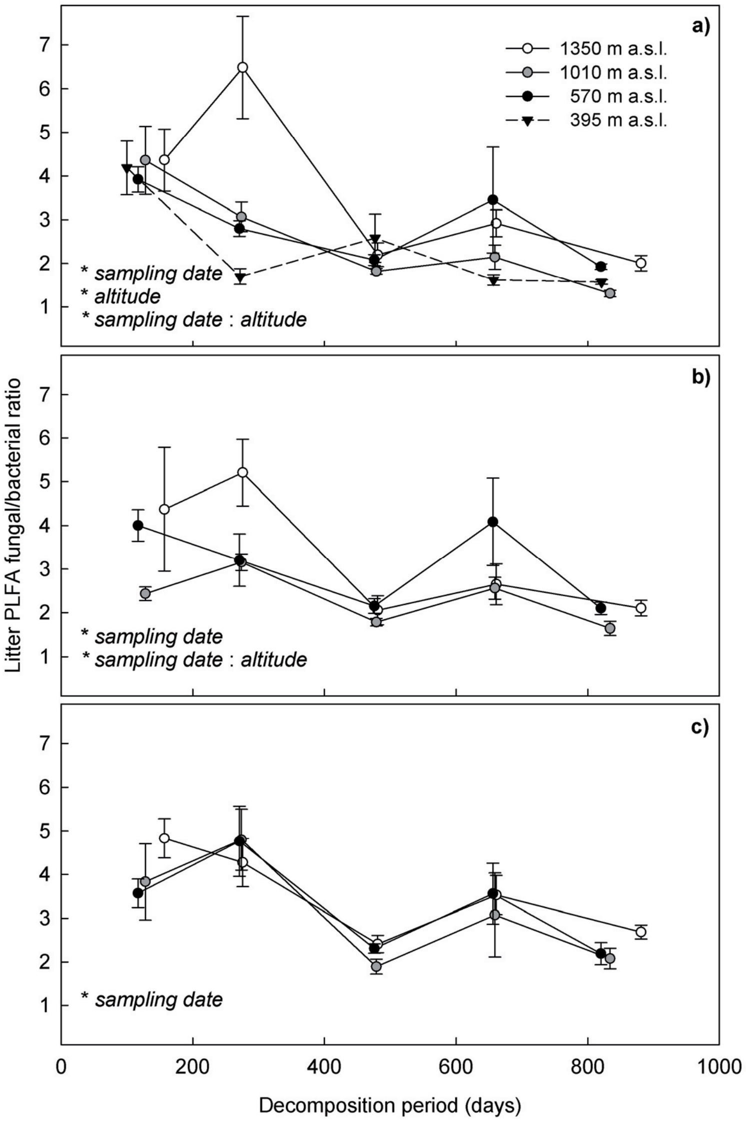


Figure 4.6. Ratio of fungal to bacterial PLFA markers in the litter bags. Land use types are: a) unwooded pasture, b) sparsely wooded pasture, and c) densely wooded pasture. Presented are mean values and standard errors for five replicate mesocosms. At the lowest altitude only the unwooded pasture type is considered. Asterisks indicate significant effects of the specified factors within each of the land use types.

4.4. Discussion

4.4.1 Climate and land use driven patterns in litter decomposition

Decomposition rates over the two and a half year incubation period were within the range of most commonly reported *K* values for leaf litter on a global basis, *i.e.* 0.1 to 0.3 (Zhang et al. 2008). Based on the type of land use, the mass loss from *Fagus sylvatica* litterbags showed distinct trajectories in its response to the climate along the altitude gradient. Only in the non-shaded UW mesocosms were the decay rates affected by the altitude treatment, with higher rates at higher altitude. Such a pattern was previously reported for altitudinal transects across vegetation zones in North American (Murphy et al. 1998) and European (Duboc et al. 2012) mountains, but never, to our knowledge, for transplanted turfs and thus, standard soil conditions. Contrary to our hypothesis about a local optimum range for litter decomposition at mid-elevation, based on the offset between air temperature and precipitation along the climatic gradient, we observed either a clear linear relationship with altitude (UW land use), or no such at all (SW and DW land use). Indeed, our data provided evidence for a prevailing moisture limitation on the decomposition process. Temperature did not act as a constraint on litter decay at higher altitude, however soil moisture exerted a strong control at lower altitude. Indeed, both litter mass loss and soil moisture decreased significantly with warmer and drier climate at lower altitude within the UW mesocosms. In contrast, within the two shaded land use types (SW and DW), where no change in decomposition rates was detected in relation to altitude, temperature was consistently warmer at lower altitudes, but soil moisture experienced an idiosyncratic seasonal pattern, with no consistent altitudinal gradient over the entire incubation period. This, together with the fact that soil moisture was not a direct function of a single climatic parameter (precipitation, air temperature and air humidity), but rather a product of several in concert (as simulated by the altitude treatment), confirmed the notion for counterbalancing effects of soil temperature and moisture on the litter decomposition process (see Aerts 2006).

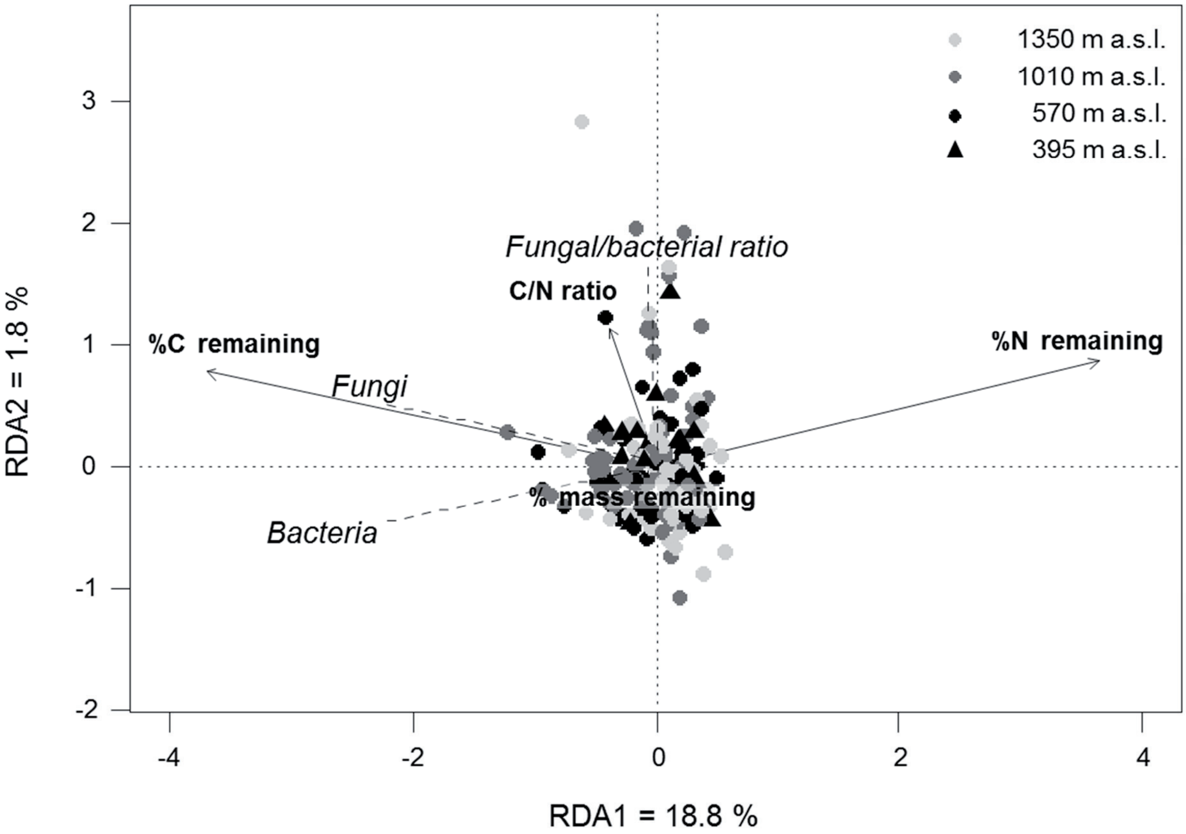


Figure 4.7. Biplot of the redundancy analysis (RDA) of microbial community variation in relation to litter physicochemical characteristics, once the effect of incubation period length is removed. Points represent the 250 individual litterbags incubated in mesocosms along the altitudinal gradient. Both axes RDA1 and RDA2 are significant (P < 0.001).

A relevant process taking place on the surface of the mesocosms is the net difference in radiative heating among the three land use types. Due to their shading, each of the two "wooded" treatments experienced, on average, cooler temperatures than the unwooded one. Hence, taking into account the intensified evapotranspiration at warmer air and/or soil temperatures (Seneviratne et al. 2006), UW mesocosms were much more prone to soil moisture limitation during persistent warm and dry periods. At the landscape scale, such a dichotomy in the response of grasslands and forests to heatwaves was demonstrated too (Teuling et al. 2010), providing evidence for a more conservative water use efficiency of forests, which preserves soil moisture in the long term and prevents excessive heating due to drought (Seneviratne 2012).

Despite the fact that litter decomposition was significantly influenced by the climatic gradient only within the UW land use, litter bags in the latter exhibited consistently higher mass loss rates along the altitude transect in comparison to those in SW and DW. Such higher decomposition rates under drier conditions could point to an abiotic degradation as in the case of photodegradation (see Austin and Vivanco 2006) where prolonged exposure to UV light renders litter more easily degradable (Foereid et al. 2010). Vegetation surveys in those mesocosms (Gavazov et al. 2013; Gavazov et al. *in press*) indicated substantial loss in plant aboveground biomass and increased bare ground area due to warmer climate and reduced precipitation which could have further facilitated such a process.

Our five biannual samplings allowed us to study the intra-seasonal decomposition pattern and the observed steady decay rates provided evidence for comparable mass loss across seasons. On the one hand, this goes in line with previous studies demonstrating substantial mass loss rates during the winter season (Sjögersten and Wookey 2004; Baptist et al. 2010; Saccone et al. 2013). On the other hand, it is in contrast to the stipulated model of faster and slower stages of litter decomposition based on a decreasing litter quality over the course of the decomposition process (Couteaux et al. 1995). This could be tentatively explained by the principle that the early stages of decay are substrate quality driven and the later stages are microbial community composition driven (Bray et al. 2012), such that the interplay between those and the seasonal change in climate and microbial structure (see Bardgett et al. 2005; and the discussion in section 4.2) has resulted in the observed steady decomposition rate over the entire incubation period.

4.4.2 Microbial community shifts in relation to litter chemistry and decomposition along the altitudinal gradient

Plant litter chemistry changed substantially over the course of time, with litter C/N ratio decreasing both as decomposition progressed and in response to the altitudinal treatment. The observed change in C/N ratio was exclusively due to an increase in N concentration in the litter, which was most probably due to immobilisation of nitrogen from the soil (Melillo et al. 1982). Since litter quality, and N content in particular, have a dominant role in determining decomposition rates globally (Cornwell et al. 2008), recalcitrant litter types (such as *Fagus sylvatica*) require that allochthonous N is brought up by microbes in order to access the C in the litter (Rutigliano et al. 1998). In this study, the process occurred only after one year of incubation, during the first plant growing season and not during the preceding winter (see Figure 4.4), indicating a preceding limitation in N-availability. Furthermore, the disproportional decrease in litter C/N within mesocosms at lower altitudes could be due to a general increase in N-availability resulting from warmer soil temperatures. Indeed, we found a concomitant increase N-mineralisation rates and leaching of N into the soil solution at lower altitudes (4.5 Appendix, Table A4.1) – a trend which has been previously established for both altitudinal gradients (Zhang et al. 2012) and globally in warming experiments (Bai et al. 2013). The land use pattern of lower C/N ratios in litterbags incubated in UW mesocosms could be further attributed to the synergetic effect of extant labile grassland litter (*i.e.* lower soil organic matter

C/N ratio, Table 4.1) on the decomposition rates of *Fagus sylvatica*, allowing the transfer of N between the two (see Schimel and Hättenschwiler 2007).

Alongside with the change in litter C/N stoichiometry, a change in microbial community structure took place, resulting in matching decrease in fungal/bacterial ratios in the litterbags both in time and in relation to the litter physicochemical characteristics. Since a gradient in fungal/bacterial ratio could result from the extent of management intensity, nutrient availability, and successional stage (van der Heijden et al. 2008), we interpret the reported decrease in fungal/bacterial ratio in litterbags at lower altitude (especially those in the UW mesocosms) as alteration of the nutrient cycle. This follows form the general concept for an increasing importance of bacteria in ecosystems experiencing a faster nutrient cycle (Wardle et al. 2004). The observed temporal dynamics in fungal/bacterial ratio, could be further attributed to the change in microbial community structure with respect to seasonality, as reported by Schmidt and Lipson (2004). The oscillating pattern, clearly seen in the two wooded pasture land use types (Figure 4.6) can be explained by the principle that senesced litter in autumn is colonised by fungi responsible for its degradation over winter, and the subsequent increase in N-availability in the soil solution in spring results in a substantial immobilisation by bacteria. Our results suggest that this process in the soil microbial community can be severely disrupted by altered climate as seen in the UW land use, but also that wooded pastures with their characteristic buffered microclimate and edaphic conditions have a much lower sensitivity to climatic perturbation.

4.4.3 Outlook

The spatial and temporal continuum of leaf litter decomposition rates presented with this experiment demonstrated the potential of climate gradient studies for the detection of causal relationships between ecosystem processes and climate variability. The linearity in the response of litter decomposition within unwooded pastures to climate change revealed the controlling role of soil moisture on this process, but also the threshold level of change needed for a significantly detectable effect. Surprisingly, we did not find evidence for temperature limitation on this process. The observed land use driven response of litter decomposition to climate has furthermore important implication for carbon cycling under climate change. Besides exerting a direct microclimatic effect on litter decomposition, wooded pastures also supported a community of microbial decomposers which was more resistant to the experimental change in climate. Since climate scenarios predict *Fagus sylvatica* encroachment into higher subalpine altitudes (Bolliger et al. 2000; Kramer et al. 2010) and into abandoned mountain pastures (Peringer et al. 2013), one should foresee the role of its litter decomposition in this process, especially under various land use practices. Given our results, we expect that the tight linkages between above and belowground ecosystem processes related to carbon and nutrient turnover (Wardle 2002) may grant leaf litter decomposition of *Fagus sylvatica* an important role in the formation of soil organic matter but also in the establishment of vegetation successions, where land use management strategies could form an important tool for climate change mitigation.

4.5. Acknowledgements

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4.6 Appendix

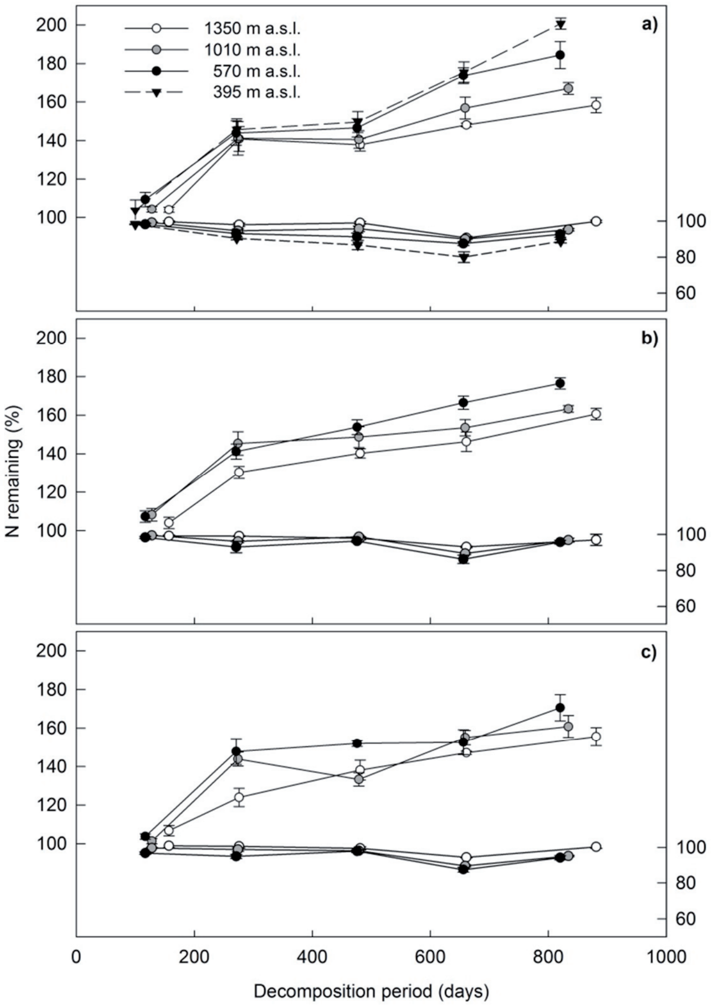

Figure A4.1. Percentage of initial nitrogen (N) and carbon (C) remaining in the decomposing litter at bi-annual sampling intervals. Litterbag incubation started in autumn 2009 on the surface of mesocosms from: a) unwooded pasture, b) sparsely wooded pasture, and c) densely wooded pasture land use type. Presented are mean values and standard errors for litterbags from five replicate mesocosms. At the lowest altitude (359 m a.s.l.) only the unwooded pasture land use was considered

Table A4.1. Soil nitrogen dynamics in the transplanted mesocosms.

Altitude (m a.s.l.)	1350			1010			570			395
Land use type [1]	UW	SW	DW	UW	SW	DW	UW	SW	DW	UW
N-mineralisation rate (µg g^{-1} $month^{-1}$) [2]	9.0 ± 4.0	7.4 ± 1.2	10.6 ± 2.0	16.4 ± 1.9	4.7 ± 3.0	13.7 ± 4.1	20.4 ± 8.5	12.1 ± 3.7	21.9 ± 4.8	39.1 ± 18.7
Soil solution DIN (mg l^{-1}) [3]	0.74 ± 0.16	0.61 ± 0.09	3.70 ± 0.63	0.41 ±0.05	0.40 ± 0.06	5.04 ±0.82	1.98 ± 0.35	0.80 ± 0.26	4.84 ± 0.62	7.84 ± 2.22
Soil solution DON (mg l^{-1}) [3]	0.35 ± 0.06	0.27 ± 0.04	0.28 ± 0.05	0.65 ± 0.10	0.29 ± 0.04	0.50 ± 0.10	0.95 ± 0.17	0.33 ± 0.05	0.76 ± 0.16	1.27 ± 0.35

[1] Land use type codes, where UW refers to unwooded pasture with 0% canopy shading, SW – sparsely wooded pasture with 40% canopy shading, and DW – densely wooded pasture with 80% canopy shading.

[2] Nitrogen mineralisation rates (production of NH_4^+ and NO_3^-) were established at peak growing season in 2011. Homogenised soil cores from each mesocosm (2.5 cm diameter x 10 cm depth) were incubated in gas permeable 50 µm thick polyethylene zip bags (5 x 7.5cm) by burying them in the soil and replacing the humus and litter layer on top (Hart et al. 1994). Data are means and standard errors for five replicates.

[3] Inorganic (DIN) and organic (DON) nitrogen concentrations in leached soil solution collected in zero potential lysimetres from each mesocosm. Presented data are monthly averages for the period February 2010 – January 2012, with means and standard errors for five replicates.

Chapter 5

Sub-alpine pasture response to simulated climate change; moisture drives diminished soil function, yet heterotrophic temperature response indicates resilience

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Mills, R., K. Gavazov, T. Spiegelberger, A. Buttler and D. Johnson (*in review*). "Sub-alpine pasture response to simulated climate change; moisture drives diminished soil function, yet heterotrophic temperature response indicates resilience." Science of the Total Environment.

Abstract

The pressure of climate change is disproportionately high in mountainous regions, and small changes may push ecosystem processes beyond sensitivity thresholds, creating new dynamics of C and nutrient cycling. As the rate of organic matter decomposition is in part dependent upon temperature, the sensitivity of soil respiration to temperature is highly relevant when considering soil-atmosphere feedbacks under a changing climate. To assess the effect of changing climate on soil respiration and heterotrophic sensitivity to temperature in a mountain pasture system, we transplanted soils along an altitude gradient and monitored *in situ* soil respiration and conducted a temperature sensitivity incubation of collected soils. *In situ*, transplantation reduced soil moisture and increased soil temperature, with concurrent reductions in soil respiration. Soil moisture acted as an overriding constraint to soil respiration, and significantly reduced the sensitivity to temperature. Under controlled laboratory conditions, removal of moisture constraint to heterotrophic respiration led to a significant respiration-temperature response. However, the response function was comparable among sites, and therefore unaffected by antecedent conditions. Our findings highlight the resilience of the microbial community to severe climatic perturbations, but also that soil moisture stress during the growing season can significantly reduce soil function in addition to direct effects on plant productivity. This demonstrates the sensitivity to subalpine pastures under climate change, and possible implications for sustainable use given such reductions in organic matter turnover and feedbacks to nutrient cycling.

Keywords

Altitudinal gradient; climate warming; mountain grasslands; pH; soil moisture; soil respiration; soil organic matter density fractionation

5.1 Introduction

Through altering temperature and precipitation patterns, climate change is projected to place increasing pressure on the sustainable use and productivity of semi-natural grassland systems. This is thought to be especially so for mountain grasslands such as those in the alpine and sub-alpine zones (Dunne et al. 2003). Elevated growing-season temperatures and more frequent occurrence of drought periods have the capacity to alter carbon (C) and nutrient cycling at the ecosystem level (Walther et al. 2002), with potential for significant soil-plant feedbacks (Melillo et al. 2002). Higher temperatures may lead to enhanced C losses from soils (Kirschbaum 1995; Bond-Lamberty and Thomson 2010) and faster nutrient cycling (Ineson et al. 1998; Shaw and Harte 2001; Zhang et al. 2012), yet these increases may be offset, or even reversed by the effect of reduced moisture status (Davidson and Janssens 2006). Whilst dependent upon antecedent conditions and biological community adaptation, moisture stress, especially during the growing season, can lead to considerable reductions in C fixation, and rates of C and nutrient cycling. This is of particular concern given that soil respiration is the second largest annual flux (after photosynthesis) of C between the atmosphere and terrestrial systems (Houghton 2007). It is therefore highly relevant to assess change in soil respiration under changing climate. Soil respiration represents a sensible and logistically simple measure of general soil function, as it encapsulates the end product of a range of metabolic processes involved in C and nutrient cycling, as well as organism activity. This is particularly important given the long-term sustainability of ecosystems depends upon maintaining soil function, therefore respiration provides a broad yet sensitive indicator of change.

The fundamental metabolic dependence upon temperature suggests that rate should increase with temperature according to a simple response function (Arrhenius 1889). In the case of soil respiration, this must assume that all other constraining factors are not limiting, but *in situ*, this is rarely the case over any significant spatial or temporal scale. Therefore, when measured in the field, the observed response to temperature is in fact the ‘apparent’ sensitivity, and recognises the myriad drivers that exist. The sensitivity to temperature is often encapsulated by the Q_{10} function, which essentially describes the change in rate over a 10 degree change in temperature. This function carries the benefit of being simple and comparable among systems, but is influenced by the statistical model used to derive the temperature-respiration fit (Lloyd and Taylor 1994). Soil moisture also strongly constrains ecosystem function, and its effect on soil respiration has been the subject of research for a considerable time (Orchard and Cook 1983; Davidson et al. 2000; Xu et al. 2004; Flanagan and Johnson 2005). The conceptual moisture-respiration model of Suseela et al. (2011) serves to summarise the occurrence of a moisture optimum, which approximately coincides with field capacity. The broad applicability of such a model, especially along gradients of drying from optimum is evident (e.g. Chen et al. 2008), and such a relationship provides a basis for modelling dependencies. However, the interaction of soil moisture with temperature requires consideration of multi-factor approaches, and this dual-driving of function by moisture and temperature has been the focus of a considerable research effort (e.g. Davidson et al. 2000; Raich and Tufekciogul 2000; Janssens and Pilegaard 2003). This interaction becomes especially apparent when considering how moving away from soil moisture optima can strongly reduce the temperature sensitivity of soil respiration (Sowerby et al. 2008; Lellei-Kovács et al. 2011; Suseela et al. 2011). To assess the intrinsic temperature sensitivity of soil respiration, incubations of soil cores across temperature manipulations (Fang and Moncrieff 2001; Curiel Yuste et al. 2007) can be used. This approach could also provide information on whether apparent sensitivity *in situ* is the product of real changes to intrinsic sensitivity, or more a function of other constraining factors.

Investigating change in soil function, and its sensitivity to moisture and temperature can be contextualised by considering changes to soil organic matter (SOM) quality and quantity, primarily as an indicator of any trajectories in C accumulation or loss. Whilst SOM is an inherently complex material that exists along a decomposition continuum, fractions of SOM that reflect early stages of decomposition can be separated to serve as a more sensitive indicator than bulk SOM. This is usually carried out by density separation, where a light fraction organic matter is separated (Sollins et al. 1984; Leifeld and Kögel-Knabner 2005; Schindlbacher et al. 2010), is assumed to be relatively available due to a lack of mineral interactions or aggregate occlusions. Not only does this fraction serve as a sensitive indicator of change, but the quality of the light fraction could also be related to temperature sensitivity (Schindlbacher et al. 2010). This relationship could be used to explore whether changes in temperature sensitivity are related to so-called 'thermal acclimation' (Bradford et al. 2008), or to changes in substrate quality (Fierer et al. 2005), which is central to respiration-temperature debate (Subke and Bahn 2010).

Much experimental work to consider the role of climate change on soil and plant function has been based on *in situ* manipulations, yet natural climate gradients can also be used to study spatial variation in ecosystem processes (Emmett et al. 2004; Zhang et al. 2012). Using the established natural gradient of mean annual temperature (MAT) decrease and a precipitation (MAP) increase with higher altitude in temperate mountain regions, one can conveniently substitute space for time in ecological climate change research (Körner 2007). Soil monolith transplantation from high to low altitudes has been shown to effectively simulate warmer climate in various studies (see Ineson et al. 1998; Hart and Perry 1999; Olofsson 2001; Link et al. 2003; Sebastia 2007), and across much larger spatial scales in general climate change contexts (Breeuwer et al. 2010). Such an approach provides a natural year-round experimental warming, which also accounts for associated changes in precipitation, snow-to-rain ratio, snowmelt, and length of the vegetation growing-season. Transplantation also allows combined temperature and moisture (multifactor) treatments to be incorporated without possible issues relating to observed infrastructure effects and uneven treatment effect throughout the year (Carlyle et al. 2011).

To assess the impact of experimental climate change on soil respiration and SOM in sub-alpine pastures, we used an existing mesocosm transplantation experiment in the Swiss Jura Mountains (Gavazov et al. 2013) where soil and vegetation were transplanted to four altitudes representing a climate gradient in moisture and temperature. Soil respiration was measured *in situ* during the growing season of 2011, and we explored the relationships to moisture and temperature, and the apparent temperature sensitivity. To assess the intrinsic temperature sensitivity of the heterotrophic component of soil respiration, we sampled the uppermost organic layer of the soil and carried out a laboratory incubation across a temperature range. We also considered change to chemical characteristics of the soil organic matter, which we assessed on bulk soil, and on a light fraction of SOM separated by density. The translocation approach used in this study spans the whole range of scenarios outlined by Meehl et al. (2007) and incorporates expected changes to precipitation for Switzerland (Frei et al. 2006). This set up allowed for the detection of thresholds in response parameters, *i.e.* tipping points (see Lenton 2011), which when reached, can trigger rapid changes in ecosystem function, with feedbacks to ecosystem resilience and sustainable use.

Given the previous observation of changes in community composition and productivity (Gavazov et al. *in press*), and the established driving of soil respiration by moisture, we first hypothesised respiration would be reduced at transplantation sites as a function of soil moisture. Secondly, soil temperature was expected to have a control over soil respiration, but the strength of the relationship was hypothesised to reduce down the transplantation gradient in response to increasing moisture stress. For the laboratory incubations, we expected that removal of moisture constraints would establish temperature sensitivities among all soils, and that the strength of this relationship might vary as a function of antecedent *in situ* conditions. Finally, we assumed that lower productivity down-slope would result in lower abundance of light fraction organic matter, and a lower quality of the separated light fraction (*i.e.* higher CN ratio).

5.2 Methods

5.2.1 Site description and experimental design

Soils of mountain pastures were translocated (in 2009) from the initial donor site in Combe des Amburnex, Switzerland (N 46°55', E 6°24') at 1350 m a.s.l. to four recipient sites: the disturbance control at 1350 m a.s.l. (Marchairuz, N 46°54', E 6°23'), and the downslope sites at 1010 m a.s.l. (St George, N 46°52', E 6°26'), 570 m a.s.l. (Arboretum d'Aubonne, N 46°51', E 6°37') and 395 m a.s.l. (Bois Chamblard, 46°47', E 6°41'). Detail of the translocation procedure, which forms part of an ongoing CCES–MOUNTLAND research initiative (http://www.cces.ethz.ch/projects/sulu/MOUNTLAND), can be found in Gavazov et al. (2013). Briefly, each site received five replicated pasture turfs measuring 60 x 80 cm and 35 cm in height, which were contained within lysimeter mesocosms of the same dimensions. At each site, mesocosms were arranged in a common garden by being dug down to ground surface as to avoid lateral heat exchange. In each mesocosm, ECH$_2$O EC-TM sensor probes coupled to Em50 data-loggers (Decagon Devices, Inc., USA) 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. Parameters vary along the transect as a simulation of climate change, spanning a gradient from wet and cold (subalpine zone) to warm and dry (colline zone) growing season conditions.

5.2.2 In-situ soil respiration

Soil respiration was measured fortnightly or monthly throughout the snow-free period using a Li-Cor LI8100 infrared gas analyser (IRGA) on a permanent 10cm PVC collar cut ~2 cm into the soil. Enclosures lasted 2 minutes with a 30 second deadband, and flux estimates were calculated automatically after data inspection using a non-linear regression. Fluxes were expressed per unit area and were a mean of the five replicated pasture mesocosms.

5.2.3 Soil sampling and preparation.

Soil cores were taken in June 2011 from the five replicated mesocosms of the open pasture system at each of the four translocation sites. The top 4 cm of soil was sampled with a 5 cm diameter steel corer, with vegetation being cut and removed prior to sampling. Soil was stored in a cooled box and transported to the laboratory for temporary storage at 4 °C until analysis. Soils were weighed and measured (for volume calculation) before being lightly homogenised by hand, and having large root (>2 mm) material removed. Soils were not sieved, so as to reduce disturbance, especially to fungal components. For soil chemical analysis, a 5 g subsample was dried at 40 °C and ball milled. For respiration analysis, a ~10 g subsample of soil was adjusted to 100 % of water holding capacity (WHC) by addition of deionised water (the quantity being determined previously on separate pasture cores by wetting and draining under gravity to determine WHC per unit of mass) and incubated at 5 °C for 24 hours in an unsealed 50 ml polypropylene centrifuge tube prior to respiration analysis.

5.2.4 Respiration analysis

After the 24 hr settling period at 5 °C, adjusted soils were subjected to a temperature ramp from 5.5 – 30.5 °C, at 5 degree intervals. Each incubation period lasted for 1.5 hours, after which respiration was determined by closing the centrifuge tube and connecting via tubing to a Li-COR 8100 infrared gas analyser. Centrifuge tubes were sampled at random on each temperature sampling-occasion, where headspace CO_2 was allowed to accumulate for 60 seconds and the ppm concentration was automatically recorded every second. After sampling, tubes were returned to the incubator at the next temperature. Respiration rates were calculated using the slope from a non-linear regression to raw ppm data and converting to a mass flux via a simple equation using the ideal gas law, taking into account incubation temperature and the volume of the centrifuge tube plus gas lines, whilst assuming atmospheric pressure of 1 atmosphere. Initial variation in ppm data were excluded to give a 10 – 15 s dead band using the Li-COR regression analyser tool. Fluxes were expressed as a function of dry soil mass. Temperature dependence of soil respiration was estimated by fitting a simple non-linear model to the derived flux rates (equation 5.1) and calculation of a Q_{10} function (equation 5.2).

$$R = ae^{(bT)} \qquad \text{(Eq. 5.1)}$$

Where R is the flux (ppm CO_2 per second), T is the temperature, and a and b are parameters of the fitted data.

$$Q_{10} = e^{(b10)} \qquad \text{(Eq. 5.2)}$$

5.2.5 Soil physico-chemical analysis

Soil C and N were determined under high-temperature oxidation using a CN analyser (CE Instruments model NA2500 Nitrogen Carbon Analyser). Ca, Mg, Al, K and Fe were determined using atomic absorption spectroscopy (Perkin Elmer AAnalyst 100) after nitric acid digestion. Total phosphorus was determined using flow injection analysis (Foss FIA-star 5000 auto analyser) after digestion in sulphuric acid with hydrogen peroxide. To obtain a light fraction

SOM_{lf}, 20 g samples of field-moist soil were mixed for 1 hour in a 1.2 g cm^{-3} solution of NaI, and then centrifuged at 4000 RPM after which the material floating on the surface was separated by decantation. This procedure was repeated and separated fractions were washed in deionised water, dried and weighed. Total C and N content of fractions were analysed as for bulk soils after ball milling. Soil moisture and organic matter were determined gravimetrically at 105 °C and 375 °C respectively.

5.2.6 Statistical analysis

The effect of experimental climate change on *in situ* field respiration rates, as well as on daily values of soil temperature and moisture, was analysed using linear mixed effects (LME) models for repeated measures, with site as a fixed factor with four levels (*i.e.* altitude of transplantation). Incubation flux estimates were analysed for between-site differences using a LME model with site as a fixed factor, temperature as a continuous co-variable, and their interaction term. Significant differences between individual transplantation sites were determined using linear combinations of contrasts, thus accounting for the model's nested structure. Between and within-site effects of concurrent soil temperature and soil moisture on *in situ* soil respiration rates were determined using simple linear regression models. Between-site differences in soil physico-chemical characteristics were tested using analysis of variance (ANOVA), followed by Tukey's HSD *post-hoc* tests. Linear associations among edaphic variables were assessed via Pearson's correlation coefficients. Assumptions of normality and homoscedasticity of the residuals in all final models were verified visually using diagnostic plots, with log and square-root transformations being applied to data when necessary. All analyses were carried out using R v2.15 (R Development Core Team 2012).

5.3 Results

5.3.1 Soil micro-climate

Transplantation of soil and vegetation monoliths had substantial effects on the soil micro-climate (Figure 5.1) during the period May-September (inclusive). Significant overall differences were found among all sites for soil temperature ($F_{3,16} = 293.7$, $P < 0.001$), and for soil moisture ($F_{3,16} = 22.6$, $P < 0.001$), all transplantation sites were significantly different from the control site at 1350 m. All sites experienced substantial fluctuations in both metrics, and variations among sites in soil moisture were reasonably correlated (all $r > 0.62$), but much more so for temperature (all $r > 0.84$).

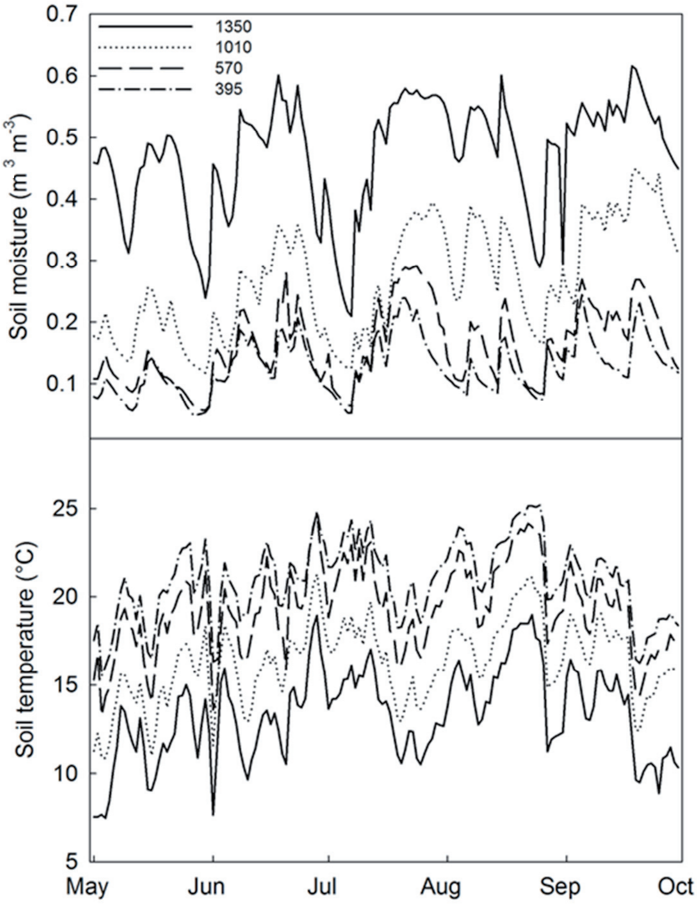

Figure 5.1. Daily mean topsoil moisture and temperature across the study period (May – September 2011).

5.3.2 Soil chemistry

A summary of selected chemical variables and broad measures of macronutrient and carbon content and ratios are presented in Table 5.1. Comparison of total C, N and P content among sites showed comparable values, and therefore ratios, of key macronutrients and C remained similar for bulk soil. Soil pH was significantly lower at sites 395 m and 570 m than the control site at 1350 m ($P = 0.016$, 0.002 respectively), and correlated strongly with changes in Ca ($r = 0.84$) across all sites. Lower levels of Ca at 570 m ($P = 0.019$) and 395 m ($P = 0.013$) than 1350 m also coincided with higher within-site correlations between Ca and pH (570 m, $r = 0.97$; 395 m, $r = 0.84$). Variation among sites in cation content (Table 5.1) was dominated by significant differences between sites 1350 m and 1010 m in Al ($P = 0.011$), Fe ($P = 0.006$) and K ($P = 0.036$), with remaining cations (apart from Ca) following no apparent trend.

Table 5.1. Soil physical and chemical parameters in the transplanted mesocosms

Site (m a.s.l.)	1350	1010	570	395
Bulk Density (g cm^{-3})	0.54 (0)	0.6 (0)	0.56 (0.1)	0.59 (0)
pH ($CaCl_2$)	5.4 (0.1)	4.6 (0.2)	5 (0.1)	4.7 (0.2)
C %	10.4 (0.5)	10.1 (1.4)	11.6 (0.6)	9.4 (0.9)
N %	1 (0)	1 (0.1)	1.1 (0.1)	0.9 (0.1)
C/N	10.5 (0.3)	10.1 (0.8)	10.2 (0.4)	10 (0.9)
P (mg g^{-1})	1 (0)	1 (0.1)	1.1 (0.1)	0.9 (0.1)
Mg (mg g^{-1})	4.4 (0.6)	4.1 (0.3)	4.6 (0.3)	4.2 (0.2)
Fe (mg g^{-1})	44.5 (1.3)	30.4 (1.6)	34.9 (3.4)	38.7 (1.8)
K (mg g^{-1})	4.8 (0.2)	3.6 (0.2)	4.2 (0.4)	4 (0.1)
Ca (mg g^{-1})	7.2 (1)	3.7 (0.9)	5.3 (0.7)	3.5 (0.4)
Al (mg g^{-1})	33 (1.2)	24.6 (1.5)	29.6 (2.2)	27.5 (1)

5.3.3 Soil organic matter light fraction

Light fraction organic matter (<1.2 g cm^{-3}) separated by density fractionation made up a small (<4 %) proportion of the total soil mass (Table 5.2), but in some cases over 10 % of the total soil C in the was found in this fraction. The N content of the SOM_{lf} was typically <7 % of total soil-N. The quality of the SOM_{lf} showed it to be only partially decomposed, retaining a relatively high CN of ~18. The variation among sites in the quantity and quality of the SOM_{lf} (Table 5.2) shows a consistent pattern, with transplanted sites generally containing more SOM_{lf}, with higher C and N content than that at the control site at 1350 m. Between site differences though were non-significant for all comparisons apart from the N content between sites 1350 m and 570 m (P = 0.02). Despite the lack of significance, there is an appreciable accumulation of SOM_{lf} in transplanted soils, in some cases twice that at the control.

Table 5.2. Mass and chemical variables for the light fraction of soil organic matter obtained by density. Values are mean, with standard error in brackets.

Site (m a.s.l.)	1350	1010	570	395
Mass % total mass	1.4 (0.7)	2.4 (0.6)	3.2 (0.7)	3 (0.7)
C %	28.7 (2.1)	30.6 (1.8)	31.6 (0.6)	31.4 (1.1)
N %	1.4 (0)	0.7 (0)	1.8 (0.1)	1.8 (0.1)
LF-C % SOC	3.4 (1.4)	6.1 (0.6)	8.9 (1.9)	9.7 (1.3)
LF-N % soil-N	2 (1)	3.3 (0.4)	5.4 (1.3)	5.6 (1.1)
C/N	20.3 (1.9)	18 (1.1)	17.4 (1)	17.8 (0.6)

5.3.4 In situ respiration response to moisture and temperature

Soil translocation resulted in successive reductions in average soil respiration rates down the altitude gradient for the period May-September 2011. There was a significant effect of site on soil respiration across the period ($F_{3,16} = 19.6$, $P < 0.001$), and as shown in Figure 5.2, between site differences were evident among all sites apart from between 570 m and 395 m a.s.l.

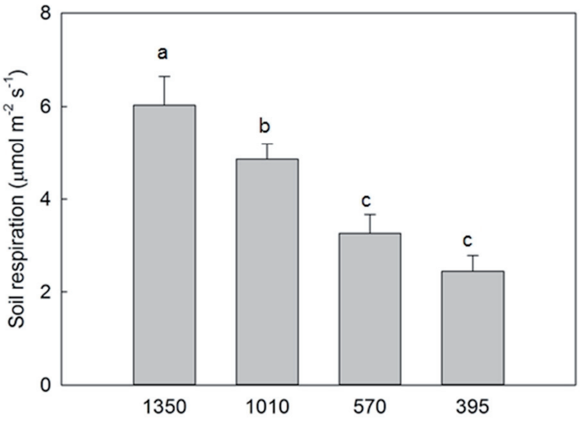

Figure 5.2. Mean soil respiration *in situ* during the growing season 2011. Different letters denote significant differences between sites (P < 0.001).

Overall, lower soil moisture content at transplantation sites coincided with lower respiration rates during the sampling period (Figure 5.3), and when all sites were grouped, moisture gave a strong and significant effect ($R^2 = 0.51$, $P < 0.001$). At the site level, moisture had an increasing explanatory power at successive downslope sites (1350 m $R^2 = 0.05$; 1010 m $R^2 = 0.14$; 570 m $R^2 = 0.41$, 395 m $R^2 = 0.66$), but only at the lowest elevation site (395 m) was the regression fit significant ($P = 0.008$). Soil temperature (Figure 5.4) had no overall significance across sites when data were combined ($P = 0.28$), and at the site level, only the control site at 1350 m gave a significant response ($R^2 = 0.85$, $P < 0.001$), with the transplantation sites all showing non-significant fits with low coefficients of determination ($R^2 < 0.1$).

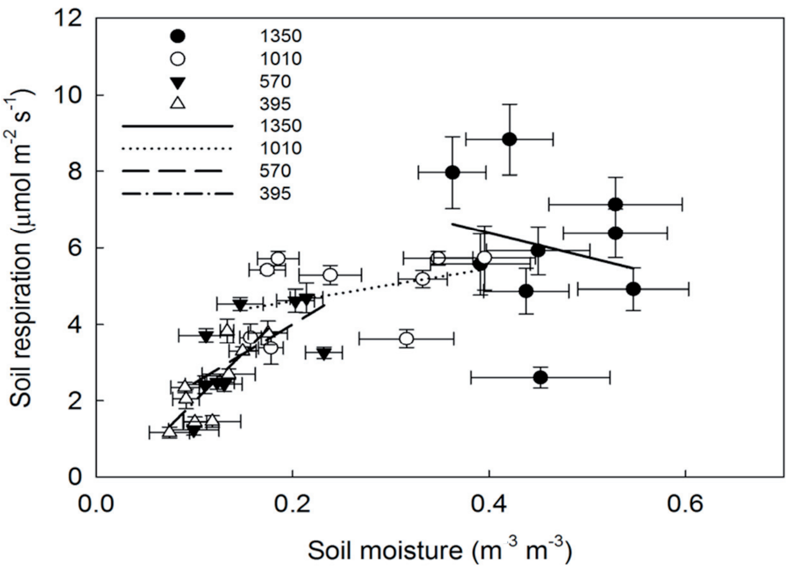

Figure 5.3. *In situ* soil respiration and soil moisture during the growing season 2011. Values are means and standard errors for five replicate mesocosm. Lines indicate regressions, for which coefficients can be found in the text.

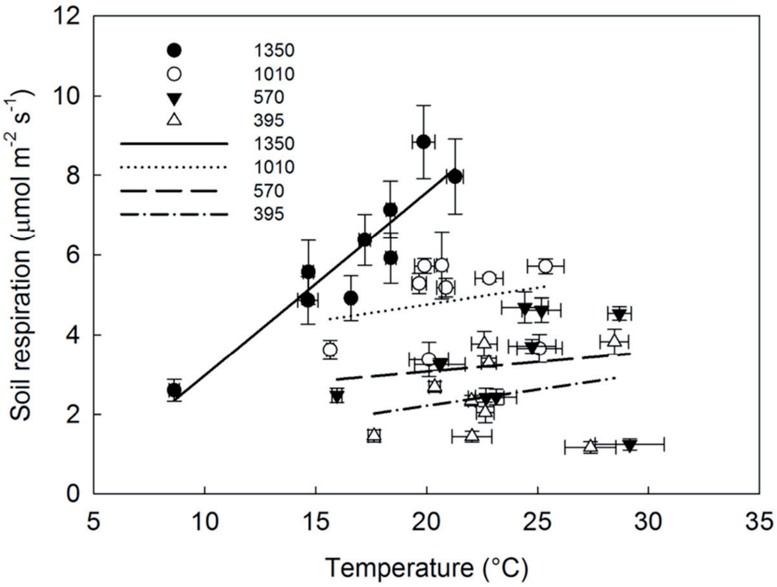

Figure 5.4. *In situ* soil respiration and soil temperature during the growing season 2011. Values are means and standard errors for five mesocosms. Lines indicate regressions, for which coefficients can be found in the text.

5.3.5 Temperature manipulations

Across the temperature ramp imposed under standardised moisture conditions, Figure 5.5 shows sensitivity to temperature among all sites, this being supported by the LME model with an overall temperature effect on flux ($F_{1,93}$ = 209.4, P < 0.001). When considering the within site effect, the LME model gave a non-significant interaction term and a low F statistic ($F_{3,93}$= 1.48) for 'site:temperature' interaction, therefore unlike the *in situ* measures, all sites displayed a comparable sensitivity to temperature. Calculation and comparison of Q_{10} values (Table 5.3) among sites also gave a non-significant output, reinforcing the similarity of responses when moisture limitation is removed. Despite the similarity in sensitivity response, the magnitude (Figure 5.5) of the flux varied among sites ($F_{3,16}$ = 9.5, P = 0.008).

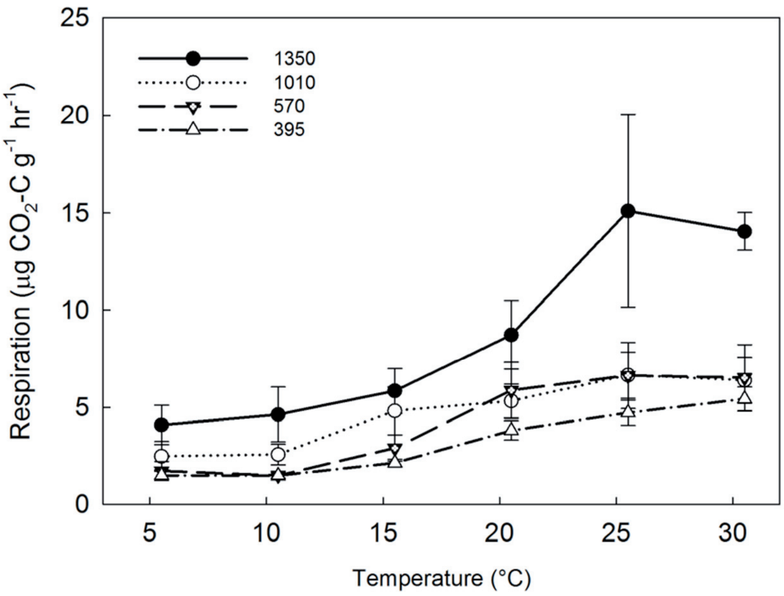

Figure 5.5. Respiration from incubated soils across temperature ramp. Values are means and standard errors for five replicates.

Table 5.3. Q_{10} values derived from incubated soils. Coefficients and significance values are derived from the fit of equation 1 (see text) to calculated flux data.

Site (m a.s.l.)	R^2	P	Q_{10}
1350	0.87	0.006	1.76
1010	0.85	0.009	1.55
570	0.82	0.014	1.88
395	0.95	0.001	1.73

5.4 Discussion

5.4.1 Moisture and temperature effects on in situ soil respiration

To consider the effect of transplantation of pasture soils along a climate gradient on soil function, we measured rates of respiration *in situ* and used soil moisture and temperature data to explore the relative strength of each driver. Here, we expected a similar change for soil function as was observed for plant productivity by Gavazov et al. (*in press*), *i.e.* a general reduction at transplantation sites from that of the control site. Specifically, we hypothesised that soil respiration would be constrained along the transplantation gradient in concert with soil moisture. Indeed, this hypothesis was supported as we observed a trend of sequentially lower soil respiration along the gradient, and this reduction coincided with lower soil moisture along the gradient, this being most heavily evident at the driest site, where moisture also significantly explained within-site variation in respiration. When viewed across all sites, our data displayed an expected trend from optimum moisture conditions to extremely water-limited conditions, which fits with the general conceptual moisture-respiration model of Sussela et al. (2011), albeit on the optimum to dry side of the bell-curve.

Given moisture has been identified as an overriding climate factor in determining rates of respiration in a range of systems (Liu et al. 2009), this finding was, in general, expected. However, the finding of a strong sensitivity to moisture at the very lowest levels was more striking. Curiel Yuste et al. (2007) considered soil moisture effects in a savannah system, and, finding similar flux rates across a comparable range of moisture to our study, proposed a Boltzman sigmoid function fit to the data. Such a fit suggests no moisture response below ~18 % volumetric water content, yet across the same range, our data (total dataset range 8 – 55 % moisture) show a very strong and significant response. This clearly highlights how mesic systems (as in the current study) have a lower resilience to such extremes when compared to the Mediterranean systems studied by Curiel Yuste et al. (2007). Indeed, soil moisture effects are strongly dependent on antecedent conditions and ecosystem type, as demonstrated by Sowerby et al. (2008). There, mesic systems became strongly water limited under simulated summer drought, yet respiration rates in hydric systems benefitted from moisture reduction. This emphasises the role of certain thresholds around moisture optima (Suseela et al. 2011; Beier et al. 2012), which can not only directly constrain respiration, but also the relative strength of temperature as a driver (Lellei-Kovács et al. 2011).

In our study, such thresholds were addressed by our second hypothesis, and here we observed a strong effect, but further than expected, only the control site at 1350m retained any significant sensitivity to temperature. This indicates that average moisture contents below the threshold of 0.25 m^3 m^{-3}, despite occasional increases, were sufficient to remove the general sensitivity to temperature. This provides evidence of a moisture threshold between the conditions at the control site (1350 m a.s.l.) and the nearest transplantation site (1010 m a.s.l.). Interestingly, the control site did experience short periods of drought conditions, with moisture contents falling to levels comparable to the mean values at transplantation sites (see Figure 5.3). Despite this, the rate and temperature sensitivity were generally maintained, suggesting that it is the cumulative effect of drought that causes the change in system response, and that at higher elevation there is a high degree of resilience to short periods of punctuated drought (Evans and Wallenstein 2011; Bérard et al. 2012). Gavazov et al. (*in press*) also suggested a threshold of moisture control on plant community exists along the gradient, yet in the case of plant productivity, this was not observed until the site at 570 m. This is also a reflection of the different temporal scales involved in each process, but reinforces how mineralisation processes are exceptionally sensitive to change during the growing season, perhaps more so for the heterotrophic component of soil respiration (Scott-Denton et al. 2006).

The combination of vegetation and mineralisation process thresholds and sensitivity to change underpins the coupling of the autotrophic and heterotrophic components, and highlights the role of plant respiration in the soil respiration metric. In the work by Flanagan and Johnson (2005), soil moisture interacted with seasonal changes in plant biomass to explain 94% of the variation in standardised ecosystem respiration, which likely encapsulates the autotrophic contribution to respiration, the indirect effect of exudate turnover, and the prevailing effect of soil moisture. In our study, whilst unable to compute a comparable biomass index, it is most likely that a large portion of the variation among sites not explained by moisture or temperature would be driven by the observed reduction in biomass at transplantation sites.

5.4.2 Temperature incubations

Following the observation of a strong *in situ* constraint by soil moisture, we expected that removal of drought stress would establish a temperature response in all soils under a controlled temperature ramp. We further expected that this sensitivity might vary such that sites that experienced greater *in situ* temperatures would have lower intrinsic temperature sensitivity. The cessation of drought conditions led to a temperature response in all soils, and contrary to our expectation, this sensitivity was comparable among sites. The derived Q_{10} values were similar to previous work under laboratory conditions (Curiel Yuste et al. 2007; Schindlbacher et al. 2010), and in the compartmentalisation exercise by Suseela et al. (2011). These findings suggest an intrinsic ability to rapidly respond to more favourable conditions upon rewetting to field capacity, and to equally augment mineralisation rates as a function of temperature, despite the variability in antecedent conditions. The similarity in temperature response must then be an underlying trait of the microbial community, whereas the differences in flux magnitude (control site being much greater than transplantation sites) most likely reflect possible variation in the quantity of available substrate and the microbial biomass size.

Fierer and Schimel (2003) suggested much of the respiration response seen after wetting of previously dried soil is derived from mineralisation of intracellular compounds as a response to osmotic stress, which might link magnitude of response to microbial biomass size. Wang et al. (2003) observed substrate availability indices to explain much of the rewetting response, and, despite their claim of less contribution from microbial biomass, still found a strong (r = 0.81) correlation to respiration. Variation in the microbial community was not explicitly addressed in the current study, but samples from the same plots taken in spring (*unpublished data*) show the control site (1350 m) to have significantly greater biomass C and N than sites at 1010 m and 570 m (site 395 m not sampled), adding some weight to the magnitude-biomass link. The similarity in 'intrinsic' temperature sensitivity (Davidson and Janssens 2006) further suggests that the quality of the dominant substrates must remain broadly similar, as the temperature sensitivities of distinct pools of SOM (Farrar et al. 2012) may have become apparent if quality varied among sites. Despite some similarity to the type II acclimation described in Bradford et al. (2008), given the complete lack of significant difference in Q_{10}, we believe this observation is not evidence of a thermal acclimation *per se*, and is more likely a response to moisture-induced effects on substrate and microbial biomass. A comparable intrinsic sensitivity also suggests that the heterotrophic component of soil respiration is unlikely to access more recalcitrant (and temperature sensitive) organic matter over the short-term under climate change. However, if productivity is reduced (Gavazov et al. *in press*), cascade effects of reduced organic matter inputs to longer-lived pools may, in the long term, reduce soil C stocks (Knapp et al. 2002).

5.4.3 Soil organic matter and chemistry

Changes in the cation content (mainly Ca) and in soil pH at drier and warmer transplantation sites suggest some fundamental alteration to base cycling. Dry-rewet events may have some contribution to this observation, especially if they result in disaggregation (Cosentino et al. 2006) and a general flushing of exchangeable cations. Reduction in base cycling from slower decomposition may also contribute, especially if important cations are retained in litter or light fraction organic matter. Direct effects of moisture are difficult to reconcile though, as evidence for reduced moisture leading to a drop in pH is confined in the literature to peats (Clark et al. 2006), following the established relationship between the oxidation of reduced sulphur and the production of protons. However, in mineral soils, to our knowledge, a moisture-induced drop in soil pH has not been observed, and whilst it is currently not possible to fully explain this observation, there are nevertheless likely to be consequences for soil function.

The hypotheses derived from lower plant productivity estimates suggest that reduced litter input should result in a lower quantity of organic matter existing as low-density material, as this material results from the initial stages of decomposition, and closely reflects litter input (Schulze et al. 2009). Contrary to our expectation, we found the proportion of SOM_{lf} and content of C and N increased downslope, albeit only significantly when comparing the N % between the 1350 m and 395 m sites. This increase suggests, perhaps irrespective of changes in litter input quantity, that the initial stages of decomposition are retarded in transplanted soils. Reduced levels of decomposition have been confirmed at these sites in a litter-bag experiment (Gavazov et al. *in review*). Most likely this will be due to direct effects of lower moisture, but perhaps also to downwards migration of litter-degrading invertebrates (Briones et al. 2009). Such an 'isolation' of recently deposited material may represent a transient store of organic matter during the drier period, but one that is rapidly accessed under wetter conditions of longer duration, such as during winter. Unlike in previous work (Schindlbacher et al. 2010), the isolated SOM_{lf} C/N ratio did not explain any of the mineralisation data, nor its temperature sensitivity. The fact that despite such large changes in function, we only observe small changes in the nature of SOM_{lf}, and none in bulk SOM would suggest that decomposer communities may have a rapid recovery capacity during the post growing-season phase which may dampen the effects of climate change over short time frames.

5.4.4. Concluding remarks

Climate manipulations of temperature and moisture along altitude gradients allow for estimation of combined effects on ecosystem processes, and here we observed a significant and overriding effect of moisture on soil respiration and its temperature response in a pasture system. The climate manipulations were shown to have affected the decomposer community response to temperature in terms of the magnitude of the flux, but not its intrinsic temperature sensitivity under standardised conditions. This highlights the resilience of the microbial community to extreme climatic change, but reinforces the reduction in the capacity to respond, and the consequences thereof for mineralisation processes and soil function. Initial observations on changes in the quantity and quality of the SOM_{lf} indicate that accumulations of unprotected organic matter may lead to a greater C and N source for decomposer communities during the winter, therefore potentially shifting a large proportion of the annual C and N budget outside of the growing season.

The consequences of reduced function during the growing season carry negative implications for the sustainability of productivity in pasture systems, especially if limiting nutrients are only slowly returned to available pools. Whilst our results do not imply an increase in the losses of C as a function of climate change, a reduction in soil function will reduce the storage capacity of C and macronutrients, which in the longer term will inevitably erode the stocks of C and N from organic matter. It is therefore pertinent that emphasis be made on understanding the seasonal dynamics of nutrient cycling in systems under climate change scenarios, especially those that exhibit reduction in soil function during the growing season. Further, there is a need to identify whether such changes feedback to community composition and productivity such to modify the sustainable use of sub-alpine pasture systems.

5.5 Acknowledgements

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Chapter 6

Soil CO_2 efflux and microbial biomass constrained by warmer winter climate and reduced snow cover in transplanted subalpine wood-pasture turfs

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Gavazov, K., R. Mills, H. Durand, T. Spiegelberger and A. Buttler (*in preparation*). "Soil respiration and microbial biomass constrained by warmer winter climate and reduced snow cover in transplanted subalpine pasture turfs."

Abstract

Recent global changes in winter snow regimes within seasonally snow-covered ecosystems have been attributed to anthropogenic climate change. Predictions for continental mountain chains are for further decreases in snowpack thickness, due to a rising snowline and increasing rain to snow ratio of winter precipitation. Aiming to evaluate the impact of warmer winter climate on biogeochemical processes, a downslope transplantation experiment was set up along an altitudinal gradient in the Swiss Jura Mountains, to act as a proxy for increased year-round temperature. Direct measures of winter soil surface CO_2 efflux and microbial carbon (C_{mic}) content under an undisturbed snowpack revealed that insufficient snow insulation at lower altitudes exposed subalpine pasture soils to naturally occurring frost events and decreased significantly their microbial biomass and respiration rates. Ambient snow cover under control conditions, to the contrary, provided efficient means for decoupling soil microclimate from freezing winter air temperatures, supporting the largest soil microbial biomass and winter CO_2 fluxes roughly comparable to peak growing season soil respiration rates at the same site. Variance partitioning revealed that mid-winter soil microbial biomass was the best predictor of mean winter season flux values. All continuously measured environmental parameters (*i.e.* snow cover thickness, soil moisture, and soil temperature) exerted a significant effect on CO_2 efflux, but their individual contribution was obscured by a large temporal and spatial variation. Substrate availability, as inferred by land use and the resulting vegetation type further contributed to the magnitude of the observed fluxes. Our data provide insights on the importance of snow for soil microbial abundance and activity in winter, and hints on possible feedbacks on the turnover of organic matter and the overall functioning of ecosystems in a future warmer climate.

Keywords

Altitude; climate warming; gradient; land use; management; transect; transplantation

6.1. Introduction

Soils represent the earth's largest terrestrial organic carbon sink and their role in carbon storage is maintained though net differences in photosynthetic uptake and respiratory loss (Kutsch et al. 2009). Recent evidence indicates that wintertime fluxes of CO_2 to the atmosphere from seasonally snow-covered ecosystems can contribute a large proportion to their annual CO_2 budgets (Liptzin et al. 2009; Merbold et al. 2011). Landscape-scale analysis of ecosystem respiration (Wang et al. 2011) shows that air temperature explains a large proportion of the spatial variation in winter CO_2 emissions. At the local scale, however, factors such as soil moisture and carbon availability become more important explanatory variables, provided the presence of consistent snowpack (Brooks et al. 2005; Aanderud et al. 2013). Time lags and hysteresis effects seem to override concurrent environmental conditions in their control over soil respiration rates (Merbold et al. 2011), which poses problems for modelling of the carbon cycle. This implies that current global circulation models for CO_2 emissions from the biosphere, which rely on a year-round Q_{10} based estimates for soil microbial activity (Jones et al. 2005), are largely underestimating the production of this greenhouse gas in cold winter soils, neglecting the insulation capacities of snow.

Snowpack is a characteristic feature of high- altitude and latitude ecosystems worldwide. It has high thermal insulation capacities and actively decouples soils lying underneath it from atmospheric temperature fluctuations (Edwards et al. 2007). This allows soils to retain circum-zero temperatures for long periods over winter, creating favourable conditions for organic matter turnover (O'Lear and Seastedt 1994; Baptist et al. 2010; Gavazov 2010) relative to snow free soils. Snow-covered soils exhibit high microbial abundance and activity (Brooks et al. 1996; Lipson et al. 2000; Schadt et al. 2003), with detectable levels of heterotrophic respiration under the snow (Sommerfeld et al. 1993; Monson et al. 2006). However, in the absence of a sufficient or consistent snow-cover, soils often freeze, or experience frequent freeze-thaw cycles of varying length and duration, which can have profound implications for soil microbial activity and carbon turnover (Sturm et al. 1997). This scenario can arise from either reduced precipitation, or milder temperatures during winter; hence the phenomenon of "colder soils in a warmer world" (Groffman et al. 2001). In light of the recent trend for reduced snow cover in mountain areas (Beniston 1997; Mote et al. 2005), and of locally predicted shorter winters with a high rain to snow ratio (Solomon et al. 2007; CH2011), it is important to understand the implications of snowpack change on belowground ecosystem processes.

The recognised importance of the winter season for ecosystem scale processes, such as nutrient turnover (Campbell et al. 2005), and litter decomposition in particular (Gavazov 2010), implies high microbial activity under the snow necessary for the breakdown of organic matter. Characteristic differences between winter and summer soil microbial communities and their substrate preferences exist: in winter, fungi that utilise complex plant residues dominate, whereas in summer bacteria that thrive on plant root exudates are more active (Lipson and Schmidt 2004). From what we know to date, the major source of CO_2 under winter snowpack is the activity of winter-specific soil microbial communities, dominated by saprotrophic fungi (Lipson et al. 2002; Björk et al. 2008; Bowling et al. 2009). Facing little competition from bacteria for nutrients, the fungi are able to proliferate under stable circum-zero temperatures (Schmidt et al. 2009), employing a fast-growth strategy and a high mineralisation efficiency (Lipson et al. 2009), which can result in considerable flux of CO_2 from seasonally snow-covered ecosystems (Liptzin et al. 2009). Furthermore, different vegetation types, defined by either plant functional traits (De Deyn et al. 2008), or land-use management intensity and succession stage (Bahn et al. 2006) have been attributed different role in the emission of CO_2 from soils. This is because fast growing early successional plants, in contrast to slow growing long-lived ones, allocate more of their carbon in photosynthetically active structures of low density and high nutrient content, thus yielding more easily decomposable litter (Aerts and Chapin 2000). Attempts to show such a link between arctic vegetation types and soil respiration rates (Elberling 2007; Bjorkman et al. 2010a; Morgner et al. 2010), or microbial community structure (Björk et al. 2008) during winter have, however, proven inconclusive. To our knowledge temperate mountain ecosystems have so far not been tested for such dependency.

In this study, we determined the effects of a milder winter, with warmer air temperature and reduced snow cover, on the activity and abundance of winter soil microbial communities in three distinct land use types within the subalpine belt of the Swiss Jura Mountains. We selected turfs from unwooded pasture, sparsely wooded pasture, and densely wooded pasture, thus spanning a gradient of decreasing pasture management (*i.e.* grazing pressure), and plant tissue quality (*i.e.* vegetation type) (Gillet et al. 1999; Buttler et al. 2009). We transplanted a set of mesocosms with turfs from each of the three land use types along a natural climatic gradient and measured soil surface CO_2 fluxes both during the vegetation season and during winter below an undisturbed snowpack. We hypothesised that: (1) earlier-developing and more consistent snow cover at higher altitudes would stimulate microbial activity and abundance due to stable micro-environmental conditions and a limited occurrence of soil frost, and (2) consistent with growing season CO_2 efflux patterns, contrasting subalpine land use types will differ in their overall fluxes based on the quality and quantity of litter input, with productive unwooded pastures having the highest rates.

6.2. Material and methods

6.2.1 Site description and design of the experimental warming

In order to simulate warmer winter climate with reduced snow cover, we used an established field experiment whereby mesocosms with subalpine soils and vegetation (*i.e.* turfs) were transplanted along an altitudinal transect. Details on the choice of study sites, the construction of the mesocosms and the type of plant communities in each land use are described by Gavazov et al. (2013). Briefly, in 2009, 45 mesocosms made of rectangular PVC boxes 60×80 cm^2 and 35 cm in height were set up, containing soils cores of 30 cm depth and the intact herbaceous vegetation. These turfs originated from Combe des Amburnex (N 46°54', E 6°23') - an area of subalpine pasture-woodlands situated along the crest of the Swiss Jura Mountains, at circa 1350 m a.s.l. Each mesocosm contained turfs from one of the following three land use types – densely wooded pasture, sparsely wooded pasture, or unwooded pasture. The given order reflects a diminishing canopy cover of the dominant tree species *Picea abies* due to an increasing intensity of pasture management and cattle grazing. In turn, this also affected the vegetation composition with unwooded pastures being dominated by graminoids, sparsely wooded pastures by forbs and mosses, and densely wooded pastures by a mixture of understory dwarf shrubs, forbs and litter debris.

In order to create a year-round effect of climate warming with respect to the ambient climate at the mountain crest, plots were transplanted to one of the three experimental sites: 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 a mean annual rainfall of *ca.*1750 mm, including more than 450 mm snow precipitation, and a mean annual temperature of 4.5 °C. The remaining two sites 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. At each site, fifteen mesocosms (*i.e.* five replicates of each land use) were transplanted to a common garden following a completely randomised design. The boxes containing the turfs were dug down to surface level into previously prepared trenches thus preventing lateral heat exchange with the atmosphere.

Climate parameters were monitored continuously throughout the experiment by means of an automated weather station (Sensor Scope Sàrl, Switzerland) in each experimental site, measuring air temperature and humidity 2 m above the ground surface at one minute intervals. Overall snowpack depth was determined manually with an avalanche probe at each of the nine winter sampling campaign in addition to daily snow height data from nearby weather stations (Source MeteoSwiss). ECH$_2$O EC-TM sensor probes coupled to Em50 data-loggers (Decagon Devices, Inc., USA) 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 are for the six months of the 2011-2012 winter season – November through April (NDJFMA).

6.2.2 CO_2 efflux measurements

Data on winter soil CO_2 efflux presented in this study were collected over nine campaigns from 11th November 2011 through 25th April 2012 (NDJFMA) using an infrared gas analyser (IRGA, LI-COR LI-8100, Lincoln, NE, USA). During late autumn and early spring when the ground was free of snow cover (see below), measurements were done with a commercial 10 cm Survey Chamber LI-8100-102 (area 83.7 cm^2, volume 835.2 cm^3) by placing it on pre-installed PVC collars (length 5cm, width 10 cm) pushed to ~ 2 cm depth in each plot and stripped of aboveground vegetation. Each measurement lasted for two minutes with an initial 1 minute dead-band, and CO_2 flux was calculated from the linear build-up of CO_2 within the closed chamber.

Shortly before snow cover built up on the ground (December 2011), the respiration collars on each plot were replaced with closed, opaque PVC respiration chambers (area 83.3 cm^2, height 10 cm, volume 832.8 cm^3) permanently inserted to ~2 cm depth (see comparison in section 6.6.1). Those remained in place until snowmelt date at the respective experimental site (March 2012 at 580 m a.s.l., April 2012 at 1010 m a.s.l., and May 2012 at 1350 m a.s.l.) thus allowing for a consistent snow cover over the entire mesocosm surface. Each PVC chamber was fitted with a pair of inlet and outlet plastic tubing whose ends were fixed on a pole above the snowpack, remaining plugged throughout the winter in order to avoid seepage of moisture and consequent frost within the tubing. At time of sampling those served to circulate the chambers' headspace air though the IRGA, without disturbing the accumulated snowpack, in a similar manner as in Sommerfeld et al. (1991; 1993). Despite these precautions, problems associated with frost and snow settling had caused blockage on a number of occasions resulting a cumulative data loss of about 10 %. The measurement protocol employed was identical to the one for the commercial LI-COR Survey Chamber, though prior to measurement the headspace of the PVC chambers and tubing was flushed with atmospheric air from above the snowpack for 1 minute using the IRGA's pump and the standard 1.7 l min^{-1} flow rate. This was done to assure that any accumulated CO_2 was released prior to efflux measurements and headspace CO_2 concentrations remained below the IRGA's calibration maximum of 3000 ppm. Addressing possible confounding effects of increased CO_2 concentration gradient between the soil and the chamber's headspace due to flushing, we carried out an independent calibration campaign (see section 6.6.2) relating fluxes from flushed and non-flushed chambers using a LI-COR 8100 system with an extended CO_2 measurement range of up to 9000 ppm. The established relationship (6.6 Appendix, Figure A6.2) indicated a significant but small in magnitude effect of flushing, rendering the absolute efflux values only slightly overestimated.

6.2.3 Sampling for soil microbial biomass

One soil core per plot (diameter 4.6 cm, length 10 cm) was sampled on 12th March 2012. At the time, the sites at 1010 m and 570 m were free of snow. At 1350 m the soil was beneath 1.2 m of snow, which was shovelled away to permit sampling. The resulting snow pit was then refilled, avoiding snow compaction as much as possible. Soil microbial biomass carbon (C_{mic}) and nitrogen (N_{mic}) were determined after chloroform fumigation (Joergensen 1996), extraction in K_2SO_4 and analysis of liquid extracts in a Shimadzu TOC-V device.

6.2.4 Data analysis

The experimental design allows for the explanation of winter-long variation in soil CO_2 efflux by six factors: two fixed categorical ones – land use and altitude of the transplantation site; and four continuous ones – gas sampling date, soil temperature, soil moisture and snowpack thickness. We used a Type I analysis of covariance, based on repeated measures linear mixed effects models, in order to incorporate data from all sampling dates (Quinn and Keough 2002). First a full model was fitted with land use and transplantation altitude as between-subject fixed factors; date as a within-subject fixed factor; and soil moisture, soil temperature and snow cover as covariables. Subsequently, we applied a backward selection using maximum likelihood (ML) to remove any interactions between factors that did not contribute significantly to the model fit. We refit the reduced final model using the restricted maximum likelihood (REML) estimation method (Zuur et al. 2009), thus accounting for cases with missing cells in the data. Further, significant differences between levels of the fixed factors were detected using pre-defined linear contrasts, thus reflecting the model's structure.

Additionally, we used simple least square linear regressions to determine if the variation in winter CO_2 efflux could be explained alone by one of the microclimatic conditions: soil temperature, soil moisture and snowpack thickness measured at the time of gas sampling. This was done since we assumed that those variables were strongly determined by the altitude of transplantation and hence intercorrelated within the mixed effects model.

Binary recursive partitioning in the form of a regression tree analysis (CART) (Breiman et al. 1984) was performed in order to select the most important explanatory variables predicting mean winter CO_2 efflux. Least sum of squares provided a quantitative assessment of the effect of diurnal soil temperature fluctuations, soil freeze-thaw cycles, soil microbial biomass, as well as preceding growing season plant biomass and soil respiration for each plot.

Assumptions of normality and homoscedasticity of the residuals in all final linear regression models were verified visually using diagnostic plots. A log-transformation of the response variable CO_2-efflux was found necessary. For all statistical tests, effects were considered significant at $P < 0.05$. All statistical analyses were performed using R version 2.14.1. (R Development Core Team 2012), mixed effects models were run using the ‘nlme’ package (Pinheiro et al. 2012), and regression tree analysis using the ‘mvpart’ package (Therneau and Atkinson 1997).

6.3. Results

6.3.1 Winter climate along the altitudinal gradient

The winter 2011-2012 was typical for the Swiss Jura Mountains with an arrival of frost in mid-November and a permanent snow cover extending between December 2011 and April 2012. Snowpack reached its maximum depth in February 2012 concurring with the lowest air temperatures recorded for this period (Figure 6.1). Mesocosms transplanted to lower altitudes experienced, on average, higher air temperature over the winter season, but the absence of snow cover subjected their soils to the direct effect of frost events (Table 6.1). This direct coupling of the soil-atmosphere boundary layer caused large diurnal soil temperature fluctuations and frequent freeze-thaw cycles (Table 6.1).

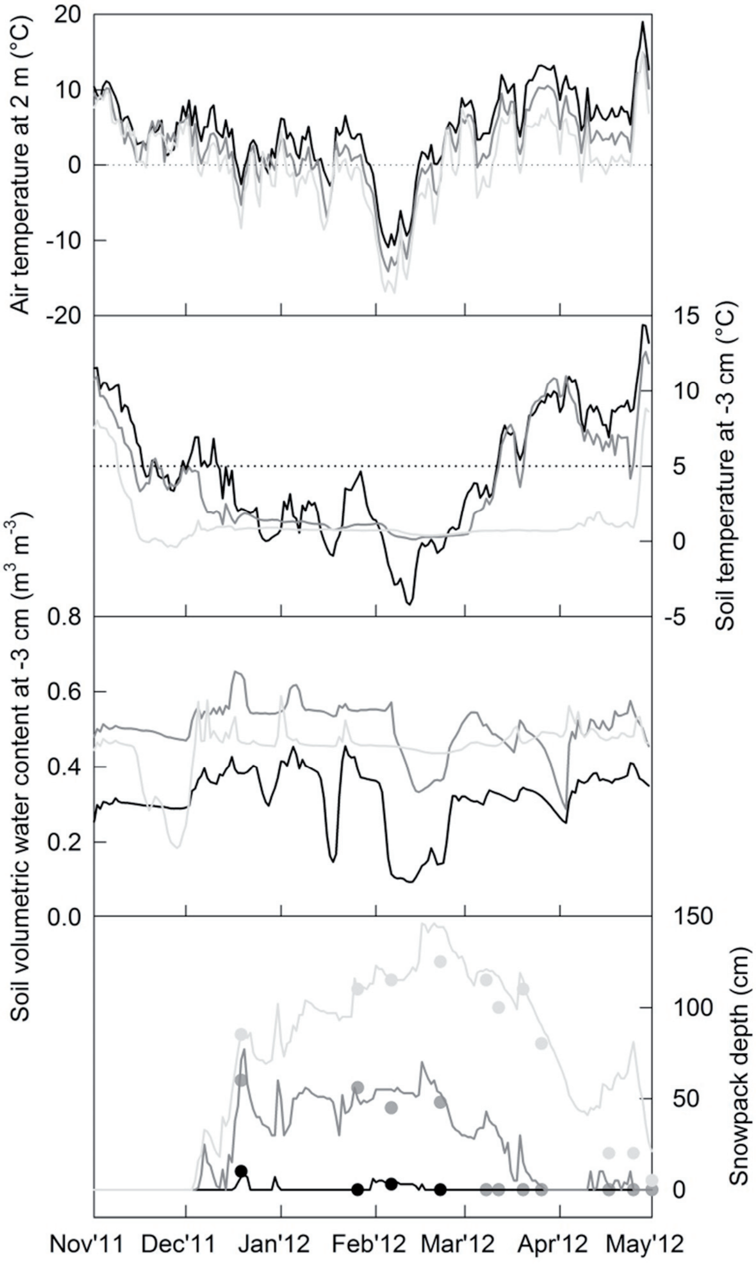

Figure 6.1. Daily climate conditions during winter 2011-2012 (NDJFMA) along the experimental transplantation gradient at 1350 m a.s.l. (light grey), 1010 m a.s.l. (dark grey), and 570 m a.s.l. (black) symbols. For clarity, at each altitude, edaphic parameters were averaged across the three land use types (n = 15). Snowpack depth was measured both locally by hand (points) or continuously (lines) at a nearby weather station (Source MeteoSwiss).

Table 6.1. Winter season (NDJFMA) averages for climatic parameters measured along the transplantation gradient.

Altitude [m a.s.l.]	1350			1010			570		
Mean air temperature [°C]	0.32			2.34			4.59		
Mean snow depth [cm]	72.5			24.1			0.5		
Snowpack duration [days]	153			124			23		
Pasture type [1]	UW	SW	DW	UW	SW	DW	UW	SW	DW
Mean soil temperature [°C] [2]	1.17 ± 0.1	1.23 ± 0.2	1.27 ± 0.2	4.04 ± 0.1	4.10 ± 0.1	3.59 ± 0.1	5.05 ± 0.2	4.60 ± 0.1	4.16 ± 0.2
Mean soil moisture [%] [2]	56.6 ± 4.9	47.5 ± 2.3	32.1 ± 1.8	48.7 ± 0.1	53.8 ± 8.4	48.2 ± 7.9	31.6 ± 2.1	36.5 ± 4.3	27.7 ± 2.6
Freeze-thaw cycles [2, 3]	4.6 ± 1.1	9.0 ± 8.0	7.8 ± 1.5	0.7 ± 0.5	0.2 ± 0.2	1.5 ± 0.9	17.0 ± 2.4	10.5 ± 1.0	13.2 ± 2.2
Diurnal temperature fluctuations [°C] [2, 4]	0.56 ± 0.1	0.47 ± 0.0	0.07 ± 0.1	2.70 ± 0.2	3.15 ± 0.3	3.59 ± 0.2	4.36 ± 0.5	2.73 ± 0.4	3.24 ± 0.1

[1] Vegetation type codes, where UW refers to unwooded pasture, SW to sparsely wooded pasture, and DW to densely wooded pasture.

[2] Means and standard errors for five replicate plots.

[3] Number of temperature oscillations around 0 °C summed over the winter season.

[4] Difference between daily minimum and maximum soil temperature measured on an hourly intervals.

6.3.2 *Effect of altitude and land use on CO_2 efflux from soils in winter*

Mesocosm transplantation to lower altitudes resulted in a significant decrease in soil respiration rates in all land use types during the winter months ($F_{2,36}$ = 73.7, P < 0.001). Figure 6.2 shows that turfs transplanted to both 1010 m a.s.l. and 570 m a.s.l. respired significantly less (P < 0.001) than the control ones at 1350 m a.s.l. This overall pattern, however, changed occasionally over the course of winter, with a significant interaction between sampling date and altitude of transplantation ($F_{2\ 263}$ = 14.0, P < 0.001). CO_2 efflux rates differed significantly among land use types ($F_{2,36}$ = 5.6, P = 0.007), with unwooded pastures differing significantly from sparsely wooded pastures (P = 0.046) but only marginally from densely wooded pastures (P = 0.069). The two types of wooded pastures did not differ in their efflux rates over the winter (P = 0.877). Overall, at the control site at 1350 m a.s.l. winter fluxes were of similar magnitude to those during the preceding growing season (Table 6.2), however those at the two transplantation sites at lower elevation were significantly (P < 0.001) smaller.

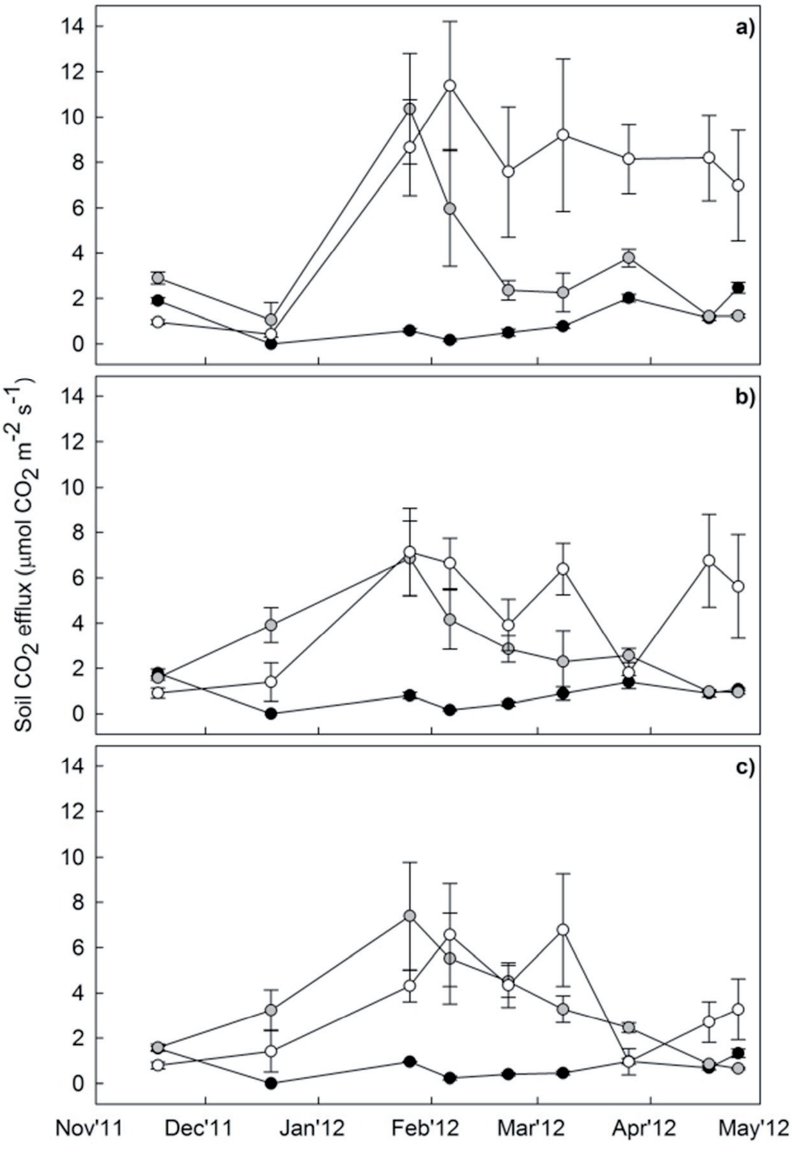

Figure 6.2. Seasonal variation in winter CO_2 efflux along the experimental transplantation gradient at 1350 m a.s.l. (white), 1010 m a.s.l. (grey), and 570 m a.s.l. (black) symbols in a) unwooded pasture, b) sparsely wooded pasture, and c) densely wooded pasture. Presented data are means and standard errors for five replicate plots.

6.3.3 Effect of soil microclimate on CO_2 efflux from soils in winter

Overall, all of the measured microclimatic parameters exerted significant effects on the rates of CO_2 efflux from the soil. Snow cover thickness had the highest explanatory power ($F_{1,263} = 63.8$, $P < 0.001$), followed by soil temperature ($F_{1,263} = 44.2$, $P < 0.001$), and soil moisture ($F_{1,263} = 29.7$, $P < 0.001$). Individual least squares linear regressions of the bulk seasonal CO_2 efflux against each of the three environmental parameters confirmed these significant relationships, although the scatter of the data was too large to detect any causal patterns and to grant credibility to the models' fits (Figure 6.3). Snow cover explained most of the variation in soil respiration rates ($R^2 = 0.28$, $P < 0.001$), followed by soil moisture ($R^2 = 0.25$, $P_{1,333} < 0.001$). Efflux rates were independent from soil temperature in this analysis ($R^2 = 0.01$, $P = 0.24$).

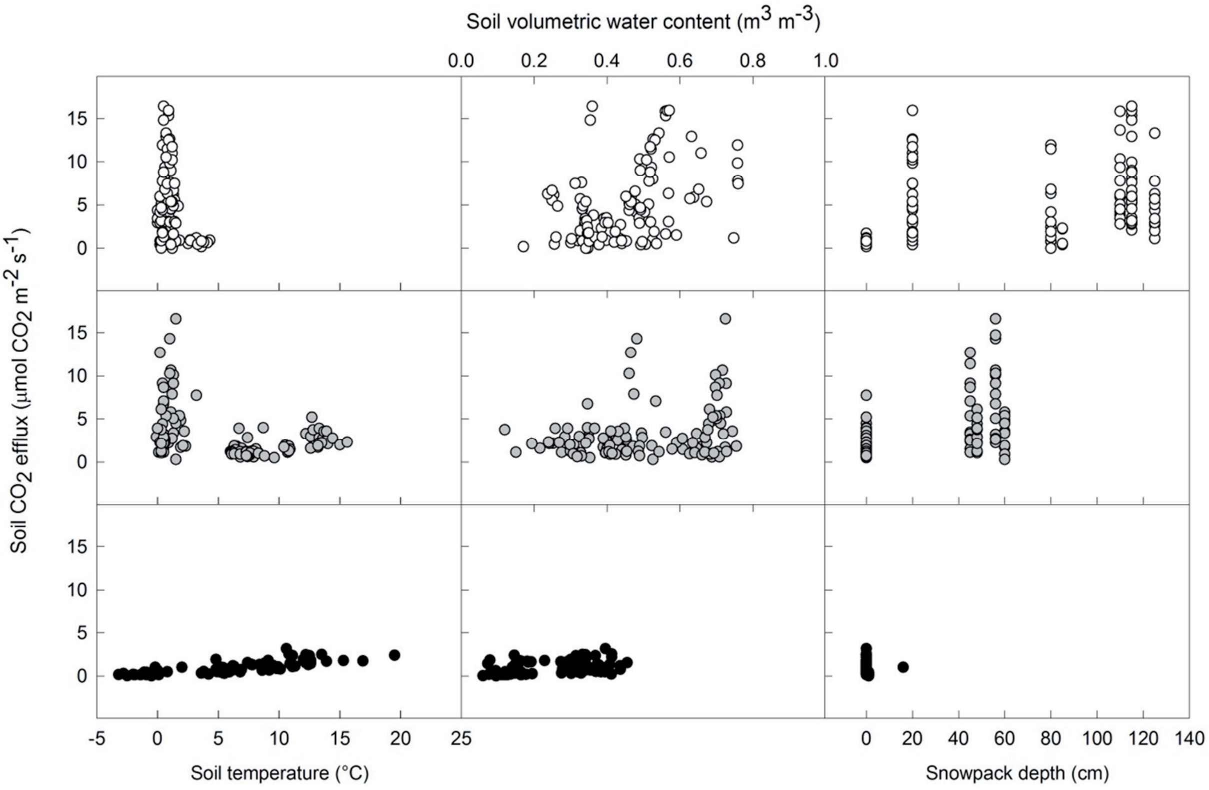

Figure 6.3. Relationship between winter season CO_2 efflux and selected environmental parameters. Colour codes for the sites along the gradient: 1350 m a.s.l. (white), 1010 m a.s.l. (grey), and 570 m a.s.l. (black).

6.3.4 Biotic and abiotic factors controlling winter CO_2 efflux

Recursive partitioning (CART) of the variation in mean winter CO_2 efflux (given in Table 6.2) indicated a dominating control of soil microbial biomass (measured as microbial carbon, C_{mic}) on fluxes. High flux rates (above 4.4 µmol CO_2 m^{-2} s^{-1}) were associated with high microbial biomass. Low flux rates were further restrained by the number of freeze-thaw cycles, but also by the number of diurnal soil temperature fluctuations; the two factors having a negative effect on mean winter fluxes. Mean summer season efflux and peak growing season plant biomass, two proxies of antecedent conditions and resource availability for decomposition, did not exert a significant effect on winter fluxes.

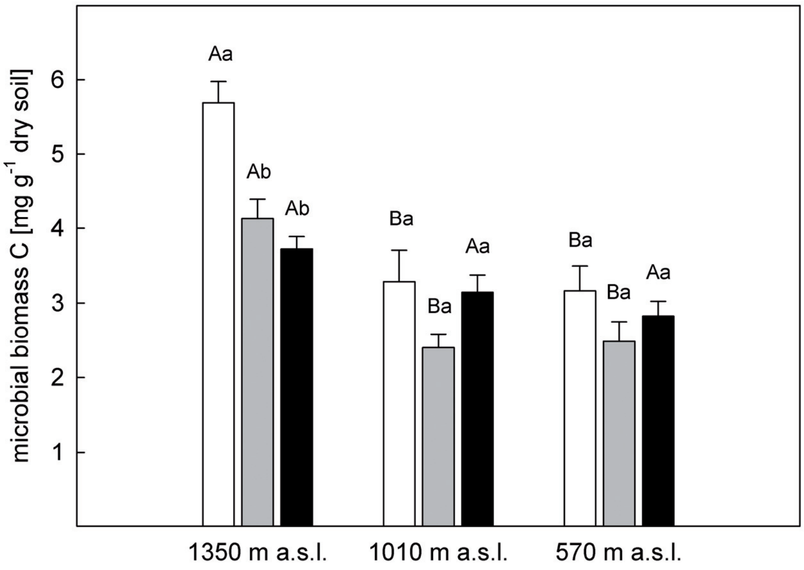

Figure 6.4. Microbial carbon (C_{mic}) in soils along the transplantation gradient from unwooded pasture (white), sparsely wooded pasture (grey), and densely wooded pasture (black). Different letters indicate statistical differences ($P < 0.05$) between a given land use at different altitudes (capital) and between different land use types at the same altitude (lower case).

Analysis of variance (ANOVA) of soil microbial biomass, the factor with highest explanatory power over winter CO_2 efflux, indicated a significant decrease of C_{mic} in soils transplanted to lower altitudes ($F_{2,35} = 39.6$, $P < 0.001$), both at 570 m a.s.l. (TukeyHSD, $P <0.001$) and at 1010 m a.s.l. (TukeyHSD, $P < 0.001$) compared to the controls at 1350 m a.s.l (see Figure 6.4). Land use also had a significant effect on the amount of microbial biomass in the soils ($F_{2,35} = 13.2$, $P < 0.001$), with unwooded pastures having higher C_{mic} than either sparsely wooded pastures (TukeyHSD, $P < 0.001$) or densely wooded pastures (TukeyHSD, $P = 0.001$). A significant interaction effect of altitude and land use ($F_{4,35} = 3.8$, $P = 0.012$) indicated that only at the control site, unwooded pastures had higher C_{mic} than sparsely wooded pastures (TukeyHSD, $P = 0.004$) and densely wooded pastures (TukeyHSD, $P < 0.001$), and that altitude did not have an effect on C_{mic} in densely wooded pastures. Data on soil microbial N revealed an identical pattern of significant differences among treatments, with unchanged C/N ratio, and were thus not presented in detail here

Table 6.2. Seasonal variation in summer (AMJJASO) 2011 and winter (NDJFMA) 2011-2012 soil respiration from each transplantation altitude and vegetation type.

Altitude [m a.s.l.]	1350			1010			570		
Pasture type [1]	UW	SW	DW	UW	SW	DW	UW	SW	DW
Summer CO_2 efflux [2]	5.04 ± 0.57	2.69 ± 0.31	2.46 ± 0.20	4.34 ± 0.30	3.30 ± 0.18	2.66 ± 0.25	2.98 ± 0.19	3.31 ± 0.32	2.75 ± 0.20
Winter CO_2 efflux [2]	6.84 ± 2.14	4.50 ± 1.24	3.46 ± 1.15	3.46 ± 0.87	2.90 ± 0.69	3.28 ± 0.78	1.06 ± 0.13	0.82 ± 0.16	0.73 ± 0.09

[1] Land use codes: UW refers to unwooded pasture, SW to sparsely wooded pasture, and DW to densely wooded pasture.

[2] Reported values for soil respiration [$\mu mol\ CO_2\ m^{-2}\ s^{-1}$] are seasonal means and standard errors for five replicate plots.

6.4. Discussion

6.4.1 Annual contribution of winter CO_2 efflux

The importance of winter season for the carbon cycle in seasonally snow covered ecosystems is well known (Campbell et al. 2005). Research in this field indicates that C loss from soils in winter due to heterotrophic respiration amounts to 30 % of the annual CO_2 efflux in an alpine vegetation zone (Liptzin et al. 2009), and anywhere between 1 and 40 % in subarctic and arctic ecosystems (Elberling and Brandt 2003; Elberling 2007; Bjorkman et al. 2010a). Our data show comparable winter and summer CO_2 fluxes under ambient snow conditions (control site at 1350 m a.s.l.) and thus corroborate these previous findings. Nevertheless, soils remaining snowless partially (site at 1010 m a.s.l.) or for extended periods (site at 570 m a.s.l.) during the winter season, as an effect of simulated climate change, had overall a much lower winter season contribution.

6.4.2 Biotic controls on CO_2 efflux beneath the snow

Similar to other studies showing a controlling role of snow insulation on soil biotic activity during winter (Aanderud et al. 2013; Bokhorst et al. 2013), in this experiment the presence of snow insulation proved to be of vital importance for the abundance and activity of soil microbes, characterised by a strong decrease in winter CO_2 production and soil microbial biomass in response to experimental climate change. We found consistently higher C_{mic} in soils exhibiting high CO_2 efflux during the winter, paralleled by higher CO_2 concentrations at the soil-snow interface. Such congruity was found both along the altitude gradient and among the land use types and consequently mid-winter soil microbial biomass was the best predictor for the average winter flux rates. The observed land use differences in microbial biomass and CO_2 production at the control site at 1350 m a.s.l. indicated that perhaps, with all environmental conditions being equal, substrate availability and quality could have exerted a secondary control (see Merbold et al. 2011). This, however, was not directly evident from the regression tree analysis. Plausible differences in the microbial community structure such as mineralisation efficiency and growth rate could have further contributed to the observed pattern (Lipson et al. 2009; Schmidt et al. 2009).

6.4.3 Abiotic controls on CO_2 efflux beneath the snow

Previous research has indicated that snow cover thickness has a controlling effect on field-measured winter soil CO_2 both spatially (Brooks et al. 1997) and temporally (Monson et al. 2006). Having chosen our transplantation stations at fixed rather than random sites along the altitudinal transect, we were not able to interpolate (*i.e.* through statistical regression modelling) the minimum snow depth threshold at which CO_2 efflux becomes limited at a given point in time. Nevertheless, we found that transplantation to lower altitudes, simulating warmer winter climate and reduced snow cover, resulted in a significant reduction in soil respiration. Snow cover itself had a rather low predictive power for efflux rates, its direct effect being possibly masked by intra-seasonal variation in substrate availability (Brooks et al. 2005; Liptzin et al. 2009).

In accordance with previously published literature (Brooks et al. 1997; Mast et al. 1998; Hirano 2005; Liptzin et al. 2009), we could not detect a straightforward relationship between topsoil temperature and CO_2 flux rates within the entirety of our dataset. When individual transplantation stations were considered separately, however, a clearer pattern emerged. At 570 m a.s.l. we observed a linear dependence between topsoil temperature and CO_2 flux, whereas at 1350 m a.s.l. they were completely independent. We believe that this resulted from snow insulation decoupling the soil respiration process from its temperature dependence; the 'Q_{10} paradigm' (see Mikan et al. 2002; Elberling and Brandt 2003). Our data suggest that temperate mountain ecosystems, characterised by ample seasonal snow cover, do not fall in line with assumptions of global carbon circulation models for a year-round temperature-driven heterotrophic soil respiration (Jones et al. 2005) and thus their winter season CO_2 efflux rates are severely underestimated. In our opinion, such a discrepancy should be accounted for, with future research focussing more on winter biogeochemical processes.

6.4.4 Experimental considerations

To our knowledge, the design of our winter respiration chambers was innovative, though very close in principle to the prototype gas collectors designed by Sommerfeld et al. (1991). Their small size allowed for the headspace and soil temperature inside to closely follow the sub-nivean temperature (Bokhorst et al. 2013). The method allowed us to measure directly at the soil-snow interface without disturbing the snowpack, thus avoiding previously reported problems associated with snow pits and with trace gas diffusion gradients through an irregular snowpack with frequent ice lenses, which often cause accumulation of CO_2 beneath the snow and subsequent "chimney effects" (Bjorkman et al. 2010b). The extensive validation tests, outlined in the Appendix (section 6.6), provided ample evidence that the method is suitable for between treatment comparisons due to its results being unbiased by environmental factors. We believe that overall the choice of sampling methodology was well adapted to a steep natural gradient in snow cover and a relatively small plot size. Whilst our fortnightly sampling strategy, integrating the temporal variation over the entire period of the winter, provided a robust estimate of the comparative CO_2 efflux across sites, a greater level of detail, and the ability to construct C-budgets, would be gained from intensive, continuous sampling (Seok et al. 2009). This is a crucial and much needed direction for such measurements of CO_2 efflux under snow.

6.4.5 Ecosystem-scale implications and conclusions

Even though the intricacy in the interactions of environmental parameters over space and time prevented us from pointing out their individual contribution to the process of winter soil respiration, we claim here that consistent snow cover exerted a positive effect on belowground ecosystem processes. Since tight linkages between belowground and aboveground processes exist (Wardle 2002), we believe that this effect has strong implication for ecosystem functioning and stretches out beyond the boundaries of the winter season (Bardgett et al. 2005). For example, during the growing season, plant performance is indirectly affected by soil nutrient availability resulting from overwinter organic matter turnover (Schimel et al. 2004). Nutrient reserves, immobilised in microbial biomass under the snow, become plant-available upon snowmelt due to a shift in soil microbial community composition (Schmidt and Lipson 2004), thus changes in the winter snowpack could indirectly influence the competitive advantage of plants during their early phenological development. Changes in snow cover will subject plants to increased tissue mortality, but also cause changes in phenology, productivity, and reproduction as a result of absent snow insulation (Bokhorst et al. 2011) or altered snowmelt timing (Wipf and Rixen 2010). Such shifts in productivity and carbon mineralisation resulting from experimental snowpack modulation may not necessarily go in parallel with the well documented effects of experimental summer warming (Bokhorst et al. 2012). Future work should address the availability of carbon source for microbial growth under the snow and its interaction with plant productivity and litter deposition, and possible feedbacks and hysteresis effects, where using stable and/or radioactive C isotopes may shed more light on these processes.

Prior to launching this field experiment, we hypothesised that milder winter climate would have negative impacts on soil microbial activity and abundance. Our data unequivocally show that naturally occurring warmer average winter temperatures resulted in thinner and inconsistent snow cover, which promoted soil frost and large diurnal temperature amplitudes. These exerted strong negative effects on soil microbial biomass and respiration rates during the winter. Considering we found below-snow CO_2 efflux to be of greater magnitude than that during the growing season, we conclude that a reduction in microbial activity due to climate warming may impede organic matter turnover and nutrient cycling in these subalpine pasture systems, with broad implications for ecosystem scale processes.

6.5. Acknowledgements

This work was supported by the CCES (Competence Center Environment and Sustainability of the ETH Domain, Switzerland) as part of the Mountland project. Method validation was carried out at the University of Innsbruck, with grants to Konstantin Gavazov from SNFS (The Swiss National Science Foundation) and COST (European Cooperation for Science and Technology). We thank Arboretum National d'Aubonne, Commune of St-George (VD), Parc Jurassien Vaudois, and Fondation Les Bois Chamblard for their logistics and infrastructure support. Special thanks go to Manuel Froidevaux and Jacobus Melis for their assistance during the sampling campaigns in Jura.

6.6 Appendix

Here we present a number of validation tests of the PVC respiration chamber system and its applicability across a range of environmental conditions. Additionally we also explore the relationship between snow depth, CO_2 efflux and CO_2 concentration, as to determine possible biases in the measurements.

6.6.1 Performance test of the PVC chambers in the absence of snow

A comparison test was run between the hand-made PVC chamber designed for CO_2 measurements under snow and the commercially available LI-COR Survey Chamber LI-8100-102 on snow-free ground before snow cover built up. In November 2011 fifteen plots from all three land use types at the St. George experimental site were measured in parallel with both techniques. We detected a significant positive bias (P < 0.001) of the PVC-chamber method and a strong linearity ($R^2 = 0.84$) across a range of flux estimates (Figure A6.1). We attribute this bias to altered soil microclimate (*i.e.* excess heating of the soil and moisture accumulation) due to the direct sunlight irradiation of the chamber. Due to this artifact, the PVC chamber was exclusively used for measurements under snow, whereas the LI-COR survey chamber and soil respiration collars were employed in late autumn and early spring at lower altitudes when the ground was snow free.

6.6.2 Effect of flushing the PVC chambers with atmospheric air

Furthermore, we evaluated the possibility that the measurement of CO_2 efflux with a closed PVC chamber under undisturbed snowpack might induce a positive bias due to flushing with atmospheric air prior to flux estimation. An independent validation experiment was set up during the subsequent winter. Four sampling campaigns were carried out between February and March 2013 on five fixed subalpine grassland plots at 1850 m a.s.l. in the Tirolean Alps – Kaserstattalm, Stubaital, Austria. Snowpack depth during this period varied between 90 and 120 cm.

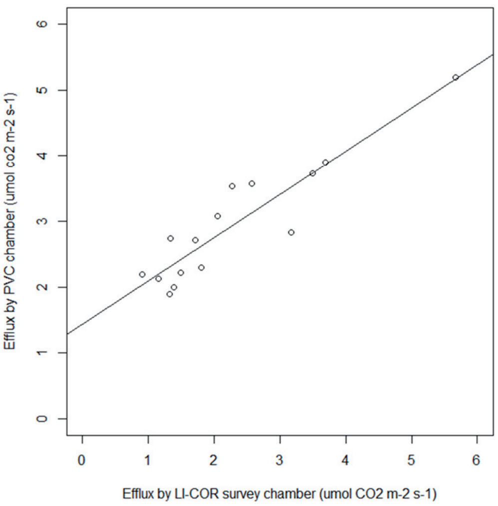

Figure A6.1. Relationship between CO_2 efflux measurements with the LI-COR survey chamber LI-8100-102 and the PVC chamber from snow free plots, N = 15.

Previous work (Bjorkman et al. 2010b) had shown that measuring CO_2 efflux at the soil-snow interface by digging snow pits can create a chimney effect stimulating the apparent soil respiration rates through increasing the CO_2 diffusion gradient between the snow-covered soil and the atmosphere. In our set-up a similar effect was considered to arise from the flushing procedure meant as a means of evacuating the trapped CO_2 in the PVC chambers prior to flux measurements. The following protocol was put in place to test this possibility. A LI-COR 8100 IRGA was manually calibrated, using the commercially provided software, for measurements within an extended CO_2 concentration range 0 – 9000 ppm by using pure N_2 gas and two CO_2 gases with different concentrations: 381 ppm and 8608 ppm, and fitting a linear algorithm relating the IRGA's optical bench CO_2 absorptance and CO_2 ppm. Field measurements with this system were done by consequently measuring the CO_2 flux in the PVC chambers, first under ambient conditions at the time of sampling, and second after flushing for 1 minute with ambient air as done in the main experiment the preceding winter. This allowed us to establish an empirical relationship between efflux measurements with flushed and non-flushed chambers (Figure A6.2), which was highly significant ($P < 0.001$, $R^2 = 0.87$) and provided evidence for only a slight overestimation of CO_2 flux due to flushing.

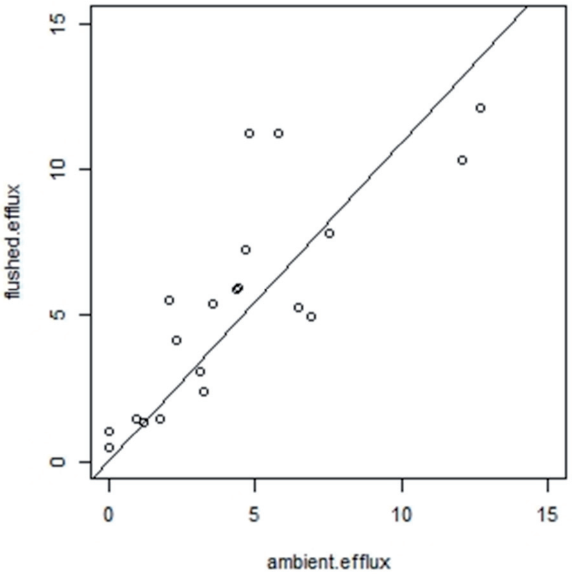

Figure A6.2. Relationship between CO_2 efflux measurements under ambient headspace conditions in the PVC chambers and after flushing the headspace with air from above the snowpack. Measurements come from four samplings (N = 20) at Kaserstattalm, Austria.

The model's performance was independent of initial CO_2 concentration in the chambers and the magnitude of change in ppm resulting from the flushing of the respiration chambers with atmospheric air (Figure A6.3).

As a result of this experiment, we were confident that the measured fluxes in the main study were not biased by the brief flushing of the PVC chambers under snow, but remain cautious about the slight positive offset of the reported absolute values.

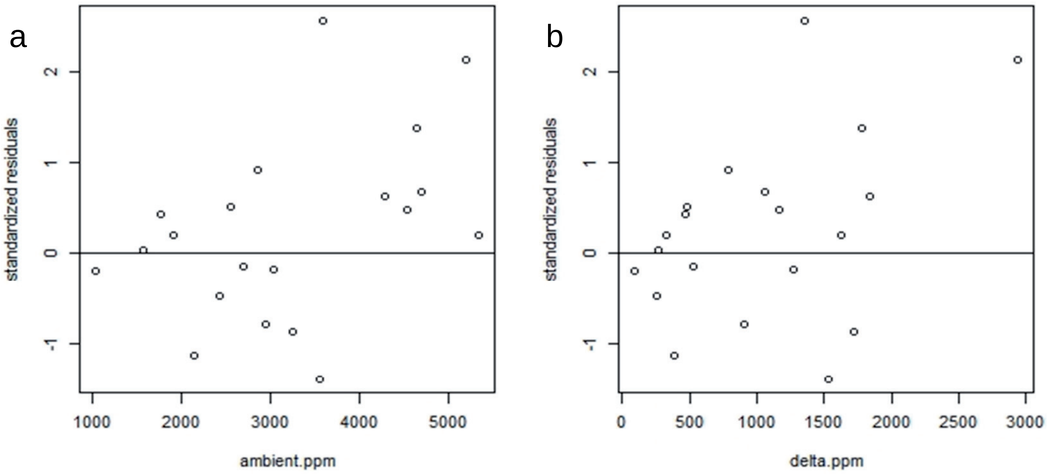

Figure A6.3. The influence of a) initial CO_2 concentration (ambient.ppm) and b) the change in CO_2 concentration (delta.ppm) in the chambers due to flushing on the performance of the model in Figure A6.2, represented by the independence of the model's residuals from those parameters.

6.6.3 Effect of initial CO_2 concentration on flux estimation

Following the idea that the diffusion to the atmosphere of CO_2 produced in the soil during winter is slower due to the presence of snow, we tested the relationship between CO_2 concentration in the PVC chambers prior to measurements and the calculated efflux. Plotting the existing data from all measurements carried out during winter 2011-2012 in the presence of snow cover on the ground, we observed a clear pattern of higher fluxes associated with higher initial CO_2 concentrations (Figure A6.4). The established relationship ($R^2 = 0.71$, $P < 0.001$) suggests that higher CO_2 production in the soil results in higher fluxes regardless of the special and temporal variation in the snow conditions during the experiment. This point is further explored in the following section 6.6.4 of this Appendix.

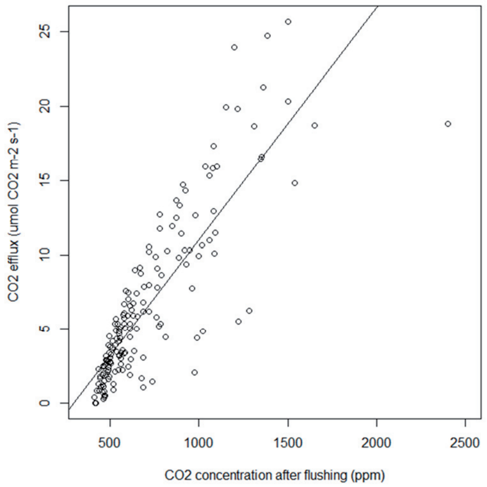

Figure A6.4. Relationship between initial CO_2 concentration in the respiration chamber and calculated efflux for all data (N = 167) obtained during the main experiment in 2011-2012 in the presence of snow cover on the ground.

6.6.4 Effect of snow depth on CO_2 concentration

We did not detect any clear relationship between the depth of the snowpack and the CO_2 concentration beneath the snow for the entire period of the winter (Figure A6.5). Snow did not affect the measured fluxes neither (as reported in the main text, Figure 6.3).

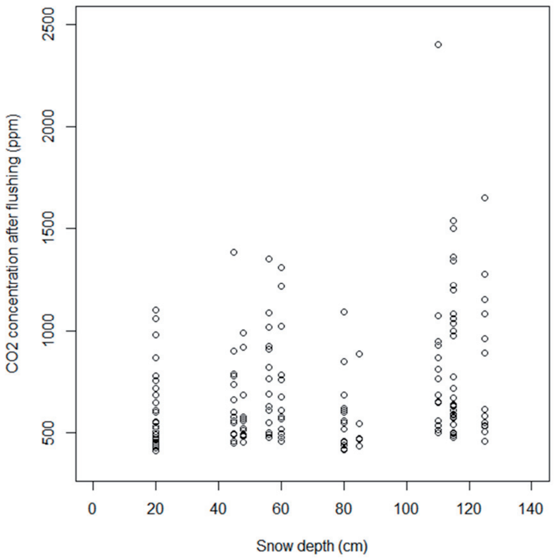

Figure A6.5. Relationship between snow cover thickness and CO_2 concentration in the respiration chambers prior to flux estimation.

Chapter 7

Synthesis

This PhD thesis summarises the findings of a four year experimental climate manipulation on the ecosystem response of three land use types, characteristic of the pasture woodlands landscape of the Swiss Jura Mountains. In this chapter a general synthesis of the main findings is provided focusing on linkages between different ecosystem processes above and below ground, and backing them up with supplementary observations which are not presented in the preceding chapters. Chapters 2 and 3 deal with the aboveground vegetation response to climate manipulation; chapter 4 establishes the climate impacts on the rates of litter turnover on the soil surface and on the responsible microbial agents; chapter 5 goes in depth to elaborate on the microbial communities activity and functioning in the most affected by climate change land use type (unwooded pastures) and the repercussions for soil organic matter accumulation; and chapter 6 demonstrates the importance of the winter season for ecosystem carbon cycling in relation to climate change. Considering that the aim of this PhD is the comparison of land use driven response to climate change, most chapters in this dissertation touch upon this aspect. In contrast, chapter 5 provides an in-depth investigation of the response of a single land use type (unwooded pastures), which is essential for acquiring further process understanding.

7.1 Aboveground vegetation

During the first three years (2010, 2011, and 2012 (*unpublished data*), reported in Chapters 2 and 3 and 7, respectively) after the transplantation in 2009 of turf monoliths to warmer and drier climates, a rather consistent pattern emerged for the response of plant aboveground biomass to the intensity of the climate change treatment. The simulated moderate (+2 K) climate change scenario achieved through a transplantation from 1350 m to 1010 m a.s.l. had barely an effect on the aboveground biomass (AGB) in the mesocosms in comparison to the intensive (+4 K) scenario involving a transplantation to 570 m a.s.l. (Table 7.1). Effects of the +2 K treatment were observed exclusively in the unwooded (UW) pasture land use with plant growth form (PGF) specific AGB decrease in the first year and an increase in the third year. In contrast, the effects of the +4 K treatment were observed during all years following the transplantation and also across all three land use types. It is interesting to note that during 2010 all land use types were affected by this treatment, however during the following years first DW, and then both SW and DW showed a marked resilience (recovery and resistance) to the effects of warmer and drier climate. Within these wooded pasture types mainly graminoids responded to the treatment (see Table 7.1). It is also remarkable that after two years of consistent reduction in AGB in UW pastures exposed to the intensive (+4 K) treatment, the third year was marked by a substantial increase in AGB from graminoids. This goes in line with our observations for a change in community species composition (Figure 7.1) and the role of *Agrostis capillaris* in this grasslands system gaining dominance over other extant or extinct species (see Chapter 3, and Figure 7.2b).

Table 7.1. Vegetation aboveground biomass dynamics in the turf mesocosms in the years following transplantation in autumn 2009. Results are presented as a directional response to the +2 K and the +4 K scenario treatments.

Year of sampling	2010						2011						2012					
Land use type [1]	UW		SW		DW		UW		SW		DW		UW		SW		DW	
Treatment	+2K	+4K	+2K	+4K	+2K	+4K	+2K	+4K	+2K	+4K	+2K	+4K	+2K	+4K	+2K	+4K	+2K	+4K
Forbs	↓	↓	-	↓	-	-	-	↓	-	-	-	-	↑	-	-	-	-	-
Graminoids	-	-	-	-	-	↑	-	↓	-	↓	-	-	-	↑	-	-	-	-
Mosses	-	-	-	-	-	-	-	↓	-	-	-	-	↑	-	-	-	-	-
Woody	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TOTAL	-	↓	-	-	-	↑	-	↓	-	↓	-	-	↑	↑	-	-	-	-

[1] Land use type codes, where UW refers to unwooded pasture with 0% canopy shading, SW – sparsely wooded pasture with 40% canopy shading, and DW – densely wooded pasture with 80% canopy shading.

↑ indicates a significant increase in AGB for that treatment combination. ↓ indicates a significant decrease. – indicates no significant change

Plant communities did not show an inter-annual variation in their species richness and once the treatment effects were established, those remained in place in the following years. Figure 7.1 demonstrates this negligible role of 'year' for explaining the variation in species assemblages, but also the major partitioning in relation to land use ('shade') separating grassland species (left) from forest understory ones (right). Mesocosms at lower altitude showed an increased frequency of species from the top half of the graph, possibly due to recruitment from the soil seed bank, whereas those at higher altitude (controls) were represented most frequently by species from the lower part of the graph.

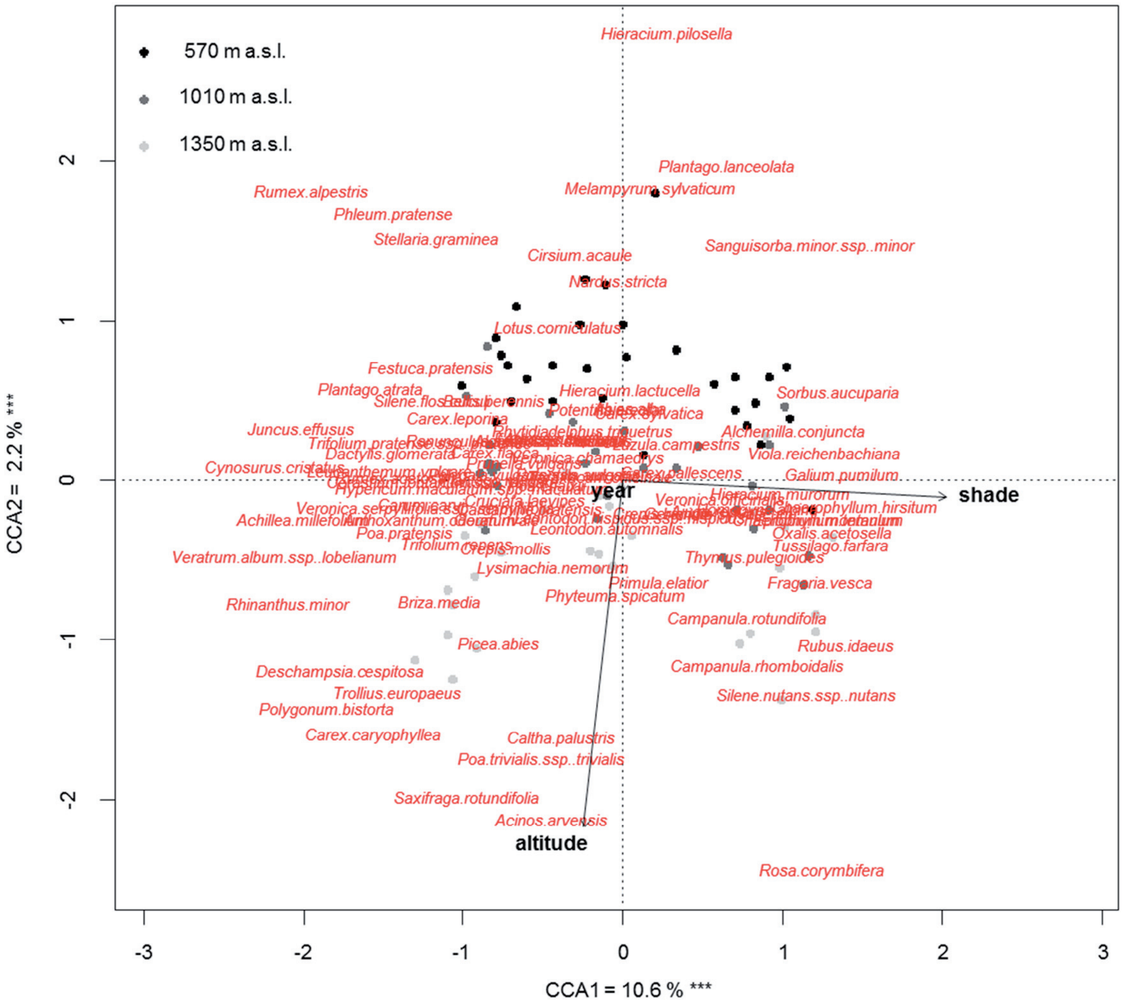

Figure 7.1 Canonical correspondence analysis (CCA) of species richness data (presence/absence) from the entire surface of the mesocosms in 2010, 2011, and 2012. Only the two first axes of the CCA are significant, however, 'year' is not.

Plant species abundance, however, was more dynamic in its response to experimental climate change. As in the case of total and PGF-specific AGB, individual species biomass was fluctuating from one year to the next, as shown in Figure 7.2. It is interesting to see that the response of the graminoid *Agrostis capillaris* in 2011 did not follow the common trend of plant community shifts in relation to the treatment and hence became a dominant species at the lowest site of transplantation (Figure 7.2b). The ubiquitous moss *Rhytidiadelphus*, as well as important pasture species such as *Anthoxanthum, Poa, Festuca, Ranunculus, Trifolium* decreased drastically in their abundance at lower altitudes due to the warm and dry climate.

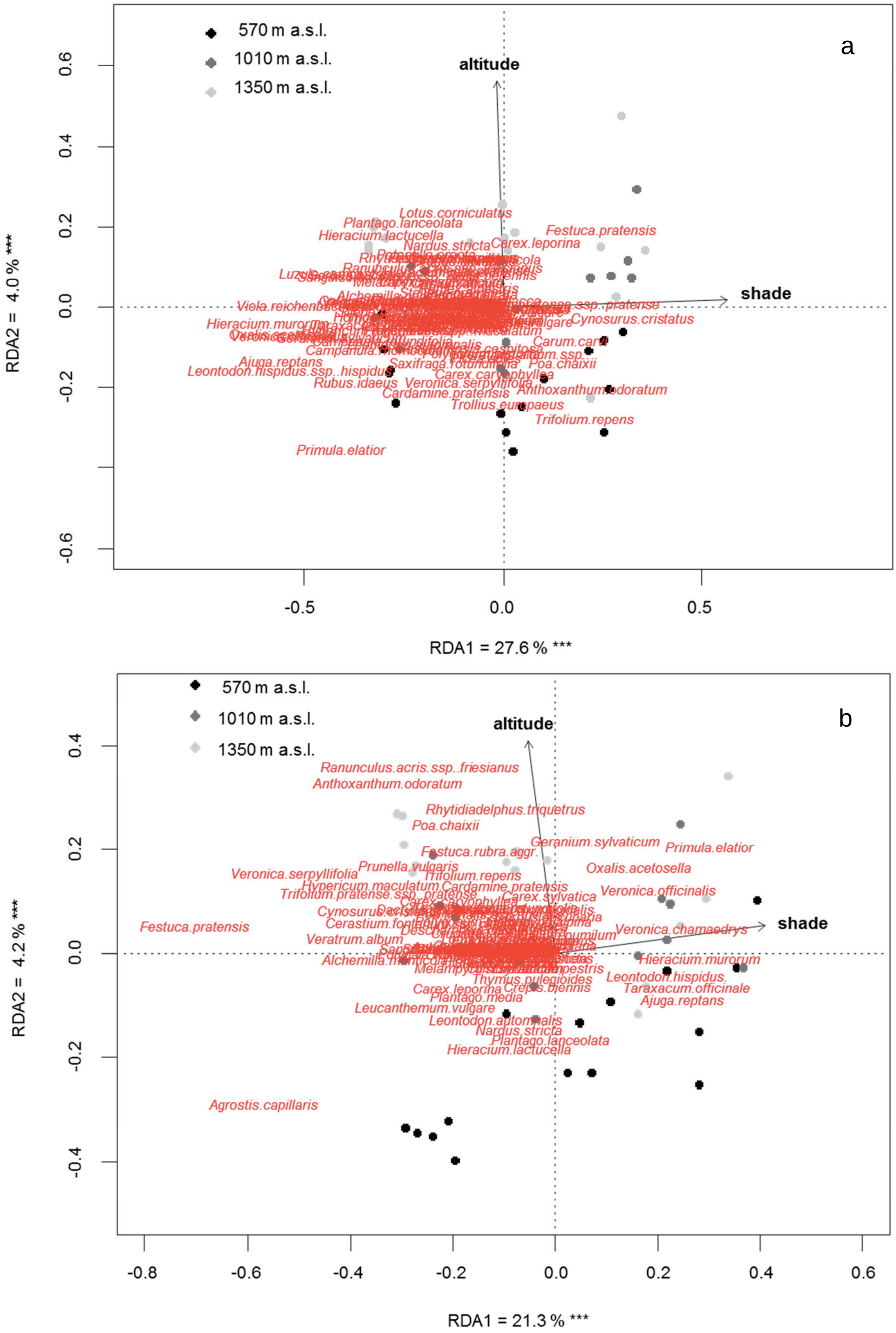

Figure 7.2 Redundancy analysis (RDA) of species abundance (AGB) per mesocosm measured in a) 2010 and b) 2011. In both models the first two axes are significant, explaingn the respective variation in percentage (%).

The suite of ecophysiological measurements carried out in 2011 (Chapter 3), allowed us to pinpoint the mechanisms behind the observed AGB patterns, bringing to light the predominant control of soil moisture regime and evapotranspiration pressure on the performance of transplanted turfs. A plausible explanation for the observed inter-annual variation in the response of plant AGB to the transplantation treatment is the precipitation and temperature patterns during these three years. The growing season of 2011 was the warmest and the precipitation that fell was much less (especially at the lowest site at 570 m a.s.l.), but also the preceding snow cover was negligible. This was reflected also in the substantially lower soil moisture in the soils during 2011. Overall 2011 had the lowest AGB across the three years of data collection. In contrast, the growing season of 2013 was the wettest with almost no gradient in precipitation along the altitudinal transect (all stations received approximately 650 mm during the months of AMJJAS). This could provide an explanation for the observed increase in AGB in the UW land use, however, the lack of response in SW and DW mesocosms remains hard to interpret. One tentative line of argumentation would be that these wooded land use types are more light- than temperature-limited, such that under conditions with ample precipitation an increase in temperature does not result in an increasing biomass. One should also remain cautious about the interpretation of the AGB results in terms of plant performance, since we did not explicitly address the issue of belowground plant biomass allocation under the different climate treatments.

Plant responses to the experimental treatments were often times species specific, and grouping into PGFs was not always useful for predicting general vegetation community structure or productivity under climate change. Overall the plant species loss was observed across all PGFs and without a particular emphasis on a given life strategy (*i.e.* plant functional types such as legumes, annuals, mycorrhizal association). Plant AGB in the different PGFs was a good predictor for the response to experimental climate change, however, inter-annual variability in the response of individual PGFs was too big to serve as a useful predictor. Further understanding of the differential response of species and/or PGFs could be gained through more frequent ecophysiological measurements during the entire growing season (as demonstrated in Chapter 3 with the use of a normalised difference vegetation index, NDVI), which could provide a better link between plant performance and climatic conditions during the growing season. Such are planned for instance for the 2013 growing season when continuous measurements of biomass accumulation (*i.e.* net ecosystem exchange NEE and gross primary production GPP) would provide a better means to characterise the system's response to climate change.

Modelling of landscape vegetation dynamics (Chapter 2) was performed exclusively with AGB data from the first year after experimental climate change, hence we limited our scope to upscaling the effects of recurrent heat waves rather than those of gradual increase in annual temperatures. We assumed that resilience is an inherent feature of the studied wooded-pasture ecosystems, with extreme climatic events triggering disproportionate vegetation changes in the landscape based on the land use type of pasture systems and their individual resistance potential, and that recovery takes place after individual heat wave events. As observed in the subsequent vegetation seasons, besides a high level of resistance to climate perturbation, extensive land use wooded pastures exhibit also a strong potential for recovery and thus resilience. We find this as a nice perspective for landscape scale mitigation of climate change impacts on subalpine pasture systems.

7.2 Carbon and nutrient cycling

In the studied pasture woodlands system the annual carbon assimilation in herbaceous biomass is partly taken up by grazing (annual clipping in the mesocosms), however a large proportion is metabolically respired back into the atmosphere through plants and soil microbes, and some enters the soil through the decomposition pathway. The suite of measurements related to this processes have revealed that soil moisture limitation is the predominant control of growing season carbon dynamics in the system, with unwooded pasture land use experiencing the largest impact of experimental climate change (Chapters 4 and 6). Both restrained litter decomposition (Chapter 4) and accumulation of undecomposed light organic matter fractions (Chapter 5) were observed in the UW mesocosms exposed to warmer temperatures and reduced precipitation. This was paralleled by a decrease in microbial and root (soil) respiration (Chapter 5) but also by a change in the soil microbial community structure (Chapter 4) and function (Chapter 5) which is further discussed in section 7.3. Unpublished data on soil solution carbon content (Figure 7.3) shows that a significantly higher concentration of dissolved organic carbon (DOC) was found in the drainage water of the turf mesocosms over the two years following the onset of the experimental climate change. We believe that the observed pattern is not due to an increased production of DOC in the soil (*i.e.* an indication of higher productivity and root activity), but rather to a physical damage of root and microbial membranes after prolonged periods of drought.

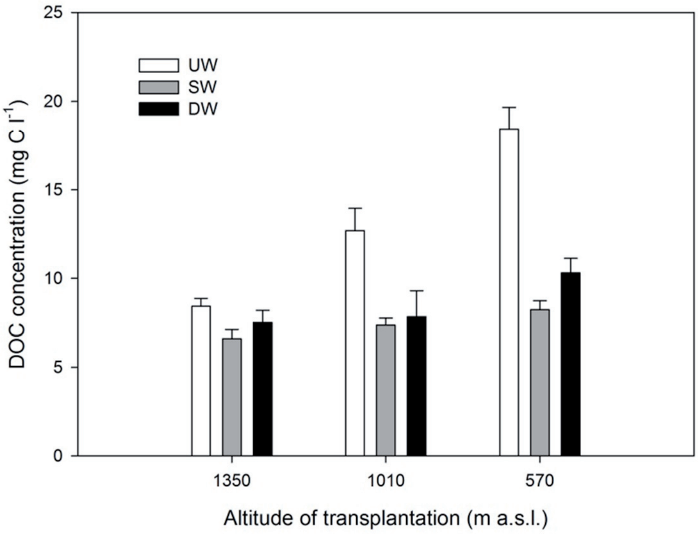

Figure 7.3 Dissolved organic carbon (DOC) concentration in soil solution collected by zero tension lysimeters for each transplanted mesocosms (5 replicates). Data are averages and standard errors of 18 sampling dates between Feb-2010 and Jan-2012.

The retarded decomposition process and accumulation of undecomposed light organic matter fraction in the soil is a clear sign for the malfunctioning of the system under warmer and drier conditions with strong implications for the turnover of nutrients too. This is evident from the sequestration of nitrogen in the soil which remains either immobilised in the SOM (Chapter 5), or leached through the water phase (Chapter 4), and hence becomes unavailable in the long term for plant growth and animal nutrition.

Considering the multifaceted effects of year-long experimental climate change on the functioning of mountain ecosystems, a field campaign for measuring soil respiration was set up during the winter season in 2011-2012. Winter soil carbon dioxide (CO_2) efflux and soil microbial communities appeared largely dependent on the insulating cover of snow during the cold winter months and as such responded strongly to the experimental treatments (Chapter 6). It was interesting to note that land use driven differences in ecosystem processes were sustained during the winter (*i.e.* higher soil CO_2 efflux in UW both in summer and winter). In contrast to the growing season, however, land use did not show an interaction with the climate treatment and all three types responded with equal magnitude to the experimental climate change.

Despite being indicative of biological activity in the soil the results on CO_2 efflux obtained in this study are hard to interpret in the context of absolute CO_2 respired by the soil per unit area and time. The reported values are often (by an order of magnitude) higher than previously reported values and indicate some experimental limitations and the need for further calibrations. During a sequel experiment in the Tirolean Alps in the winter of 2012-2013 much lower rates of soil CO_2 efflux were detected in a similar subalpine grassland ecosystem. This indicates a potential confounding effect of the turfs enclosure in PVC mesocosms, which could have restricted the lateral CO_2 diffusion in the soil under the snowpack and caused accumulation of the gas. Further calibrations and method verifications using cross comparisons between different methods have been carried out in collaboration with the lab of Michal Bahn in the University of Innsbruck and subsidised by grants from COST-SIBAE and SNFS to Konstantin Gavazov, the results of which should shed more light on the credibility of this method for studying winter ecosystem processes.

7.3 Microbial communities

Various measures of microbial biomass, activity and functional diversity have been recorded during the three years of experimental climate change in the mesocosms. The most exhaustive of all was the determination of *in situ* fungal/bacterial ratio in decomposing litter over a course of 2.5 year through the phospholipid fatty acid PLFA technique (Chapter 4). This revealed a significant alteration in the size and composition of microbial communities in the litter incubated in the mesocosms due to the experimental climate change. As a result, a measurable indirect effect on the ecosystem functioning, and litter decomposition rates in particular, were observed. Furthermore under standardised laboratory conditions temperature sensitivity (Chapter 5) and carbon mineralisation potential (*unpublished data*) revealed that such structural changes in the communities can potentially have persistent effects on the ecosystem and its functioning even upon the reestablishment of optimal environmental conditions. The reported increase in bacterial dominance in the turfs exposed to warmer and drier climate is prone to disrupt the carbon and nutrient cycling in the system, but potentially also the symbiotic interactions between plants and microbes.

7.4 Main conclusions

The global picture emerging from the ensemble of individual studies presented in this thesis is that unwooded pastures are disproportionately more prone to experience profound impacts from future warmer temperatures and reduced precipitation in comparison to their wooded pasture counterparts. The established pattern for overall resistance of the ecosystems to a moderate change in climate goes is in line with the fact that these subalpine pasture systems are already experiencing a large annual and inter-annual variability in climate and are buffered to such moderate disturbance. Their response to an intensive experimental climate change, however, is strong and can have large impacts on the sustainable provision of ecosystem services. The reported resistance of wooded pastures to experimental climate change could and should be used as a natural buffer for counteracting the impacts of future climate.

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Appendix

Other work published in collaboration with project MOUNTLAND

Réchauffement en montagne

Une équipe de chercheurs du laboratoire ECOS de l'Ecole Polytechnique Fédérale de Lausanne et de l'Institut Fédéral de Recherches sur la forêt, la neige et le paysage (WSL) s'intéresse à l'impact du changement climatique sur le sol et les interactions entre plantes et microorganismes dans les écosystèmes caractéristiques des montagnes jurassiennes.

THOMAS SPIEGELBERGER, KONSTANTIN GAVAZOV UND ALEXANDRE BUTTLER

Le pâturage boisé, écosystème emblématique du Jura, nous rend régulièrement de multiples biens et services. Les forêts stockent beaucoup de carbone dans la biomasse, ce qui contribue à l'équilibre climatique, et nous fournissent du bois. La végétation très diversifiée des prairies fixe le sol et réduit le risque de glissement de terrain et d'érosion. Elle est le support de l'agriculture de montagne. La capacité filtrante du sol rend l'eau des sources potable. Et finalement, ce paysage hospitalier permet de nombreuses activités de loisirs à proximité des grands centres urbains. Le changement climatique constitue une menace pour ces milieux fragiles et pour son utilisation par l'homme. L'augmentation de la température de l'air et la réduction des précipitations estivales pourraient notamment influencer la distribution des espèces végétales, dont celle des arbres, le fonctionnement des sols, et

Site expérimentale au Col du Marchairuz: La bacs avec les monolithes de terre des habitats forestiers et pâturages boisés sont ombragés pour une toile laissant passé uniquement une partie de la lumière. (Photo : Konstatin Gavazov).

en conséquence bouleverser l'équilibre de ces écosystèmes. On peut donc se poser la question de la durabilité des pâturages boisés du Jura et de leur exploitation traditionnelle en estivage. Ce paysage a-t-il encore un avenir ?

Transplantation d'altitude vers la plaine

Différentes techniques existent pour simuler expérimentalement le réchauffement climatique: mini-serres, réchauffement de parcelles par lampes infrarouges et transplantation le long d'un gradient d'altitude. Dans le cadre du projet Mountland (www.cces.ethz.ch/projects/sulu/MOUNTLAND), financé en partie par le Competence Center Environment and Sustainability du domaine des EPFs, nous avons opté pour une expérience de transplantation de blocs de sols avec leur végétation. Prélevés dans le site donneur du Marchairuz à 1450 mètres, les sols ont été transplantés à trois altitudes inférieures de manière à simuler l'augmentation de la température de l'air prévue par les scénarios climatiques pour le Jura: de plus deux degrés à plus cinq degrés.

Plus de 700 blocs de terre ont été extraits dans trois habitats représentatifs du Jura à l'aide d'une tarière et ensuite assemblés dans des cuves lysimétriques d'une contenance de 144 litres. Ces bacs ont ensuite été transportés vers 1) un site de contrôle à même altitude (Marchairuz à 1450 mètres), 2) un site à 1000 mètres (St.-Georges), 3) un site à 600 mètres (Arboretum national d'Aubonne) et 4) un site de plaine à 400 mètres (Bois-Chamblard près de Buchillon).

Un gradient d'intensité d'exploitation

En plus du changement climatique, les pâturages boisés sont soumis à des changements de gestion, liés notamment à la difficulté de l'exploitation en montagne et aux contraintes légales et économiques. Ces dernières années, une radicalisation est visible dans le paysage jurassien : intensification agricole et coupe du bois dans les endroits les plus productifs et d'accès facile, abandon graduel dans les zones moins favorables. Le résultat est une dynamique dichotomique du paysage vers des milieux soit entièrement ouverts, soit en voie de fermeture. En conséquence, nous avons choisi d'étudier trois habitats herbacés représentatifs de trois types d'utilisations par le bétail : la forêt parcourue, le pâturage boisé et le pâturage ouvert.

Le lien entre les changements de la végétation et du sol

Le climat dans chaque site de transplantation est enregistré en continu, de même que la température et l'humidité du sol dans les bacs. Outre les changements qualitatifs et quantitatifs dans la végétation et la capacité de germination et de développement des plantules d'épicéa et de hêtre, ce sont les interactions avec le sol et ses changements de propriétés, notamment l'activité biologique et les conséquences sur la décomposition de la litière, sur la fertilité et sur le devenir du carbone fixé, qui sont en point de mire.

L'enjeu du stockage de carbone dans le sol

Une des fonctions importantes des sols est leur capacité à stocker le carbone. Ce phénomène est bien connu dans les sols organiques des milieux humides, mais il apparaît que dans le cas des sols terrestres et en particulier ceux des prairies et pâturages de montagne, cette capacité est plus importante qu'on ne le pensait. Une fois séquestré dans le compartiment souterrain, ce carbone ne contribue plus aux gaz à effet de serre qui sont responsables du réchauffement planétaire.

A intervalles réguliers pendant toute l'année, les chercheurs de l'EPFL suivent la dynamique du carbone en mesurant les pertes dans l'atmosphère, par respiration du sol ou celles dans les eaux de drainage collectées sous les cuves. La résilience des milieux dans un contexte de réchauffement pourrait être différente selon l'habitat.

Des signes inquiétants après une année de manipulation expérimentale ?

Les mesures faites pendant la première année de l'expérience montrent clairement, dans le cas des pâturages ouverts, qu'une augmentation de la température jusqu'à quatre degrés Celsius dans les transplantations à 1000 et 600 mètres, mène à une perte de matière organique dissoute dans l'eau jusqu'à deux fois supérieure à celle de la situation de contrôle à 1400 mètres. Cependant, avec une augmentation de cinq degrés Celsius à 400 mètres, où la sécheresse estivale se marque plus fortement, la respiration par les microorganismes du sol et les racines est plus de deux fois inférieure par rapport aux sols de contrôle.

Cette tendance doit être vérifiée à plus long terme pour tenir compte des variations interannuelles.

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Erhaltung der Wytweiden im Jura: klimatische und agrarpolitische Herausforderungen

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Kontrollstandort les Amburnex beim Col du Marchairuz (Vaud). (Foto: Alexandre Buttler, WSL)

Einleitung

Wytweiden sind vom Menschen geschaffene Weideflächen auf denen sich bestockte und reine Weideflächen abwechseln. Diese dienen in erster Linie als Futtergrundlage für Kühe und Rinder und werden zur Holzgewinnung genutzt. Im jahrhundertelangen Zusammenspiel von Natur und Mensch wurden kleinräumige Mosaikstrukturen geschaffen, die einer Vielzahl von Pflanzen und Tieren einen passenden Lebensraum bieten, darunter emblematische Arten wie Auerhahn, Luchs oder verschiedene Orchideen. Die Wytweiden sind ein typischer Bestandteil der Juralandschaften und dienen sowohl im Winter als auch im Sommer als Erholungs- und Freizeitgebiet, insbesondere für die Bevölkerung der nahegelegenen urbanen Gebiete des Genfersees. Die Wytweiden-Ökosysteme stellen noch weitere, für die Gesellschaft grundlegende Ökosystemdienstleistungen bereit, wie beispielsweise die Speicherung und Reinigung von (Trink-)Wasser, die Reinhaltung der Luft oder die attraktiven Kulturlandschaften (Miéville-Ott und Barbezat 2005).

Zusammenfassung

Die für den Jura typischen Wytweiden dienen als Futterweiden und Holzlieferanten. Darüber hinaus haben diese artenreichen Ökosysteme weitere Funktionen, insbesondere als Raum für Erholungs- und Freizeitaktivitäten. Die Wytweiden reagieren empfindlich auf Klima- und Landnutzungsänderungen. Dieser Artikel zeigt mit Hilfe eines Transplantations-Experiments und Modellrechnungen, wie sich die prognostizierten Klimaänderungen auf die Grasproduktion der Wytweiden auswirken und welche zusätzlichen Effekte durch die nächste Agrarreformetappe (AP14–17) zu erwarten sind. Die Resultate zeigen, dass unter zukünftigen Klimabedingungen die Futterproduktion auf Wytweiden stabiler verläuft als auf Weiden ohne Bäume. Die Modellsimulationen prognostizieren, dass die bestehende Nutzungsintensität zu einer Übernutzung auf offenen Weiden führen kann, wenn das Futterangebot trockenheitsbedingt zurückgeht. Im Gegensatz dazu führt die AP14–17 zu einer Extensivierung der Landnutzung, wodurch längerfristig die Zunahme geschlossener Waldflächen gefördert wird. Die in der AP14–17 vorgesehenen Landschaftsqualitätsbeiträge sollten es ermöglichen, spezifische Massnahmen zur Erhaltung der Wytweiden zu unterstützen.

Wytweiden reagieren empfindlich auf Landnutzungsänderungen, weil die Vegetationsentwicklung durch ein komplexes Zusammenspiel von Beweidung und Forstwirtschaft geprägt ist. In den letzten Jahrzehnten wechselten sich verschiedene Phasen der Landnutzung ab (Chételat *et al.* 2012). Nach dem 2. Weltkrieg wurden viele Flächen gerodet, um die Nachfrage nach Holz und Nahrungsmitteln decken zu können. Die Kombination einer protektionistischen Landwirtschaft mit der fortschreitenden Mechanisierung der Landwirtschaft hielt in der Folgezeit die Intensität der Nutzung hoch. Gleichzeitig führte der Strukturwandel in der Landwirtschaft zu voneinander abgetrennten Nutzungseinheiten. In den Siebzigerjahren führte die Einführung der Milchkontingentierung zu einer Abschwächung der Nutzungsintensität. Die Trennung von Einkommens- und Preispolitik anfangs der neunziger Jahre resultierte in einem starken Rückgang der Produzentenpreise, wodurch sich der Trend verstärkte, dass Flächen entweder intensiv genutzt oder aber aufgegeben wurden. Dieser Trend konnte auch durch die Einführung der (ökologischen) Direktzahlungen mit dem neuen Verfassungsartikel von 1996 nicht wesentlich gebremst werden. Parallel zu den unterschiedlichen Phasen der Landnutzung spielten auch die Veränderung des Klimas und Wetterereignisse wie Stürme und Dürreperioden eine wichtige Rolle in der Entwicklung der Wytweiden (Peringer *et al.* 2012). Durch die kalkhaltigen Unterböden und den damit verbundenen raschen Wasserabfluss sind die Wytweiden im Jura insbesondere anfällig auf Trockenheit. Die Zunahme der mittleren jährlichen Temperatur um 1,5 Grad führte im vergangenen Jahrhundert zu extremen Sommertemperaturen und vermehrten Dürreperioden, welche sich negativ auf die Futterproduktion auswirkten (Gavazov *et al.* 2012). Für viele landwirtschaftliche Betriebe im Jura erhöhte sich dadurch das Einkommensrisiko, weil fehlende Futterreserven zugekauft oder der Tierbestand angepasst werden mussten.

Auch in Zukunft werden sich klimatische und sozioökonomische Änderungen stark auf die Vegetation der Wytweiden auswirken. Der Klimawandel rechnet in diesem Jahrhundert mit einer Fortsetzung des Temperaturanstiegs um 2,8 – 5,3 Grad und einer Verringerung der Niederschläge um 30 %, wodurch das Risiko von Dürreperioden weiter zunehmen dürfte (CH2011). Gleichzeitig sieht die nächste Reformetappe der Agrarpolitik (AP14–17) vor, dass mit der Weiterentwicklung des Direktzahlungssystems tierbezogene durch flächenbezogene Direktzahlungen ersetzt werden. Damit sollen Intensivierungsanreize in der Tierhaltung abgeschafft werden und die Landnutzungsintensität reduziert werden (Barth *et al.* 2011). Eine zusätzliche Extensivierung

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Abb. 1 | **Mesokosmos für das Transplantationsexperiment.** (Foto: Konstantin Gavazov, EPFL)

der Landnutzung im Wytweidensystem des Juras könnte jedoch die Zunahme der Walddichte beschleunigen und damit der Segregation der Flächen in offene Weiden und geschlossenen Wald Vorschub leisten.

Für diesen Artikel wurden verschiedene methodische Ansätze miteinander verknüpft, um eine ganzheitliche Perspektive zu ermöglichen (Huber *et al.* 2012b). Mit Blick auf die verschiedenen wertvollen Funktionen der Wytweiden und die daraus entstehenden Nutzungskonflikte wurden bereits in früheren Forschungsprojekten Instrumente entwickelt, welche eine integrierte und multifunktionale Bewirtschaftung unter der Berücksichtigung divergierender Interessen ermöglichen sollen (Barbezat und Boquet 2008). Die hier präsentierten Resultate verdeutlichen, wie wichtig die Berücksichtigung der klimatischen und agrarpolitischen Veränderungen in der Entwicklung von adaptiven Massnahmen sein wird.

Material und Methoden

Die vorliegende Analyse umfasst drei verschiedene methodische Ansätze. 1) Ein Boden-Transplantationsexperiment; 2) ein Vegetationsmodell und 3) ein sozioökonomisches Landnutzungsmodell.

Für den experimentellen Teil dieser Studie wurden im August 2009 Bodensoden («Mesokosmen», ca. 60 × 80 cm und 35 cm tief – Abbildung 1) entlang eines Höhengradienten von der Combe des Amburnex (Waadtländer Jura) in tiefere Lagen verpflanzt (Abb. 2). Der Standort Combe des Amburnex (1350 m ü.M., N 46° 4', E 6° 23') diente als Kontrolle vor Ort. Eine Verpflanzung nach Saint-George (1010 m ü.M., N 46°

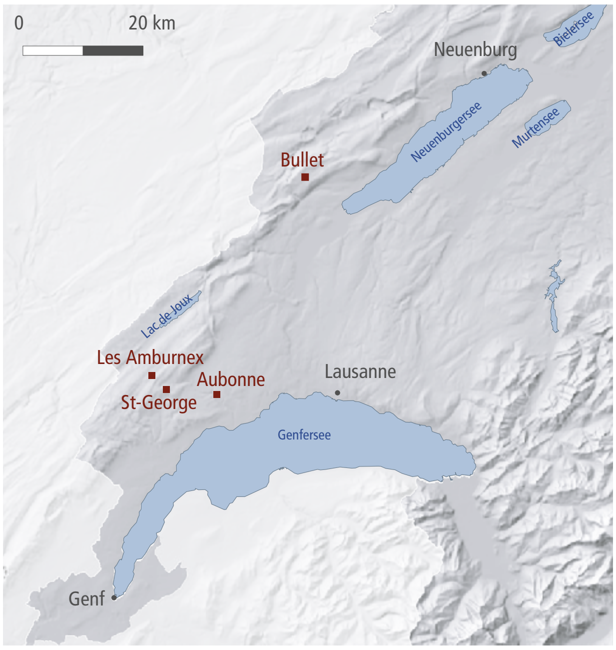

Abb. 2 | **Geographische Lage des Verpflanzungsexperiments (entlang des Höhengradienten Les Amburnex – St-George – Arboretum d'Aubonne) und der Modellregionen in Bullet. (Planets Ouest, Planets Milieu Est, Cluds sud).**

Abb. 3 | Die verpflanzten Mesokosmen auf einer offen Wytweide in der Combe des Amburnex.
(Foto: Alexandre Buttler, WSL)

52', E 6° 26') repräsentiert einen Temperaturanstieg von +2 Grad und eine Reduktion der Niederschläge von -20 %. Das Arboretum von Aubonne (570 m ü.M., N 46° 51', E 6° 37') entspricht einer Änderung von +4 Grad beziehungsweise -40 % der Niederschläge.

Die Bodensoden aus der Combe des Amburnex stammten dabei aus Wytweiden mit unterschiedlicher Walddichte: i) einer dicht bewaldeten Weide, ii) einer licht bewaldeten Weide und iii) einer baumfreien Weide. An jedem Standort wurden fünfzehn Mesokosmen (5x3 Typen Weidefläche) eingesetzt und die natürlich vorherrschenden Lichtbedingungen mit Hilfe von Beschattungsnetzen simuliert (Abb. 3). In jedem Mesokosmos wurde das Gras auf einer Fläche von 35 × 35 cm geschnitten (Ende Juli), alle Pflanzenarten bestimmt, getrocknet und gewogen. Die entsprechende Biomasse diente als Grundlage für die Schätzung der jährlichen Biomasseproduktion.

Für die Simulation der Sukzessionsdynamik in den Wytweiden wurde das dynamische Computermodell WoodPaM (Gillet 2008; Peringer *et al.* 2012) benutzt. WoodPaM ist ein räumlich explizites Modell der Wytweide-Ökosysteme, das in der Lage ist, im Schweizer Jura die Entstehung einer halboffenen Weidelandschaft unter der selektiven Beweidung von Rindern und Kühen zu simulieren. Es wurde für diese Studie auf drei Wytweiden in der Nähe von Bullet (1200 m ü.M., Abb. 2) angewendet, welche in enger Nachbarschaft zueinander liegen. Die Weiden unterscheiden sich in ihrer Landnutzungsintensität und der aktuellen Vegetationsstruktur: Planets Ouest ist eine fast baumlose, sehr intensiv genutzte Allmende (1,79 GVE/ha für 170 Tage/Jahr), Planets Milieu Est ist ein meist offenes Grasland mit einigen licht bewaldeten Flächen (1,56 GVE/ha für 135 Tage/Jahr), während Cluds Sud ein Mosaik aus Weide und Waldstücken ist (0,99 GVE/ha für 153 Tage/Jahr). Durch die Nähe zu den Versuchsflächen konnten die experimentellen Ergebnisse in die Parametrisierung des Modells einfliessen.

Die sozio-ökonomische Modellierung, welche den Einfluss der Agrarreform (AP14–17) auf die Nutzungsintensität auf den Wytweiden simuliert, basiert auf dem Optimierungsmodell ALUAM. Dieses agentenbasierte Modell optimiert die Einkommen der Landwirte unter der Berücksichtigung von agrarökologischen und betriebsbedingten Restriktionen (Huber *et al.* 2012a). Für die Auswirkungen der AP14–17 wurden die Berechnungen ohne Tierbeiträge aus dem Beitrag von Huber *et al.* (2012b) verwendet. Dieses Modell wurde mit dem WoodPam-Modell gekoppelt.

Für die Klimawandelszenarien wurden regionalisierte Temperatur- und Niederschlags-Zeitreihen benutzt, die den erwarteten Klimawandel für zwei unterschiedliche Emissionsszenarien wiederspiegeln (IPCC 2007). Für den Zeitraum von 2000–2100 werden folgende Annahmen getroffen:

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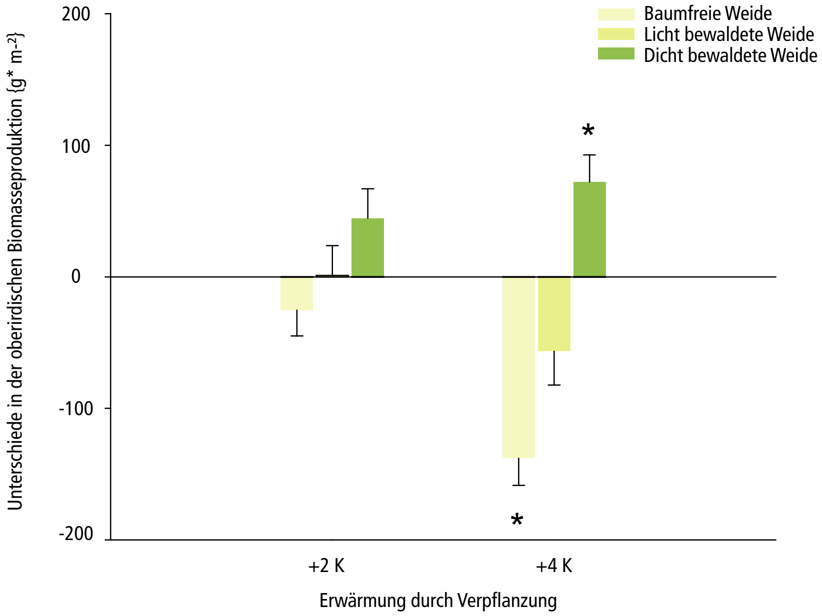

Abb. 4 | Unterschiede in der durchschnittlichen Biomassenproduktion (2010 und 2011) der Grasschicht (g*m^{-2}) der drei Habitate im Vergleich zum Kontrollstandort auf 1400m. Signifikante Unterschiede sind mit einem Stern gekennzeichnet.

- Szenario B2: Temperaturerhöhung von +4 Grad;
- Szenario A1FI: Temperaturerhöhung von +8 Grad
- Szenario B2 & A1FI: Zunahme der Trockenperioden durch Verlagerung der jährlichen Niederschlagsmengen vom Sommer- in das Winterhalbjahr.

Resultate

Abbildung 4 zeigt die Resultate der Verpflanzung von Bodensoden für zwei Höhenstufen und die drei untersuchten Habitate. Eine moderate Klimaerwärmung von +2K führte auf keiner der Flächen zu signifikanten Änderungen. Eine simulierte Erwärmung von +4K reduzierte die jährliche Biomasseproduktion auf den unbewaldeten Flächen, welche ursprünglich die höchsten Erträge aufwiesen, um 40 %. Auf den dicht bewaldeten Weiden hingegen ergab sich eine leichte Erhöhung der Futterproduktion.

In den Simulationen der Futterproduktion auf Landschaftsebene führte das zu einer unterschiedlichen Nutzung der vorhandenen Futterressourcen bei konstanter Besatzdichte (Abb. 5). Eine Auslastung von 100 % in Abbildung 5 bedeutet, dass alles verfügbare Futter abgeweidet wird und keine Waldregeneration möglich ist. Steigt die Auslastung auf über 100 %, dann reicht das heranwachsende Futter nicht mehr aus, um die entsprechende Anzahl der Tiere ausreichend zu ernähren. Dagegen ermöglicht eine kurzfristige Auslastung (d.h. einige Jahre) von unter 100 % die Regeneration der Wytweiden und eine Erhaltung des spezifischen Landschaftsmosaiks. Findet jedoch längerfristig eine Unterweidung statt, dann nimmt die Walddichte auf den entsprechenden Weiden zu. Abbildung 5 illustriert, dass mit steigender Temperatur ab dem Jahr 2000 die Auslastung der intensiv bewirtschafteten Weiden Planets Ouest die 100 %-Schwelle während einer Vielzahl von Jahren überschreitet. Im Gegensatz dazu bleibt die Auslastung der extensiv und moderat genutzten Weiden während der ersten 50 Jahre des Klimawandels (2000–2050) sowohl im moderaten Szenario B2 als auch im Szenario A1F unter der 100 % Schwelle. Nach 2050 kann je nach Klimaszenario eine unterschiedliche Entwicklung beobachtet werden. Eine moderate Klimaerwärmung liesse die Ausnutzung auf den offenen Weiden deutlich über den optimalen Ausnutzungsgrad steigen, während die licht bewaldeten Flächen sich bis 2100 dem Schwellenwert von 100 % näherten. Im extremen Szenario A1FI überschritten auch die licht bewal-

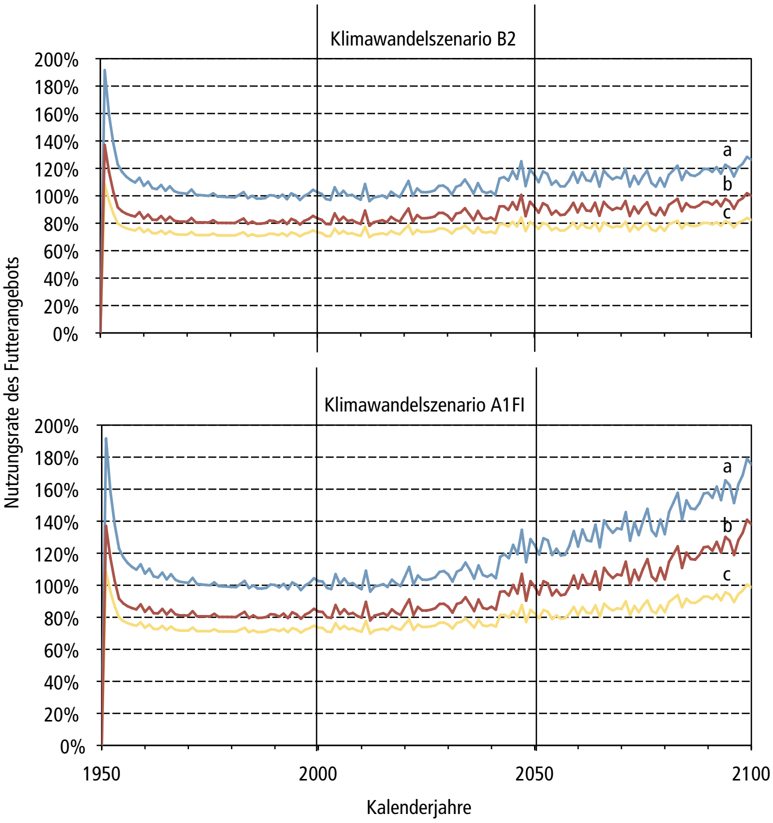

Abb. 5 | Entwicklung des Ausnutzungsgrads der totalen Futterproduktion unter zwei Klimaszenarien auf drei Wytweiden in der Nähe von Bullet, Planets Ouest (a), Planets Milieu Est (b) und Cluds Sud (c) (nach Gavazov *et al.* 2012).

deten Flächen eine Ausnutzung von 100 % und nur die extensiv genutzte Mosaikweide von Cluds Sud bliebe unter der 100 %-Schwelle. Mit anderen Worten: nur auf diesen Weiden wäre kontinuierlich ausreichend Futter vorhanden um den Bedarf der Tiere zu decken. Dies verdeutlicht das Potenzial dieser Wytweiden, dank der Schutzwirkung der Bäume, die negativen Effekte des Klimawandels auf die Futterproduktion abzumildern.

Wie wirkt sich nun eine extensivere Nutzung, impliziert durch die AP14–17 (Huber *et al.* 2012a), auf die Entwicklung der verschiedenen Wytweiden-Typen aus (baumfreie Weide, licht bewaldete Weide, dicht bewaldete Weide und beweideter Wald)? Abbildung 6 illustriert die Entwicklung bis ins Jahr 2050 und 2100 in den drei Modellregionen Planets Ouest, Planets Milieu Est und Cluds Sud für das Klimaszenario B2. Dabei können zwei Entwicklungen unterschieden werden:

1. Die Walddichte nimmt aufgrund der Extensivierung auf allen Flächen zu. In der Simulation sind im Jahr 2100 nur noch vereinzelte offene Weiden zu finden. Der Anteil der licht bewaldeten Flächen nimmt auf den zurzeit intensiv genutzten Flächen zu, während auf weniger intensiv genutzten Flächen dicht bewaldete Weiden entstehen.
2. Die Waldentwicklung ist gekennzeichnet durch eine Veränderung der Baumartenzusammensetzung von der Fichte zur Buche (Peringer *et al.* 2012). Dadurch nimmt die Waldfläche mittelfristig (bis 2050) ab, bevor sie gegen Ende des Jahrhunderts wieder ansteigt (Cluds Sud). In der Simulation verbindet dabei ein intermediäres Sukzessionsstadium mit Vogelbeere den trockenheitsbedingten Zusammenbruch von Fichtenbeständen mit der Neuetablierung der Buche. Simulationen mit einem Zeithorizont über 2100 zeigen, dass sich dieser Trend der zunehmenden Waldfläche akzentuiert und auch, dass die licht bewaldete durch dicht bewaldete Weiden und Wald ersetzt werden. Längerfristig deutet dies auf eine Simplifizierung der Landschaft hin, welche im Verlust von reichstrukturierten Lebensräumen und damit der typischen Biodiversität der Wytweiden resultieren.

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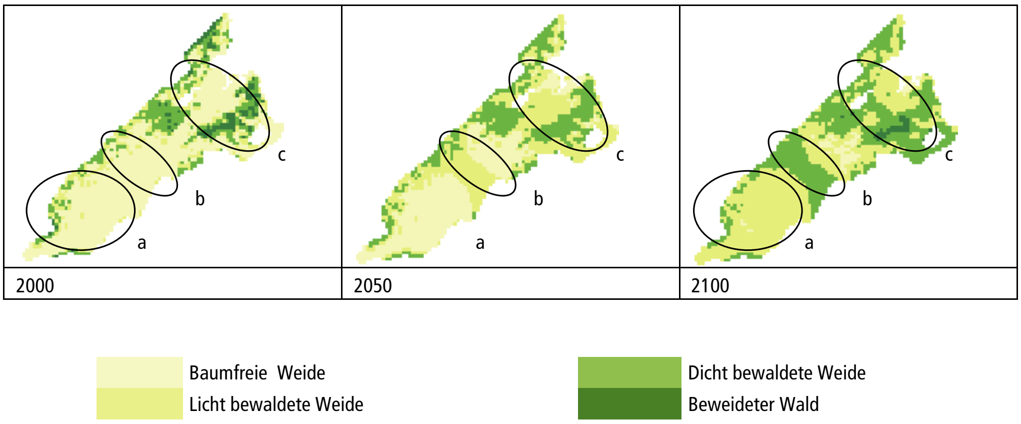

Abb. 6 | Simulation der Entwicklung von Weidetypen mit unterschiedlichem Bestockungsgrad für die Jahre 2050 und 2100 in Planets Ouest (a), Planets Milieu Est (b) und Cluds Sud (c) bei Bullet unter dem Szenario AP 14–17 und dem Klimaszenario B2.

Diskussion

Das Feldexperiment belegt, dass mit steigenden Temperaturen und einer Reduktion der Niederschläge die Futterproduktion auf den offenen Weiden des Juras zurückgeht. Im Gegensatz dazu ist die Biomasseproduktion auf den Wytweiden stabil (licht bewaldete Weiden) beziehungsweise sogar leicht ansteigend (dicht bewaldete Weiden). In der Versuchsanlage wiesen die entsprechenden Wytweiden eine (künstliche) Beschattung von 40% respektive 80 % auf, was zu einer niedrigeren Bodentemperatur und einer höheren Bodenfeuchte führte. Dadurch waren die negativen Einflüsse der simulierten Trockenheit auf diese Bodensoden begrenzt. Die Wichtigkeit des Mikroklimas zeigte sich auch in der Simulierung der Klimaveränderung auf Landschaftsebene. Die mosaikartige Zusammensetzung der Wytweiden ermöglicht eine stabile Futterproduktion trotz vermehrtem Trockenheitsstress. Halboffene Wytweide-Landschaften sollten es daher den Landwirten erlauben, trotz der prognostizierten Zunahme von Trockenperioden eine kontinuierliche Grasmenge zu produzieren. Dadurch reduziert sich auch das ökonomische Risiko, weil sich die Wahrscheinlichkeit verringert, dass man in trockenen Jahren zusätzlich Futterkäufe tätigen muss.

Die Simulationsergebnisse verdeutlichen auch, dass die Erhaltung der Wytweiden von einer optimalen Nutzungsintensität abhängig ist. Eine zu hohe Nutzungsintensität fördert die Entstehung einer offenen und damit trockenheitsempfindlicheren Weide (Gavazov *et al.* 2012, Mariotte 2012). Eine Extensivierung der Wytweiden dagegen kann das sensible Konkurrenzverhältnis zwischen Gras und Krautschicht ebenfalls ins Ungleichgewicht bringen. Insbesondere dann, wenn die klimatischen Bedingungen gleichzeitig die Konkurrenzkraft der Bäume erhöht. Schon aktuell zeigt sich in den Wytweiden eine allgemeine Tendenz zur verstärkten Waldentwicklung, weil die Klimaerwärmung im vergangenen Jahrhundert das harsche Klima milderte und die Baumetablierung förderte.

Die Wirkung der durch die AP 14–17 zu erwartenden Extensivierung der Wytweiden muss als ambivalent bezeichnet werden. Einerseits wird die Wahrscheinlichkeit einer Übernutzung der Weiden mit der Umlagerung der tierbezogenen Direktzahlungen auf die Fläche stark vermindert. Andererseits führt eine starke Zunahme der Walddichte längerfristig zu einer Simplifizierung der Landschaft. Um die verschiedenen Funktionen der Wytweiden und die landschaftliche Vielfalt längerfristig zu gewährleisten, ist deshalb die Ausgestaltung der Landschaftsqualitätsbeiträge im Rahmen der AP14–17 elementar. Diese sollten es ermöglichen, räumlich explizite Massnahmen zur Erhaltung der Wytweiden zu definieren. Dazu gehören eine gezielte Unterstützung einer standortgerechten Besatzdichte und eine räumlich explizite Reduzierung des Walddrucks durch selektive Holzeinschläge. Auch eine Anpassung der Zonenzugehörigkeit (landwirtschaftliche Nutzfläche (LN) bzw. Sömmerungsfläche) könnte dabei als Mittel zur Anpassung der Nutzungsintensität in Betracht gezogen werden. ■

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Riassunto

Conservazione dei pascoli alberati del Giura: sfide climatiche e agro-politiche

I caratteristici pascoli alberati del Giura servono principalmente da foraggio per animali e forniscono legname. Inoltre, essi sono anche importanti per la loro biodiversità, svolgono altre funzioni come aree di svago e di ricreazione per il tempo libero, come pure per la qualità del paesaggio che essi offrono in prossimità delle grandi zone urbane nell'arco lemanico. Questo articolo mostra, con l'aiuto di modelli di simulazione, l'effetto di cambiamenti climatici sulla produzione di biomassa erbacea e, in questo contesto, le conseguenze della nuova riforma agraria (PA 14–17) sull'evoluzione del paesaggio. I pascoli alberati potrebbero meglio resistere all'aumento delle temperature e alla diminuzione delle precipitazioni estive, rispetto ai pascoli non alberati, mantenendo una produzione foraggera più stabile. L'associazione del modello di vegetazione ad un modello socio-economico indica che attraverso la nuova politica agricola (AP 14–17), la pressione di pascolo diminuirà e che nell'ambito di uno scenario di moderato riscaldamento climatico questo porterà a un inforestamento con un aumento di zone boschive chiuse. La nuova politica agricola dovrebbe permettere di prendere delle misure mirate per conservare i pascoli alberati.

Summary

Conservation of pasture woodlands in the Jura mountains: climate change and agro-political challenges

Wooded pastures of the Jura mountains are mainly used for fodder and timber production, but they provide also other goods and services such as biodiversity, leisure areas as well as attractive landscapes. These ecosystems are sensitive to climate and land-use changes. In this paper we report on a transplantation experiment and model simulations to show the impact of climate change on the grass production as well as the consequences of the upcoming new agriculture policy (AP 14–17) on landscape dynamics. Results indicate that wooded pastures could better resist to climate warming and concomitant summer droughts than open pastures, and thus provide more stable fodder yields along the season. Simulations of vegetation evolution indicate that the global utilization rate of fodder in treeless intensive used pastures would be beyond a sustainable threshold. The AP 14–17 will lower the intensity of pasturing which will lead to more closed landscapes in the long run. The new policy should allow, by means of incentives in favour of landscape quality, to take targeted measures for the conservation of wooded pastures.

Key words: pasture-woodland, climate warming, vegetation dynamics, transplantation experiment, agricultural policy.

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Marital Status - Single
Nationality - Bulgarian

EDUCATION

05.2009 – 10.2013 **École Polytechnique Fédérale de Lausanne (EPFL), Switzerland**
Completed a 4-year PhD programme in Ecology

09.2006 – 02.2009 **Vrije Universiteit Amsterdam, Netherlands**
Completed a 2-year MSc programme in Ecology

09.2002 – 05.2005 **Jacobs University Bremen, Germany**
Completed a 3-year BSc programme in Biological Sciences

09.1997 – 05.2002 **First English Language School Sofia, Bulgaria**
Completed high school education in English Language & Sciences

SCIENTIFIC PROFESSIONAL EXPERIENCE

PhD Research

05.2009 – 10.2013 **“Subalpine pasture-woodlands in a changing climate: The role of land use type in ecosystem resistance to simulated climate change”** CCES funded project MOUNTLAND
Laboratory of Ecological Systems, EPFL, Lausanne
Swiss Federal Institute for Forest, Snow and Landscape (WSL)
PhD thesis supervised by Prof. Dr. Alexandre Buttler and Dr. Thomas Spiegelberger

01-06.2013 **“Snow cover effects on winter soil respiration and microbial community structure and function”** SNSF funded CanDoc project
Laboratory of Ecophysiology and Ecosystem Processes, UIBK, Innsbruck
Project supervised by Prof. Michael Bahn

MSc Research

05-12.2008 **“Reduced early growing season freezing resistance in alpine treeline plants under elevated atmospheric CO_2”**
Institute for Snow and Avalanche Research (SLF) Davos – WSL, Subunit - Alpine Ecosystems
MSc thesis supervised by Dr. Christian Rixen and Prof. Dr. Rien Aerts

01-04.2008 **"Dynamics of alpine plant litter decomposition in a changing climate"**
Vrije Universiteit Amsterdam, Department of Systems Ecology
MSc literature study supervised by Dr. Johannes H.C. Cornelissen

01-12.2007 **"Isotopic analysis of cyanobacterial nitrogen fixation associated with subarctic lichen and bryophyte species"**
Abisko Scientific Research Station, Sweden.
MSc thesis supervised by Dr. Johannes H.C. Cornelissen and Prof. Dr. Rien Aerts

BSc Research

09.2004 – 05.2005 **Jacobs University, Department of Biology**
"Analysis of the radical scavenger potential of tryptophane, glutathione and vitamin C in a chemiluminescence system". *Supervised by Dr. A. Lerchl*

"Comparative scanning electron microscopy study of the structure and function of avian eggshells". *Supervised by Prof. Dr. V.B. Meyer–Rochow*

"Electrolocation and communication in weakly electric fish". *Supervised by Dr. Günter Zupanc*

06 – 09.2004 **Umeå University, Department of Ecology and Environmental Science, Sweden** Internship in Fennoscandia : Active involvement in the EU research project LACOPE for nature conservation of large scale grazing systems.
"Plant community responses to different levels of herbivory in a Tundra Ecosystem" - *Supervised by Prof. Dr. Lauri Oksanen*

06 – 08.2003 **Sofia University Bulgaria, Department of Ecology and Environmental Protection**
Internship at the Central Balkan National Park, Bulgaria.
"*In situ* behaviour, territorial structure and social relationships of the European ground squirrel" - *Supervised by Dr. Vladimir Stefanov*

TEACHING EXPERIENCE

09.2009 – 12.2013 **Teaching Assistant** at École Polytechnique Fédérale de Lausanne
Soil Sciences
Multivariate Statistics using R

09.2004 – 05.2005 **Teaching Assistant** at Jacobs University Bremen
General Biology

AWARDS & SCHOLARSHIPS

10.2013 **Swiss Academies of Arts and Sciences Award; Network for Transdisciplinary Research**
Best transdisciplinary project for the period 2010-2013 with the CCES-funded "Mountland"

01-06.2013 **SNSF fellowship for prospective researchers**
6-month funding for a collaborative project with the University of Innsbruck

09.2006 – 06.2008	**Vrije Universiteit** 2-year academic scholarship for graduate studies
09.2002 – 05.2005	**Jacobs University** 3-year tuition grant for undergraduate studies
09.1997 – 05.2002	**First English Language School** 5-year scholarship for academic excellence by the Bulgarian Ministry of Education and Culture; Graduated with Honours

EXTRA-PROFESSIONAL SKILLS AND ACTIVITIES

Languages	English (Fluent - C2) French (Very good - B2/C1) German (Reading & understanding - A2) Bulgarian (Mother tongue)
Hobbies	Skiing (Freeride & touring) Volleyball (Indoor, beach, tournaments) Music (Drums, percussions) Contemporary literature

PUBLICATIONS LIST

Mills, R., **K. Gavazov**, T. Spiegelberger, A. Buttler and D. Johnson (*in review*). Sub-alpine pasture response to simulated climate change; moisture drives diminished soil function, yet heterotrophic temperature response indicates resilience. Science of the Total Environment.

Gavazov, K., R. Mills, T. Spiegelberger, J. Lenglet and A. Buttler (*in review*). Effects of experimental climate change on the decomposition of *Fagus sylvatica* leaf litter along an altitudinal gradient in contrasting land use types. Soil Biology & Biochemistry.

Gavazov, K., T. Spiegelberger and A. Buttler (*in press*). Transplantation of subalpine wood-pasture turfs along a natural climatic gradient reveals lower resistance of unwooded pastures to climate change compared to wooded ones. Oecologia.

Gavazov, K., Peringer, A., Buttler, A., Gillet, F., Spiegelberger, T., 2013. Dynamics of forage production in pasture-woodlands of the Swiss Jura Mountains under projected climate change scenarios. Ecology and Society. 18(1): 38.

Buttler, A., **Gavazov, K.**, Peringer, A., Siehoff, S., Mariotte, P., Wettstein, J.B., Chételat, J., Huber, R., Gillet, F., Spiegelberger, T., 2012. Conservation of pasture woodlands in the Jura mountains: climate change and agro-political challenges. Agrarforschung Schweiz 3, 346–353.

Gavazov, K., 2010. Dynamics of alpine plant litter decomposition in a changing climate. Plant and Soil 337, 19-32.

Martin, M., **Gavazov, K.**, Körner, C., Hättenschwiler, S., Rixen, C., 2010. Reduced early growing season freezing resistance in alpine treeline plants under elevated atmospheric CO_2. Global Change Biology 16, 1057-1070.

Gavazov, K., Soudzilovskaia, N.A., van Logtestijn, R.S.P., Braster, M., Cornelissen, J.H.C., 2010. Isotopic analysis of cyanobacterial nitrogen fixation associated with subarctic lichen and bryophyte species. Plant and Soil 333, 507-517.