IMPACTS OF CLIMATE CHANGE ON ALPINE GRASSLAND ECOSYSTEMS:
RESPONSES IN STRUCTURE AND FUNCTION

A thesis submitted to attain the degree of

DOCTOR OF SCIENCES of ETH ZURICH

(Dr. sc. ETH Zurich)

presented by

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2017
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1 Definitions

**Biomass production** A general term for the formation of biomass, unrelated to a specific area or period.

**Biomass pool** The amount of biomass per unit ground area at any given time. The above-ground standing biomass in alpine grassland was measured by clipping, whereas the below-ground standing biomass was sampled by taking soil samples and separating the roots.

**Biomass productivity** The amount of newly formed biomass per area and growing season. The below-ground biomass productivity in alpine grassland was measured with ingrowth cores.

**Biomass loss** The amount of biomass, which dies back per area and growing season.

**Resistance** The ability of the grassland system to stay in the initial state, when stressed by a perturbation such as summer drought. Resistance of alpine grassland was assessed based on changes in vegetation structure and biomass production.

**Resilience** The ability of a grassland system to quickly return to the initial state by recovery after a perturbation such as summer drought. Resilience was not directly measured, but the amount of below-ground biomass in alpine grassland, especially the amount of storage organs, was used as a proxy.

**Stability** The capability of an ecosystem to apply self-regulating mechanisms (such as a shift from above- to below-ground biomass production) so as to maintain or return to a steady state after a perturbation and thus to keep its structure and function in the longer term. Stability arises from an interplay of resistance and resilience.

**Integrity** The integrity of an alpine grassland ecosystem is characterised by the intactness of the system, especially concerning the capability to deliver ecosystem services such as slope stability.
As a consequence of human-induced global climate change, high elevation ecosystems may face considerable changes in their future climate. Evidence is accumulating that these changes may drastically affect plants in the sub-nival and nival zones, i.e. at the upper limit of plant life. No such evidence is available for the alpine zone, and it is unclear how stable these ecosystems are under changing environmental conditions. The future summer climate in the European Alps is predicted to be drier and warmer, with an increased probability of extreme events such as prolonged periods of drought. This doctoral thesis aimed at evaluating the potential impacts of these climatic changes (summer droughts and warming) on alpine grassland ecosystems by experimental and observational studies, carried out in the Swiss Central Alps. In a field experiment, established at three alpine grassland sites at Albula and Furka Pass, the structural and functional responses of alpine grassland to three years of simulated summer droughts differing in severity have been investigated (Studies 1 and 2). In a survey, conducted at Furka Pass, high-tech infra-red thermometry has been applied to address habitat heterogeneity and species niche specificity and hence potential responses of alpine grassland species to a warmer climate (Study 3).

Study 1 examined the above-ground structural responses of alpine grassland to summer droughts and evaluated potential implications on erosion susceptibility. Drought-induced changes in vegetation structure in the canopy layer and on the soil surface have been accurately quantified using the grid-point intercept method. The study found that, overall, three years of simulated summer droughts strongly influenced vegetation structure of alpine grassland by decreasing foliar and basal cover by up to 37% and 54%, respectively, and by increasing the area of bare ground by a factor of up to 8. Summer drought had a gradual effect, meaning that already substantial responses under moderate drought were further intensified under extreme drought. But summer drought had not the same effect at each site, since vegetation structure remained unaffected at one of the three sites. These findings show that a prolonged and recurring summer drought can significantly affect above-ground vegetation structure of alpine grassland in the short term. The drought-induced structural changes, namely the increased area of bare ground, may restrict the important function of alpine grassland to protect soil against erosion and thus, to maintain slope stability. But surprisingly, this study also demonstrates that the structural stability is clearly site-dependent. This means that some sites can strongly counterbalance the effect of drought and completely maintain above-ground vegetation integrity.
Study 2 focussed on the quantification of above- and below-ground biomass responses of alpine grassland to simulated summer droughts. Changes in pools and net production of biomass were sampled by clipping (above-ground) and using a split tube sampler and ingrowth cores (below-ground). Recurring summer droughts strongly influenced the swards by decreasing standing above-ground biomass, while increasing standing below-ground biomass, thereby leading to significantly increased root-shoot ratios. The gradual responses to increasing drought severity were already visible in the second year of drought simulation and were further intensified in the third year of the experiment, indicating carry-over effects. The changes in the biomass pools could be primarily attributed to a drought-induced modification of the biomass productivity in the respective compartments and to a changed root biomass loss. However, three years of summer droughts did not affect the overall biomass production in the alpine swards. The results of this study show that droughts affect the resource allocation in alpine grassland systems by inducing a significant shift from above- to below-ground biomass production. The intensified allocation of resources to roots and storage organs turns out to be a successful acclimation strategy of alpine plants when exposed to drier conditions. This strategy allows them to escape the damaging consequences of a drought by surviving the adverse conditions below the ground and to quickly recover afterwards when conditions become favourable again. These findings clearly emphasise the key role of below-ground biomass in alpine grassland to resist and recover from summer droughts. The fact that the overall production has not been restricted during the drought periods points to the resistance of these ecosystems under changing environmental conditions.

Bringing together the outcomes of the drought experiment, this thesis supplies evidence that alpine grassland systems are unexpectedly responsive to drier conditions in the short term, leading to changes in resource allocation, which in turn has implications on above-ground vegetation structure. These responses seem to be part of acclimation mechanisms to endure the droughts and to recover subsequently and contribute to the resistance and resilience, and thus stability, of alpine grassland ecosystems. The key ecosystem service of alpine grassland, i.e. slope stability, could be largely maintained. Although above-ground responses in vegetation structure indicated a higher erosion risk, below the ground, the rooting density was increased significantly, leading to a higher soil stability and thus lower landslide risk. This below-ground response counteracted the above-ground responses and suggests that the slope stability may not be jeopardised after prolonged summer droughts in the future.

Study 3 assessed thermal surface (plant canopy) and soil (root zone) conditions across topographically rich alpine landscapes with low stature grassland vegetation by thermal imagery techniques and miniature data loggers at different spatial resolutions. The study revealed substantial variation
in both surface and soil temperatures on several scales (among slopes, within slopes and within plots). The diverse micro-climates that occurred on alpine grassland slopes were mainly caused by micro-topography. The recorded actual habitat temperatures allowed a precise description of the current micro-habitats and thus real life conditions. Hence, this survey demonstrated that meteorological data from weather stations, captured 2 m above the ground, are clearly unable to reflect the complex thermal patterns of low stature alpine grassland vegetation. To quantify the effects of spatial sampling resolution on current micro-habitat distributions and habitat loss due to climate warming scenarios, the spatial resolution of the temperature data was artificially manipulated. Simple predictions of the habitat conditions under warmer climates revealed that the spatial resolution of sampling strongly biased the outcome of any prediction of climate warming. For example, under a 2 K warming scenario, less than 10% of the current micro-habitat conditions (climate space) disappeared from a slope, when based on the high resolution data (1 × 1 m), while at a lower resolution (100 × 100 m) more than 60% were predicted to disappear. Thus, a reduction of the spatial sampling resolution clearly lead to an underestimation of the current habitat diversity and predicted a much higher habitat loss in a warming scenario.

This study confirmed that habitats in the alpine zone are in fact more suitable for organisms to cope with climatic change than had commonly been assumed. It predicted that future warming will only lead to moderate elevational migration needs for cold-adapted plant species in the alpine zone because species have the opportunity to utilise the diverse micro-habitats occurring within the grassland slope. They may move horizontally to occupy colder niches instead of migrating upwards to higher elevations.

This doctoral thesis concludes that alpine grassland ecosystems are characterised by a high stability, when exposed to climate change. This implies that these ecosystems have the capacity to maintain their structure and function under changing environmental conditions. Furthermore, this thesis concludes that this high stability of alpine grassland will be a decisive property of these ecosystems to ensure a long-term integrity under the predicted climate change.
3 Zusammenfassung


Mit den Ergebnissen des Trockenheitsexperiments liefert diese Doktorarbeit Beweise, dass alpine Graslandsysteme unerwartet schnell auf trockenere Bedingungen reagieren können, indem sie ihre Ressourcenallokation anpassen, was Auswirkungen auf die oberirdische Vegetationsstruktur hat. Diese Reaktionen scheinen Bestandteil von Anpassungsmechanismen zu sein, um Trockenheiten zu

In der Studie 3 wurde die Oberflächen- und Bodentemperatur (Temperatur im Bereich des Blattwerks und der Wurzelzone) von niedrigwüchsiger Graslandvegetation in topografisch vielfältigem alpinem Gelände präzise erfasst. Die Temperatur wurde einerseits mit Thermografie und andererseits mit kleinen Temperaturdatenloggern in unterschiedlicher räumlicher Auflösung gemessen. Die Studie zeigte, dass eine deutliche Variabilität sowohl in der Oberflächen- als auch Bodentemperatur bei Anwendung unterschiedlicher Massstäbe (zwischen den Hängen, innerhalb der Hänge, innerhalb der Plots) vorhanden war. Die zahlreichen Mikroklimata, welche an einem alpinen Graslandhang vorhanden waren, wurden hauptsächlich durch die Mikrotopografie verursacht. Die aufgenommenen tatsächlichen Habitattemperaturen ermöglichten eine präzise Beschreibung der gegenwärtigen Mikrohabitate und damit der wirklichen Lebensbedingungen in den alpinen Rasen. Diese Studie beweist, dass meteorologische Daten, die 2 m über dem Boden mit Wetterstationen gemessen wurden, zur Beschreibung der komplexen Temperaturverhältnisse in niedrigwüchsiger alpiner Graslandvegetation sehr ungeeignet sind. Um die Auswirkungen des räumlichen Beprobungsmusters auf die aktuelle Mikrohabitatverteilung und einen möglichen Habitatverlust unter Verwendung von Klimaerwärmungsszenarien zu analysieren, wurde die räumliche Auflösung der Temperaturdaten künstlich manipuliert. Einfache Voraussagen über die Habitatbedingungen bei wärmeren Klimata ergaben, dass die räumliche Auflösung der Beprobung die Vorhersageergebnisse bei sämtlichen Erwärmungsszenarien stark beeinflusste. Zum Beispiel ergab ein 2 K Erwärmungsszenario, dass weniger als 10% der aktuellen Mikrohabitatsituationen (Klimaraum) von einem Hang verschwanden, wenn die Berechnung mit den hochaufgelösten Daten (1 x 1 m) durchgeführt wurde, wobei bei niedrigerer Auflösung (100 x 100 m) mehr als 60% Habitatverlust vorausgesagt wurde. Eine Reduktion der räumlichen Beprobungsauflosung hatte also zu einer Unterschätzung der aktuellen Habitatvielfalt und zu einer deutlichen Überschätzung des Habitatverlustes bei Erwärmung zur Folge. Diese Studie bestätigt, dass Habitats in der alpinen Höhenstufe bei einem sich wandelnden Klima tatsächlich besser geeignet sind für Organismen als bisher allgemein angenommen wurde. Die Studie lässt ver-
muten, dass kälteangepasste Pflanzenarten in der alpinen Höhenstufe bei einer zukünftigen Erwärmung kaum auf eine Höhenmigration angewiesen sind, da sie die Möglichkeit haben, die zahlreichen Mikrohabitate innerhalb des Graslandhangs zu besiedeln. Sie können horizontal ausweichen und kühlere Nischen besetzen anstelle einer Migration in höhergelegene Höhenstufen.

Diese Doktorarbeit belegt, dass sich alpine Graslandökosysteme bei Klimawandel durch eine hohe Stabilität auszeichnen. Das bedeutet, dass diese Ökosysteme ihre Struktur und Funktion bei sich verändernden Umweltbedingungen aufrechterhalten können. Diese Doktorarbeit zeigt zudem auf, dass diese hohe Stabilität von alpinen Rasen unter dem erwarteten zukünftigen Klimawandel eine entscheidende Rolle spielen wird, um eine langfristige Unversehrtheit dieser Ökosysteme zu gewährleisten.
4 General introduction

4.1 High elevation life zone

4.1.1 Life conditions

The life conditions in high elevation ecosystems are dominated by a strongly varying topography and an extremely harsh climate, forcing plants and animals to a high degree of specialisation and adaptation (Billings & Mooney 1968, Körner & Larcher 1988, Körner 2003a). High elevation site conditions are characterised by the occurrence of a variety of stress factors (Landolt 2003, Reisigl & Keller 1994, Körner 2003a). Abiotic stress at high elevation sites can be induced by the following constraints:

- low average temperature
- frost
- strong heating
- strong temperature fluctuations
- low air humidity
- low air pressure
- high irradiance (in particular in ultraviolet radiation)
- strong winds
- nutrient deficiency
- poor soil development
- excess soil moisture
- drought (only on steep scree slopes, cliffs and ridges, otherwise negligible)
- high percentage of rock and scree
- landslides
- falling rocks
- prolonged snow cover and thus a short growing season

As can be seen from this compilation, climatic and edaphic stress factors predominate, but also mechanical impacts play a role. Biotic stress, and in particular such of anthropogenic origin, plays a minor role in the high elevation life zone. However, in alpine grassland, grazing and trampling by domestic and wild herbivores may reach a stress-causing intensity.
4.1.2 Climate

The climate refers to the average meteorological conditions and the usual weather pattern at a particular location (Larcher 2003). The macro-climate relates to a large area and forms the basis for the characterisation of regional climates. The macro-climate is recorded with a network of meteorological stations. The measurements are taken 2 m above the ground. The micro-climate is the characteristic climate at the place, where plants grow. Thus, it is the climate plants directly experience. It is measured on individual plant organs (e.g. on the leaf surface) or in the vegetation (e.g. in the canopy, on the soil surface or in the soil).

With increasing elevation, the climate gets harsher and the growing seasons shorter. The climate in high elevation mountainous terrain differs from the climate in low elevation by lower atmospheric pressure, lower air temperature, higher irradiance on clear days, stronger and more frequently occurring wind, lower air humidity, higher evaporation, higher precipitation and longer duration of snow cover. In high elevation, abrupt changes in climate over relatively short distances are common and form a multitude of different micro-habitats (Körner 2003a). The micro-climatic situation for mountain plants usually strongly deviates from the macro-climate (Reisigl & Keller 1994). Often, plants profit from favourable micro-habitats (e.g. sub-nival plants in protected rock crevices) and thus are able to grow in higher elevation as they would do under macro-climatic conditions. On the other hand, the micro-climate also can lead to a higher stress exposure, e.g. at wind-exposed cliff edges.

The micro-climate depends on three main components: solar radiation, relief (inclination and aspect) and plant stature (Körner 2003a). Furthermore, it is influenced by wind velocity, ambient air temperature above the vegetation and soil properties such as surface structure, soil moisture and thermal conductivity. An interaction between the relief and the directional climatic factors radiation and wind results in an enhanced or reduced force of the corresponding climatic vector. The inclination and aspect of an area determine the orientation towards the sun and thus influence the irradiance and its consequences. An indirect effect of the relief is the interception of solar radiation leading to a certain degree of shading at a particular location. In peak, ridge, hilltop or edge positions, the full wind force takes effect, whereas depressions, rock ledges or crevices provide protection against wind.

In addition, the plants themselves influence the micro-climate by their stature, leaf arrangement, height above ground, and canopy surface roughness. For example, plants influence temperature, air humidity or wind speed to their benefit (Larcher 2003, Körner 2003a). In doing so, plants with low
stature growth forms (such as tussocks, rosettes, cushions) are most successful in generating their favourable own climate.

4.1.3 Vegetation and elevational zonation

In the high elevation tree line ecotones, the trees reach their upper distributional limits (Körner 2012). This life form boundary marks the transition from the low to the high elevation life zone. High elevation life zones occur globally and are not only restricted to the European Alps. 16.5 mio km$^2$ or 12.3% of all terrestrial land area outside Antarctica are mountains and 21.5% of this mountainous terrain (3.55 mio km$^2$ or 2.6% of the global land area outside Antarctica) is situated above the climatic tree line and thus represents the high elevation life zone world-wide (Körner et al. 2011).

Above the climatic tree line, tall-growing trees and shrubs are replaced by low stature plants. Slow-growing and cold-adapted plant species, able to cope with low nutrient availability and extreme climatic conditions are dominating alpine ecosystems. Typically, high elevation ecosystems have retained largely natural vegetation. The small-scale changes in the micro-climate, together with the changing edaphic conditions explain the high biological diversity in these ecosystems (Körner 1995). For example, the flora of the European Alps includes 4500 vascular plant species (Aeschimann et al. 2004). Perennial herbaceous plant species (forbs), often forming rosettes, and graminoids such as grasses and sedges, mostly forming tussocks, which together represent the “hemicryptophyte” category are dominating and characteristic for all high elevation floras (Körner 2003a). Other typical growth forms of high elevation plant species are:

- low stature or prostrate woody shrubs
- cushion plants of various types
- geophytes
- succulents
- annuals (sometimes biennials), which become quite rare at high elevations
- cryptogams, i.e. mostly desiccation-tolerant, non-flowering plants such as bryophytes (mosses) and lichens, in some areas also ferns and lycophodioids

With increasing elevation, a change of vegetation is evident and results in a characteristic elevational zonation. Belts of similar vegetation exist at similar elevation. In the European Alps, three zones can be distinguished: the alpine, sub-nival and nival zones (Fig. 4.1). The specific position of the transitions between the zones is determined by the local climate (primarily by the temperature), and hence differs depending on the location. In the Northern Prealps, the transitions are generally locat-
ed in lower elevation than in the Central Alps. Furthermore, they are generally situated lower on the northern compared to the southern slopes (Fig. 4.1).

The alpine zone is characterised by closed low stature vegetation. It ranges from the climatic tree line (in the Central Alps at about 2200 m a.s.l.) upwards to the point where vegetation becomes discontinuous and fragmented (at about 2800 m a.s.l., Fig. 4.1). The alpine zone is dominated by natural grassland vegetation, but encompasses also snowbed, fen, tall-herb, dwarf shrub, rock and scree vegetation. Depending on the site conditions (bedrock type, soil acidity, slope inclination and aspect, nutrient and water availability), a multitude of different natural sward communities with characteristic species compositions are formed (Reisigl & Keller 1994, Ellenberg & Leuschner 2010, Braun-Blanquet 1948/1949, Landolt 2003).

The sub-nival zone follows above the closed alpine vegetation and reaches in the Central Alps from about 2800 to 3200 m a.s.l. (Fig. 4.1). An extensive plant colonisation is restricted and only a few plant species are sufficiently specialised and adapted to cope with the demanding life conditions in this zone. The vegetation is highly fragmented and consists of patchy grassland, cushion plants, mosses and lichens. Snow is found in this zone during most of the year.

The climatic permanent snow line is the line above which snow and ice cover the ground throughout the year. It marks the lower boundary of the nival zone, which reaches up to the summits. The snow line is situated at about 3200 m a.s.l. in the Central Alps (Fig. 4.1). Vascular plants are very rare in this zone and the occurrence of isolated individuals of highly specialised species is restricted to only the most micro-climatically favourable snow-free locations. Only some individual cushion plants and patches of mosses and lichens represent the vegetation in this harsh environment. The highest-located flowering plant ever recorded in Europe was discovered at 4507 m a.s.l. on the Dom summit in the Swiss Central Alps (Körner 2011). Several individuals of Saxifraga oppositifolia forming cushions were found there at protected locations on solid siliceous rock.
Figure 4.1  Elevational zonation of vegetation in the European Alps. The high elevation life zone is situated above the climatic tree line. In the Central Alps, it can be divided into the alpine, sub-nival and nival zones. In the Northern Prealps, the nival zone is missing. The alpine zone is bordered by the tree line at the bottom and the upper edge of closed vegetation at the top. Modified from Lauber et al. (2012).
4.2 Alpine grassland

4.2.1 Sward communities in the drought experiment

Naturally forest-free habitats are rare in Central Europe, and most of the grassland in low elevation developed after deforestation. This is not the case in alpine ecosystems. Alpine swards, also called ancient swards, belong to the natural grassland and have originated without any anthropogenic influences. The two sward communities examined in the drought experiment, the *Sesleria caerulea* and *Carex curvula* swards, shape widespread natural grassland vegetation and therefore represent the prevailing sward communities in the alpine zone (Ellenberg & Leuschner 2010). The swards are usually located on steep mountain slopes with up to 40° inclination and consist of perennial sward-forming hemicyryptophytes, chamaephytes and heliophilous cryptogams. Graminoids such as grasses and sedges, mostly forming tussocks, are dominating.

The *Sesleria caerulea-Carex sempervirens* sward (Seslerio-Caricetum sempervirentis, or Seslerietum for short) is formed on calcareous bedrock and dominated by the graminoids *Sesleria caerulea* (Blue sesleria) and *Carex sempervirens* (Evergreen sedge). In addition, plant species such as *Anthyllis vulneraria* ssp. *alpestris*, *Aster alpinus* and *Helianthemum nummularium* ssp. *grandiflorum* are characteristic in this sward. Most of the plant species are calciphilic. *Sesleria caerulea* swards are multicoloured and species-rich (Reisigl & Keller 1994). The *Sesleria caerulea* swards evolve directly on calcareous scree, and therefore the soils are poorly developed and shallow. The swards are always slightly terraced and some of them are susceptible to solifluction and erosion. The topsoil of *Sesleria caerulea* swards on steep south facing slopes may temporarily dry out, but the two dominant species in these swards survive such events without any enduring damage (Ellenberg & Leuschner 2010).

The *Carex curvula* sward (Caricetum curvulae, or Curvuletum for short) is formed on siliceous bedrock and dominated by the sedge *Carex curvula* (Curved sedge), which is accompanied by *Helicotrichon versicolor*, *Trifolium alpinum*, *Leontodon helveticus* and *Homogyne alpina* as characteristic plant species. Often, the swards consist of a high proportion of lichens. The swards develop exclusively on acidic substrates and hence contain acidophilic, often calciphobic plant species. The *Carex curvula* swards are not as colourful and diverse as the *Sesleria caerulea* swards. The olive-brown, never green leaves of *Carex curvula*, with the curved leaf tips often turning brown because of infection by the fungus *Clathrospora elynae* and other endophytes, let the swards appear monotonous. The soils, on which the *Carex curvula* swards evolve, are more developed and deeper than those of the *Sesleria caerulea* swards. They are as nutrient-poor, but not as dry as at climatically similar sites on calcareous bedrock (Ellenberg & Leuschner 2010). This means that sites with *Carex curvula*
swards generally contain more moisture than sites with *Sesleria caerulea* swards and hence are less drought-prone.

### 4.2.2 Ecosystem services of alpine grassland

Alpine grassland ecosystems deliver several ecosystem services such as slope stability, water provision and quality, forage quantity and quality, carbon sequestration, conservation of botanical diversity and aesthetic value of landscape (Lamarque et al. 2011). For most of these services, plant growth and thus biomass productivity, but also vegetation structure of alpine grassland plays a decisive role. Therefore, a drought-induced change in the biomass productivity and vegetation structure could compromise the provision of these services.

Generally, a relatively high natural erosion risk exists on alpine slopes due to the steepness of the terrain, geological conditions, shallow soils and the often sparse vegetation. The most important service of alpine grassland vegetation is to ensure the protection of alpine soils on steep slopes by preventing erosion and landslides, and thus, to secure slope stability (Körner 2003a). On slopes, soils persist only as long as vegetation persists and vegetation integrity rests upon an adequate ground cover and intact root system. Hence, both above- and below-ground biomass pools are relevant to ensure slope stability. A reduction in the above-ground biomass pool results in an increased area of bare ground and consequently a decreased ground protection and higher erosion risk, whereas a reduction in the below-ground biomass pool leads to a decreased rooting density involving a decreased soil stability and higher landslide risk, both changes negatively influencing the slope stability. Summer droughts may change the above- and below-ground biomass pools of the swards and thus the structural parameters of the vegetation in such a way that the alpine grassland sites become more susceptible to erosion and landslides. As heavy rainfall events are predicted to occur more frequently in the future, erosion is likely to be enhanced at alpine grassland sites, which will be damaged by summer droughts. Thus, slope stability as an ecosystem service may be jeopardised after prolonged summer droughts and therefore may play a key role at such sites under a future climate.

### 4.3 Study sites

#### 4.3.1 Albula and Furka Pass

The three studies presented in this thesis all focus on the alpine zone of the Central Alps (Fig. 4.1). The climate change experiment investigating the impact of a drier summer climate on alpine grass-
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land (Studies 1 and 2) was conducted in the centre of the alpine zone at about 2500 m a.s.l., whereas the observations to describe the habitat temperatures of low stature alpine vegetation (Study 3) were made across the entire elevational gradient of the alpine zone (see Fig. 4.1).

The sites and areas of the three studies were located in two regions: at Albula Pass, Grisons (46°35’ N, 9°50’ E) and Furka Pass, Valais (46°34’ N, 8°25’ E), both situated in the Swiss Central Alps (Fig. 4.2). The climate at this elevation is characterised by cold winters with permanent snow cover followed by short summers limiting the growing season to about 75 days (from late June to mid-September). Both regions have a similar mean annual temperature (-2.2 °C at Albula Pass and -2.1 °C at Furka Pass, ETH Zurich et al. 2004), but significantly differ in the mean annual precipitation (845 mm at Albula Pass and 1920 mm at Furka Pass, ETH Zurich et al. 2004) and monthly distribution of rainfall (Figs. 4.3 and 4.4). In addition, the regions considerably differ in the frequency of high intensity rainfall events (days with precipitation > 70 mm d⁻¹: Albula Pass 10–20 d, Furka Pass 50–100 d, ETH Zurich et al. 2004).

The experimental site at Albula Pass was situated on the Ela Nappe, which is part of the Upper Austroalpine and consists of calcareous sediments (Bearth et al. 1987). Main Dolomite, Dolomite and Allgäu Schist are the most represented rocks in this area. The swards on the slopes are formed on calcareous scree material, which originates from calcareous bedrock, located at the upper edge of the corresponding slopes. The Furka Pass is situated in the geologically interesting Ursern Zone, which is characterised by a multitude of rocks and minerals (Labhart 2004). The zone is located between the Gotthard and Aare Massif. The Furka Pass area is dominated by siliceous rocks (granite, gneiss, clay and quartzite layers). The vertical Piora Layer, which crosses the Furka area from East to West, consists of sedimentary rocks and yields calcareous substrate. Although calcareous bedrock occurs only in a very small area, a site was found providing enough area for 12 experimental plots. The contrasting geology was essential for the site set-up of the drought experiment. Calcareous vs. siliceous bedrock leads to different species compositions of the swards, as well as different edaphic conditions, which both may impact the response of the vegetation to drought.

The two regions have been selected because they represent ideal conditions to test the effects of extreme climatic events under widely differing climatic and geologic conditions that occur in the Swiss Alps. In addition, their selection was based on the availability of suitable grassland plots for the drought experiment, on data availability from former long-term scientific engagement, offering excellent base-line information on vegetation composition, micro-climate and ecosystem processes, and on suitable infrastructure in close vicinity to the experimental locations (lab and office space, telecommunication, accommodation etc.). At Albula Pass, the Department of Environmental Systems Science, ETH Zurich runs a research station (Alp Weissenstein) and a complete vegetation mapping
and determination of plant functional traits has been performed (Schmid 2007). At Furka Pass, the Institute of Botany, University of Basel, runs a research station (ALPFOR) and has performed a variety of projects that yield highly relevant information, including a CO₂ enrichment experiment (Körner et al. 1997).


4.3.2 Experimental sites and observational areas

The drought experiment (including Studies 1 and 2) was established at three characteristic grassland sites with contrasting conditions in macroclimate and geology: (1) a site at Albula Pass with low precipitation and calcareous bedrock, (2) a site at Furka Pass with high precipitation and calcareous bedrock, and (3) a site at Furka Pass with high precipitation and siliceous bedrock. The sites were located on steep mountain slopes representing the predominant landform at this elevation. The slopes with calcareous bedrock were characterised by a 30° inclination and a southern aspect and the one with siliceous bedrock by a 40° inclination and a western aspect. The vegetation at the three sites consisted of typical alpine grassland communities: two Sesleria caerulea-dominated swards (Seslerio-Caricetum sempervirentis) on calcareous bedrock and a Carex curvula-dominated sward (Caricetum curvulae) on siliceous bedrock. Most of the plant species at the three grassland sites were perennial, and many of them were able to form below-ground storage organs. Grazing by domestic and wild herbivores played only a minor role and thus, grazing intensity was very low at the three grassland sites.

Study 3 used observational areas, which were situated in the region at Furka Pass, well above the climatic tree line (which is at c. 2150 m a.s.l. in this region). Within an area of about 2 km² (study area), we chose three steep mountain slopes with NNW (centre at 2500 m a.s.l.), W (2480 m a.s.l.) and SSE (2430 m a.s.l.) exposure. All slopes showed strong variation in micro-topography but no change in macro-exposure and covered elevation ranges of 400–600 m on the NNW and W slope and 200 m on the SSE slope. Within each slope, we defined four 1 m² plots (near the centre) which were used for detailed small-scale measurements. For logistical reasons (power supply, road access and a field station for night measurements), we designated the NNW slope as our core site.
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Figure 4.2  Geographical position of Furka and Albula Pass. F: Furka Pass, A: Albula Pass. General map of Switzerland (swisstopo).

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Figure 4.4 Climate charts of Furka Pass and Albula Pass. Data from ETH Zurich et al. (2004). The line represents mean monthly temperature, bars depict mean monthly precipitation. Numbers below names are mean annual temperature and mean annual precipitation.
4.4 Climate change

4.4.1 Global and regional climate change

In its Fifth Assessment Report, the Intergovernmental Panel on Climate Change (IPCC) states that human-induced climate change is unequivocal and ongoing, with a further increase of global air temperatures and globally changing precipitation regimes (IPCC 2013). Furthermore, in a Special Report, the IPCC points to the higher occurrence of extreme weather events in the future, such as extreme droughts, heat waves or high intensity rainfalls (IPCC 2012). Localised climate change scenarios of mean temperature and precipitation project that Switzerland will experience increased temperatures in all seasons, with a maximum in summer, while precipitation will slightly increase in winter, but strongly decrease in summer towards the end of the 21st century (CH2011 2011, Fischer et al. 2012, Zubler et al. 2014). Additionally, Switzerland is predicted to be subjected to an increased year-to-year variability of the summer climate, so that extreme events such as severe summer droughts might occur more frequently in the future (Schär et al. 2004).

4.4.2 Climate change impacts on plant communities

Consequences of climate change have been documented convincingly for a broad range of organisms, with impacts on phenology, species distributions, community composition and ecosystem structure and function (Walther et al. 2002). Such biological effects may be considered as “fingerprints” of climate change, which are expected to have a greater amplitude at high latitudes and altitudes (Root et al. 2003).

Research on climate change impacts on plant communities mainly applies three approaches: (1) modelling projected species distributions (e.g. Thuiller et al. 2005), (2) document ecosystem changes after natural climate anomalies (e.g. Reichstein et al. 2007), or (3) experimentally manipulating some aspects of predicted atmospheric and subsequent climate change, such as CO₂ enrichment (e.g. Lüschler et al. 2004), warming (e.g. Harte & Shaw 1995), drought (e.g. Kahmen et al. 2005), or rainfall (e.g. Suttle et al. 2007).

Climate change experiments in alpine ecosystems have focused on CO₂ enrichment (e.g. Körner et al. 1997, Inauen et al. 2012), warming (e.g. Henry & Molau 1997), nitrogen deposition (e.g. Bassin et al. 2012), and snow depth and snowmelt timing (e.g. Wipf et al. 2009). However, the response of alpine vegetation to drought has rarely been investigated.
4.4.3 Drought impacts on grassland ecosystems

Research on drought impacts on grassland ecosystems mainly follows two approaches: (1) monitoring the effect of naturally occurring droughts on grassland systems in observational field studies (e.g. Weaver et al. 1935, Gibbens & Beck 1988, Stampfli & Zeiter 2004) or (2) measuring the responses of grassland systems to simulated droughts in field experiments manipulating rainfall amounts. Such experimental field studies were conducted in arid or semi-arid regions, which are regularly exposed to drought conditions (e.g. Sternberg et al. 1999, Köchy & Wilson 2004, English et al. 2005, Schwinning et al. 2005, Yahdjian & Sala 2006, Arredondo et al. 2016), but also in temperate regions, where droughts did not occur frequently so far (e.g. Morecroft et al. 2004, Kahmen et al. 2005, Gilgen & Buchmann 2009, Hartmann & Niklaus 2012, Vogel et al. 2012, Cantarel et al. 2013, Prechsl et al. 2015, Deléglise et al. 2015, Hofer et al. 2016). However, there is a significant lack of experiments simulating droughts in alpine regions and thus, the response of alpine grassland systems to drier conditions has been poorly investigated so far. De Boeck et al. (2016) studied the influence of drought and heat waves on alpine grassland in a short-term experiment. But to our knowledge, no multi-year experiment exists so far, which examined the impact of recurring summer droughts with rainout shelters on grassland in the alpine zone, i.e. above the climatic treeline.

The biomass responses of temperate grassland systems to simulated droughts have been widely studied. In general, the studies yielded consistent results and revealed that drought conditions clearly reduced above-ground productivity, while the allocation of carbon to below-ground organs was enhanced. Alpine grassland systems differ fundamentally from temperate systems by a comparatively low overall annual biomass production and a proportionately large below-ground biomass compartment, with possible implications on the drought responses.

In contrast to temperate grassland systems with a growing season of up to six months (Gilgen & Buchmann 2009), the period with favourable growth conditions in alpine systems lasts only a few months (2.5 months at our study sites). Alpine grassland productivity is in fact not necessarily low, if expressed per unit of growing period duration rather than per year (Körner 2003a). Thus, the low annual biomass production in alpine grassland compared to temperate grassland is due to the short growing season. This suggests that a drought period of the same duration during the growing season may have a stronger impact on the alpine system than on the temperate one, since a drought-induced production loss is proportionately bigger and may hardly be compensated in the current season due to time constraints. In contrast, a temperate grassland system with a much longer growing season is able to largely compensate a production loss after a drought in the ongoing season (Hofer et al. 2016).
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The below-ground biomass compartment, consisting of roots and storage organs, plays a major role in high elevation ecosystems and especially in alpine grassland systems (Körner & Renhardt 1987, Hitz et al. 2001). This large below-ground biomass compartment may have the capacity to better buffer the drought-induced dieback of above-ground biomass in alpine grassland compared to temperate grassland. This allocation pattern suggests that alpine grassland vegetation is optimised for surviving a drought period in the soil and quickly recovering thereafter from below the ground. Both resistance and resilience of grassland vegetation are basic requirements to maintain ecosystem stability when subjected to drought disturbances.

4.4.4 Effects of climate change on alpine ecosystems

The future summer climate in the Swiss Alps is predicted to be drier and warmer (see above). It is expected that alpine vegetation will be influenced by an overall warming and associated changes in precipitation patterns and thus snow cover (Theurillat & Guisan 2001). There is ample observational evidence, which indicates that recent climatic changes have already substantially affected high elevation ecosystems. High elevation vegetation may be a sensitive “ecological indicator” of climate change effects, because of its low biotic complexity (Pauli et al. 2003). In high elevation environments, abiotic factors, in particular climatic constraints, dominate over biotic factors such as competition. This may lead to more pronounced impacts of climate change on vegetation at high elevation, compared to low elevation. In addition, potential signals can be unambiguously related to climate, because they are not masked by effects of human land use, which is largely negligible in these ecosystems. Short-term climatic fluctuations may have weak impacts on alpine vegetation due to the slow growth rates and extended life cycles of alpine plant species (Pauli et al. 1999). However, high elevation vegetation is expected to be sensitive to long-term climate change (Gottfried et al. 1998).

4.4.5 Consequences of a warmer climate in alpine ecosystems

Due to the steep environmental gradients and the reduction in land area with increasing elevation, high elevation environments are supposed to be particularly sensitive to global warming (Beniston et al. 1996, Diaz et al. 2003, Beniston 2006). In addition, temperature change patterns are spatially not uniform, with the European Alps being a hotspot of warming, especially during the last decades (Beniston 2005, Rebetez & Reinhard 2008). The Alps warmed by +1.5 K compared to the global average of +0.7 K during the last century and therefore are often considered as particularly threatened (Beniston et al. 1997, Theurillat & Guisan 2001, Schröter et al. 2005, Nogués-Bravo et al. 2007). Furthermore, most climate warming scenarios predict higher than average future warming in most al-
pine areas (Meehl et al. 2007, Nogués-Bravo et al. 2007). Alpine plant communities may be seen as early indicators of warming impacts (Cannone et al. 2007). It is widely believed that the recent and future climate warming is driving species ranges polewards and towards higher elevations (Beniston et al. 1996, Theurillat & Guisan 2001, Walther 2004, Colwell et al. 2008) and may cause regional species extinctions.

In fact, there is observational evidence of **upslope migration** of plant species in the Alps (Walther et al. 2002, Cannone et al. 2007, Pauli et al. 2007, Lenoir et al. 2008), resulting in increased species richness on mountain summits (Grabherr et al. 1994, Bahn & Körner 2003, Walther et al. 2005, Pauli et al. 2012, Wipf et al. 2013). A large-scale study by Gottfried et al. (2012), including 60 summit sites in all major European mountain systems, confirms a continent-wide response of mountain summit vegetation to a warmer climate. Evidence was found that the more cold-adapted plant species decline in abundance, while the more warm-adapted species increase, a process described as **thermophilisation**. At the continental scale, a significantly higher abundance of thermophilic species was found in 2008, compared with 2001. This observed transformation in summit regions suggests a progressive loss of cold mountain habitats and thus a challenge for cold-adapted plant species. In the long term, warming may result in local extinctions of cold-adapted species due to the losses of their habitats, but also due to invading taller species from lower elevations outcompeting them.

In contrast to these observed responses to a warmer climate in the sub-nival and nival zones in the last decades, there is also evidence for substantial resistance to climatic forcing in plants living in high elevation and inhabiting the same location over thousands of years (Steinger et al. 1996, De Witte & Stöcklin 2011, De Witte et al. 2012). The large-scale study by Grytnes et al. (2014), using data on observed upward shifts in the upper range limit of alpine plants on 114 European mountains, does not support the hypothesis that climate warming is the dominant factor causing the observed elevational range shifts of alpine plant species. This conclusion arises from the fact that the extent of change in species assemblages on the summits was not statistically related to the extent of climate warming, and those species that moved upwards were not particularly warmth demanding. At this point, it has to be mentioned that most of the observations of elevational species shifts originate from the sub-nival and nival elevational zones. Due to the lack of appropriate historical reference data, weak empirical evidences on recent upward migrations exist for the sub-alpine and alpine zones of the Alps (Pauli et al. 2003).

habitat conditions with occurrences of a species (Guisan & Thuiller 2005, Araújo & Guisan 2006). Strong impacts of climate change on biodiversity and species abundance have been predicted (Bakkenes et al. 2002, Thuiller et al. 2005), especially in mountain ranges.

Yet, the predicted habitat loss in mountainous regions strongly depends on model selection (Araújo et al. 2005, Algar et al. 2009) and the spatial resolution of the SDMs (Trivedi et al. 2008, Randin et al. 2009). Scherrer & Körner (2010) showed that in alpine landscapes there is substantial variation in actual plant surface and soil temperature within 1 km² test areas, not reflected in the commonly referred to 2-m-above-ground air temperature. The thermal mosaic created by micro-topography, in fact, offers suitable habitats for many species with different thermal preferences requiring hardly any migration for a 2 K warming scenario (Scherrer & Körner 2011). This results from both geo-diversity (topography) as well as aerodynamic decoupling of low stature alpine vegetation from atmospheric conditions at a centimetre scale (Körner 2003a). Most models work on interpolated weather station data at much larger scales, with the noteworthy exception of an attempt for a small-scale resolution by Randin et al. (2009). Although not based on actual plant temperatures, this study revealed the significance of scale. Given the key role of spatial sampling resolution of climatic conditions to describe patterns of current micro-habitats, fact-based life conditions need to be assessed, the aim of Study 3 presented in this thesis.

4.4.6 Consequences of a drier climate in alpine ecosystems

Precipitation inputs increase with increasing elevation in the European Alps (Frei & Schär 1998, Ellenberg & Leuschner 2010). Hence, alpine vegetation is commonly less constrained by moisture deficiency than vegetation at lower elevations, and local water shortages occur only temporarily (Körner 2003a). In the last centuries, long-lasting severe summer droughts have been very rare in alpine ecosystems (Van der Schrier et al. 2007), but alpine regions are predicted to experience increases in the frequency and intensity of droughts in the near and long-term future (Gobiet et al. 2014). Here, the question arises how alpine grassland ecosystems will respond to altered precipitation regimes, and particularly to prolonged summer droughts. It is unclear how stable these ecosystems are, when exposed to such climate extremes, which did not occur so far. During the growing season, the limiting site factor for biomass productivity of alpine grassland is the availability of nutrients, in particular the supply of enough plant-available nitrogen. Furthermore, if summer droughts will become more frequent, water availability could be restricted temporarily leading to a water shortage. In addition to direct effects of water deficiency causing physiological drought stress, a water shortage may also have indirect effects such as a restriction of the nitrogen availability (through reduced decomposi-
tion and mineralisation) or a reduction of the transpirative cooling capacity, leading to nutrient and heat stress, respectively. All these drought-induced effects may co-limit plant growth and thereby reduce the productivity and thus the biomass production of alpine grassland. It is unclear how recurring summer drought events of different severity affect alpine grassland biomass production above and below the ground. The biomass responses to drought might vary dependent on local environmental conditions such as geology or macroclimate and might change over time. Studies 1 and 2 of this thesis aim at experimentally examining the influence of recurring summer droughts on alpine grassland.

4.5 Plant stress

4.5.1 Conceptions of stress

In plant ecology, different conceptions of plant stress exist. Grime (2001) divides the “external factors” that limit plant biomass into “stress” and “disturbance”. He defines stress as “the external constraints which limit the rate of dry matter production of all or part of the vegetation” (p. 48) and disturbance as “the mechanisms which limit the plant biomass by causing its partial or total destruction” (p. 80). Thus, he differentiates between long-term external influences, which affect photosynthetic production and hence growth of a plant (such as shortages of light, water and mineral nutrients, or sub-optimal temperatures) and short-term external impacts, which result in a partial or total destruction of existing plant material (such as grazing, mowing, trampling, wind, frost, drought and fire). According to his concept, the impact of low rainfall on plants can be associated with either stress or disturbance. It is necessary to distinguish whether the lack of water constantly reduces the productivity or abruptly destroys plant material leading to a die-back of vegetation. Whether low rainfall results in stress or in disturbance depends primarily on the constancy of the occurrence, but also on the severity of the water shortage (Grime 2001).

Larcher (2003) defines stress as “the manifold unfavourable but not necessarily immediately lethal conditions occurring either permanently or sporadically in a locality” (p. 345). In his concept, he does not clearly distinguish between stress and disturbance. He divides the environmental constraints into abiotic and biotic stress factors. Abiotic factors include edaphic and climatic influences related to water, minerals, radiation, temperature and gases as well as mechanical impacts. Biotic factors include influences caused by plants, micro-organisms and animals as well as anthropogenic impacts. Stress affects all functional levels of an organism. The induced changes and responses may be reversible initially, but they may also become permanent. Non-specific effects of stress are alterations
in membrane properties, increased respiration, inhibition of photosynthesis, reduced dry matter production, growth disturbances, lower fertility, and premature senescence. The longer the plant is exposed to stress, the weaker becomes its vitality. A plant is able to adjust to some extent, but when a certain limit is reached, latent damage develops into chronic disease or irreversible injury.

Lichtenthaler (1996) defines stress as “any unfavourable condition or substance that affects or blocks a plant’s metabolism, growth or development” (p. 4). He differentiates between short- and long-term stress impacts as well as between moderate and extreme or chronic stress events. Thus, plant and vegetation stress is determined by both, the duration and intensity of the impact of the stress factor. Physiological and morphological adaptations allow plants to cope with stress up to a certain severity. As soon as the stress exceeds the adaptive capacity, plants suffer from acute and permanent damage or even die.

Körner (2003b) does not provide a clear definition of stress. He considers “stress” as, in part, a synonym for resource limitation (e.g. water shortage), and in part, a general term for physical impacts (e.g. temperature, mechanical forces). He associates stress with limitation. But he adds for consideration that, from an ecological point of view, the concept of limitation is problematic. Cold-adapted alpine vegetation is not cold-limited. Once, the ability to cope with low temperatures has evolved, such an environmental extreme has become an element of normal life (Körner 1999). And the low biomass production of the cold-adapted alpine plants does not imply that a limitation exists. As long as they are able to grow and reproduce in their habitat, they are fit and thus not limited. A limitation exists only if such plants become extinct due to a lack of fitness, i.e. because they are unable to successfully reproduce. In fact, alpine vegetation is dependent on low temperatures and warming may threaten these highly adapted and specialised species, a topic of this thesis. In a warmer environment, which might be from our human perspective a less stressful habitat, most local species would either die, or be outcompeted by invading species.

### 4.5.2 Drought stress

A drought is a period with reduced rainfall, during which the water content of the soil is shortened to such an extent that plants suffer from water deficiency (Larcher 2003). Drought stress, the adverse effect of a water deficit, does not occur abruptly, but develops slowly during the drought and increases in intensity the longer the drought lasts. Thus, the duration of the period with drought conditions plays an important role in the survival of drought stress. The time of greatest need of water for plants is during their growing season and therefore, droughts coinciding with the growing season are most detrimental to plant life.
Survival of both drought and frost requires cell membranes which can tolerate dehydration (Körner 2003a). Alpine plant species are able to survive low temperatures, i.e. they are cold-adapted. This suggests that they innately embody also a drought resistance to a certain extent. Plants that are specialised in living on nutrient-poor, shallow soils, grow slowly and are often small (Larcher 2003). In the case of an inadequate water and nutrient supply, as could happen during a summer drought, the low productivity may enable them to maintain sufficient concentrations of mineral elements and an adequately high tissue water potential. Also in this respect, alpine plant species may inherently be equipped with a certain drought resistance.

4.5.3 Physiological responses during drought stress

At cellular level, the first and most sensitive response to water deficiency is a decrease in turgor and a cell growth inhibition (Larcher 2003). In addition, protein metabolism, synthesis of amino acids, and activity of nitrate reductase are soon impaired. Water stress also affects mitosis and meiosis and thus meristematic growth and pollen development. A water deficit triggers the synthesis of the plant hormone abscisic acid in the roots, which is then transported to the leaves, where it initiates stomatal closure and thus a limitation of gas exchange and inhibition of photosynthesis. If water deficiency continues, other hormones are released and induce a change in the allocation of assimilates, an altered ratio of root to shoot growth, a development of characteristic morphological features such as denser hairiness, and changes in reproductive processes. Increasing dehydration leads to an accelerated senescence and older leaves dry out. The accumulation of low-molecular organic substances in the cell promotes the osmotic influx of water and thus helps to delay the loss of turgor in the mesophyll of leaves. As soon as the turgor can no longer be maintained, plant cells shrink (cytorrhysis) and cell compartments become deformed. This becomes visible by the wilting of the leaves. In a further step, the biomembranes of the cell compartments disintegrate and subsequently, the cell dies.

4.5.4 Survival of drought stress

The capacity of plants to survive dry periods is drought resistance. Levitt (1980) divides the strategies of plants to cope with stress in “stress escape”, “stress avoidance” and “stress tolerance”. In the case of counteracting drought stress, these strategies are “escaping drought”, “avoiding desiccation” and “tolerating desiccation” (Larcher 2003).
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**Drought escape** Drought-escaping plants are not truly drought-resistant. They grow and reproduce in a period when sufficient water is available. They survive the drought by an appropriate timing of the formation of seeds or perennating organs, which are protected from desiccation. Geophytes e.g. have below-ground storage organs such as rhizomes, tubers or bulbs, which store carbohydrates and water. They are able to quickly resprout by using stored carbohydrates in a rainy period after a drought. For such species it is essential to quickly flower and develop seeds within a very short period of time, when conditions are favourable again. Alpine grassland consists to a large proportion of hemicryptophytes with rhizomes and other below-ground storage organs. This predominant life form in alpine grassland may be an important advantage to survive droughts.

**Desiccation avoidance** Plants that avoid a desiccation are able to delay a harmful decrease in the water potential of the protoplasm despite dry conditions (Larcher 2003). They are capable of maintaining an adequate tissue water content as long as possible and thus sustaining the plant water status. Desiccation avoidance can be achieved by an enhanced water uptake from the soil, by a reduced water loss by transpiration, or by the storage of water in plant tissue.

An extension of the root system leads to an **improved water uptake**. In alpine soils, rooting depth is limited due to shallow soils and a growth into deeper soil layers may be largely impossible. But also an increase in rooting density in the upper soil layer may result in an improved water uptake and especially graminoids are able to develop a very dense root system. During drought exposition, the root-shoot ratio may be shifted in favour of the roots to forage larger soil volumes for water.

A **reduced transpiration** prevents an extensive water loss. Plants are able to temporarily close the stomata. Especially alpine plants have developed a multitude of morphological adaptations to reduce transpiration (Landolt 2003, Körner 2003a, Reisigl & Keller 1994), such as low stature growth forms (tussocks, rosettes, cushions), small and rolled leaves, leaves protected by hairs, cutinised epidermises and wax layers, leaves with a higher stomatal density on the bottom side and small stomata, often hidden in depressions or covered with hairs.

Another mechanism to avoid desiccation is **water storage**. Plants that store water in specialised tissue are called succulents. Several alpine plants, which are adapted to shallow soils that dry out soon, show a high degree of succulence.

**Desiccation tolerance** Most plants have a protoplasm that is highly responsive to water loss, making them desiccation-sensitive. On the other hand, a desiccation-tolerant plant is characterised by a protoplasm that can dry out without becoming damaged and thus tolerates a severe loss of water (Larcher 2003). Protection mechanisms stabilise the cell structure of such plants with increasing dehydration. To survive an extreme degree of cellular dehydration, these plants remain in an anabiotic
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state, in which their metabolism is almost at a standstill. The capacity of the protoplasm to tolerate dehydration varies over a wide range and is species-specific. Several species of the cryptogams endure severe desiccation. Lichens e.g. can withstand long periods without water in a completely dehydrated state and resume metabolic activity as soon as they are moistened again. Also various mosses are capable of sustaining complete desiccation. In addition, most of the mosses and lichens preserve their pigments during drought and are able to quickly resume photosynthesis after it. The bristly leaves of graminoids and the coriaceous leaves of dwarf shrubs both are morphological adaptations of alpine plants to maintain the stability of the leaves under dry conditions and thus to tolerate desiccation. Graminoids, mosses and lichens can make up a high proportion of the biomass of alpine grassland and thus may contribute to a desiccation tolerance of this vegetation.

4.6 Drought experiment

4.6.1 Experimental design

To assess the impact of a drier summer climate on alpine grassland ecosystems we simulated summer droughts with rainout shelters in a field experiment. This drought experiment was based on a multi-site multi-year approach. It was conducted at three sites in the Swiss Central Alps during the growing seasons of three consecutive years. An essential element of the site set-up was that the sites differed in the macroclimate (low vs. high annual precipitation resulting in a continental-dry vs. temperate-moist climate) and geology (calcareous vs. siliceous bedrock leading to different edaphic conditions and thus different sward communities, Fig. 4.5). This site set-up allowed to test for the effect of drought on alpine grassland under the widely differing environmental conditions that occur in the Swiss Central Alps and thus made it possible to draw more general conclusions about the effect of summer drought on alpine grassland. We have chosen one site at Albula Pass (low precipitation), which was situated on calcareous bedrock (referred to as LC site) and two sites at Furka Pass (high precipitation), one on calcareous bedrock (HC site) and another on siliceous bedrock (HS site, Fig. 4.5).

At each of the three sites, twelve $1 \times 1$ m experimental plots were arranged in four replicated units (blocks), each containing three plots. The sward plots have been selected such as to achieve homogeneity in species composition, vegetation structure, micro-topography and rock cover preferably within each site, but necessarily within each block. The experimental treatments included ambient rainfall (control conditions, referred to as CT treatment), six weeks rainfall exclusion (moderate drought, MD treatment) and twelve weeks rainfall exclusion (extreme drought, ED treatment). The
three treatments were randomly assigned to the three plots of each block (Fig. 4.5). Hence, the application of each treatment was replicated four times at each site. This experimental set-up yielded a total of 3 (sites) × 4 (blocks) × 3 (treatments) = 36 plots, equivalent to a total of 24 rainout shelters installed. It corresponds to a locally reproduced randomised complete block design.

4.6.2 Rainout shelter design and sampling plot

The design of the rainout shelters, which I used in the drought experiment, was based on a shelter template that had been proven to be suitable for realistic drought simulations in temperate grassland systems (Kahmen et al. 2005, Gilgen & Buchmann 2009). In order to be installed on a slope in a tilted position and to resist the harsh alpine weather conditions, I had to adapt the shelter design. Important aspects were that the shelter had a lower height to provide stability to withstand strong winds and a ridged roof to facilitate the gliding of snow (Fig. 4.6). The shelter consisted of a triangular aluminium construction that was covered by an UV-B-transmissible greenhouse film (Luminance AF Window, Folitec, Germany). The base area of the shelter was 2.4 × 3.0 m, the ridge height 1.2 m and the roof inclination 45°. In essence, the shelter was tunnel-shaped and installed with the openings in slope direction to ensure a constant wind flow and thus to prevent artificial warming beneath the shelter. At the HS site with the steepest slope, I inserted plastic shields into the soil upslope of the plots to interrupt surface and sub-surface runoff during heavy rainfall events (Fig. 4.7).

The alignment of the shelter with the longer side in slope direction provided enough buffer area at the top of the covered area to absorb runoff water and thus to keep it away from the effective sampling plot, which was established in the lower part of the covered area. As runoff or precipitation may reach the periphery of the covered area and to minimise potential edge effects of the shelter, the effective sampling plot was limited to 1 × 1 m, which accounted for just one sixth of the covered 2.4 × 3.0 m base area of the shelter (Fig. 4.7). To evaluate the position of the effective sampling area and to determine if the buffer zone around was chosen in the appropriate dimensions, the spatio-temporal pattern of the soil moisture content was accurately recorded with ThetaProbe measurements on the entire covered area several times during the experimental treatment period. Based on the analysis of this pattern, Bitter (2010) showed that there was runoff and precipitation reaching the buffer zone, especially in the upper part, leading to moisture gradients at the outer border of the covered area. But she also showed that the effective sampling area was characterised by the driest moisture conditions once the drying of the soil has started and that these conditions were homogeneous on the entire 1 m² plot. Thus, the size of the buffer area and the position of the sampling plot were well chosen.
4.6.3 Rainfall manipulation

I simulated recurring summer droughts at the three grassland sites by covering the experimental plots with rainout shelters and thereby excluding the ambient rainfall in the summers of 2008, 2009 and 2010. In order to create droughts at different severity levels, I manipulated rainfall during periods varying in length. After installing the shelters at the beginning of each growing season (late June), I excluded rainfall during approximately six weeks (late June until early August) to simulate moderate drought (MD treatment) and during approximately twelve weeks (late June until mid-September) to simulate extreme drought (ED treatment). Control plots remained uncovered and thus received ambient rainfall (CT treatment). At the end of each growing season (mid-September), rainout shelters were removed and plants overwintered under snow.

During the experimental treatment period in 2009 (July, August, September), the total precipitation amounted to 305 mm at LC site (Albula Pass), to 291 mm at HC site and to 280 mm at HS site (both at Furka Pass). Surprisingly, all three sites had approximately the same summer precipitation amount and thus, the clear differences in the precipitation regimes of the Albula and Furka Pass regions showed by the climate data (cf. climate diagrams of the two regions) were not confirmed in this year.

It has to be mentioned that the rainout shelters did not exclude the whole amount of precipitation during the treatment periods. The shelters reduced the water supply to the sampling plots by about 50% compared to the control treatment with ambient rainfall. This is a conservative estimate that is based on personal observations and on the soil moisture data, which showed that the soil moisture content has not dropped as strong as without any water supply (Fig. 4.8). Some alternative water sources such as (1) surface and sub-surface runoff reaching the sampling plot during strong rainfall events, (2) snow and rain drifted by wind under the shelter and deposited on the sampling plot or (3) fog and dew deposited on the sampling plot have partially compensated for the reduced water supply by the excluded rainfall and ensured that the simulated droughts were not too severe.

I am aware that for a true assessment of the drought effects, shelters should also have been established on control plots, with the excluded water collected and added back. However, given the amount of labour and financial resources involved, only treatment plots could be covered and potential shelter artefacts were identified with micro-meteorological measurements.
4.6.4 Assessment of the drought simulation with micro-meteorological measurements

To assess the effect of the rainout shelter on the micro-climate, we took detailed micro-meteorological measurements during the experimental treatment period. The objectives were (1) to ensure significant treatment effects, i.e. differences in the water availability between covered (MD, ED treatment) and uncovered (CT treatment) plots and (2) to monitor possible shelter artefacts such as warming, which could interfere with the drought treatments.

Micro-meteorological measurements

At each of the three experimental sites, we measured air temperature, relative air humidity, soil temperature and wind speed on an uncovered area with control conditions (CT treatment) and under a shelter used to simulate extreme drought (ED treatment). To prevent disturbances on the sampling plot, these measurements have been carried out on a separate area above the plot (Fig. 4.1). For this, a combined air temperature and air humidity sensor (TRH-100, Pace Scientific Inc., Mooresville NC, USA) was fixed 17 cm above the ground on a metal mast. In addition, a soil temperature sensor (PT940, Pace Scientific Inc., Mooresville NC, USA) was buried 5 cm into the soil at 30 cm distance from this metal mast. Finally, a cup anemometer (Type f.555.1.18, Schiltknecht, Gossau, Switzerland) was fixed 30 cm above the ground on a wooden post next to the metal mast.

At each site, we counted the amount of precipitation by a rain gauge (ECH2O ECRN100, Decagon Devices Inc., Pullman WA, USA), which was attached to a wooden post 1 m above ground. To improve the measurement conditions, the rain gauge was installed at a minimal distance of 1.5 m from obstacles (rainout shelter or fence).

On each of the 12 experimental plots at the three sites (CT, MD and ED treatments) we determined soil moisture by a mobile measurement device (ThetaProbe type ML2x, Delta-T Devices Ltd, Cambridge, UK). Measurements have been carried out at 9 (3 × 3) regularly arranged positions on a 40 × 40 cm grid on the 1.0 × 1.0 m sampling plot (Fig. 4.7). The measured voltage $V$ indicated by a voltmeter was transformed to the volumetric soil moisture content $\theta$ as

$$\theta = \frac{1.1 + 4.44 \times V - a_0}{a_1}$$

using a generalised calibration for mineral soils with $a_0 = 1.6$ and $a_1 = 8.4$ (Delta-T Devices Ltd, 1999).

Air temperature, relative air humidity, soil temperature, wind speed and precipitation amount have been measured automatically and continuously from June 2009 until September 2009. Several bat-
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tery-powered data loggers (XR 440, Pace Scientific Inc., Mooresville NC, USA and ECH2O Em5b, Decagon Devices Inc., Pullman WA, USA) recorded the data at 10-min intervals using CEST (Central European Summer Time). Soil moisture data have been collected just before the start of the drought simulation (late June), at the end of the moderate drought simulation (early August) and at the end of the extreme drought simulation (mid-September).

Development of the soil moisture content under experimental drought conditions

Just before the start of the drought simulation (late June), the soil moisture content did not differ between the three treatment plots in both years 2009 and 2010 (Fig. 4.8). This shows that the soil moisture content of the MD and ED plots reached the level of the CT treatment over winter and hence, there were no carry-over effects on soil moisture on the sheltered plots from the previous years. At the end of the moderate drought simulation (early August), i.e. after six weeks of the experimental treatment period, soil moisture content has dropped on both the MD and ED plots from c. 45 to 30% at LC site, from c. 40 to 25% at HC site and from c. 35 to 25% at HS site in both years (Fig. 4.8). Up to this date the two drought treatments did not differ, which is visible in the same level of the soil moisture content of the MD and ED plots. From this date onwards, the two drought treatments differed, as the shelters were removed from the MD plots, which resulted in a divergence of the soil moisture content of the MD and ED plots. At the end of the extreme drought simulation (mid-September), i.e. after twelve weeks of the experimental treatment period, the soil moisture of the MD plots has reached the level of the CT plots, whereas the ED plots clearly had a lower moisture content as the plots under control and moderate drought conditions (Fig. 4.8). The development of the soil moisture of the ED plots towards the end of the experimental treatment period depended on year and site. In 2009 the ED treatment induced a further drop of the soil moisture to c. 20% at LC site and to less than 10% at HC site, whereas it stayed constant at c. 25% at HS site. In 2010 there was a slight increase of the soil moisture of the ED plots at each of the three sites (Fig. 4.8).

These soil moisture measurements were essential for the evaluation of the experimental drought simulation. The measurements revealed that the drought simulations were successful, as the desired drying-out under the shelters was observed, which shows that the used rainout shelter design was suitable to simulate drought in alpine grassland. The measurements also show that the two drought treatments (MD and ED treatments) actually led to droughts differing in severity. At both sites with calcareous bedrock (LC and HC sites) the drought simulations were very effective. However, at the HS site the experimental drought simulation led to less pronounced reductions in soil moisture in
general. The most likely explanation for the limited effectiveness of the rainout shelter in preventing water from reaching the covered area at this site might be the steepness of the slope, which allowed surface and sub-surface runoff to occur during heavy rainfall events. Therefore it was essential that we have installed plastic shields upslope of the plots, which interrupted runoff to optimise the drought treatment.

Influence of the rainout shelter on air temperature, soil temperature, relative air humidity and wind speed

The micro-climate of an uncovered area (CT treatment) as well as of an area, which was covered by a rainout shelter (ED treatment) was characterised by several micro-climatological parameters calculated from air temperature ($T_a$), soil temperature ($T_s$), relative air humidity (rH) and wind speed (v) data at each of the three sites (Table 4.1). These parameters showed that the rainout shelters affected the micro-climate at two of the three experimental sites. At both the LC and HC sites, the wind was slowed down and the air and soil temperatures were increased beneath the shelters (Table 4.1). The increase of the temperature was more pronounced above the ground, with increases in the mean air temperature of about 1 K at LC site and about 1.4 K at HC site. However, these warming effects of the shelters were within the seasonal variation of the temperatures. In contrast, there was no significant reduction of the wind speed and no warming observed at the HS site. At this site, there was even a tendency for lower temperatures beneath the rainout shelters (Table 4.1).

Surprisingly, the extent of the shelter-induced warming effect depended on the site. At the two sites, where warming has been detected (LC and HC sites), the wind speed was significantly reduced beneath the shelters (Table 4.1). This suggests that the wind flow reaching the covered area and allowing for ventilation mainly determined the extent of warming beneath the shelters. Since the main wind direction was probably not parallel to the slope direction at the two sites, the ventilation was restricted and resulted in a temperature increase. Nevertheless, it was essential to install the shelters parallel to the direction of the slope to allow for sufficient buffer area above the sampling plots to capture runoff. Another explanation for the site dependency of the warming effect could be the varying slope inclination and slope aspect. The two sites, where warming has been detected (LC and HC sites), were characterised by a lower slope inclination (30°) and by a southern slope aspect, whereas the site without warming (HS site) had a higher slope inclination (40°) and a western slope aspect. The lower inclination might have led to a reduced ventilation capacity and the southern slope aspect to a stronger solar radiation, both promoting warming beneath the shelters.
This micro-meteorological investigation revealed that the used rainout shelter can influence the micro-climate, mainly the air temperature. A warming beneath the shelters is undesirable, because it may cause some additional effects that can not be separated from the effects of drought. But we assume that the extent of the observed warming beneath the shelters (1–1.4 K) was too low to strongly affect the grassland systems. Here, it also has to be noted that drought events in alpine areas are usually accompanied by higher temperatures due to lower clouding. Thus, the observed increases in temperatures beneath the shelters go in line with the predicted changes in climate.

4.6.5 Classification of the simulated droughts in relation to climate change scenarios and other drought experiments

A central aim of the drought experiment was to simulate a summer drought, which corresponds to the projected future change of precipitation. For this, we used a localised projection for southern Switzerland (CHS) for 2085 based on the emission scenario A2, which amounted to -27.0% summer precipitation, with summer referring to the period from June to August (CH2011 2011). In the drought experiment, the decrease of precipitation was simulated during the period from July to September, which corresponded to the growing season in the alpine zone and which was of equal duration as the summer period to which the projection applied.

The moderate drought treatment (MD treatment) excluded rainfall during 6 weeks. Under the assumption that the rainout shelters reduced the water supply by 50% and when relating the simulated precipitation reduction to the whole summer period (12 weeks), this corresponded to a precipitation change of -25%. Hence, the moderate drought treatment was very close to the projected precipitation reduction of 27% under the climate change scenario (CH2011 2011). This clearly shows that the moderate drought conditions were realistic concerning the projected changes in precipitation and thus were suitable to simulate the expected future summer precipitation regime in alpine ecosystems. On the other hand, the extreme drought treatment (ED treatment) excluded rainfall by 50% during 12 weeks. This treatment corresponded to a precipitation change of -50% for the summer period, which significantly exceeded the projected change based on the climate change scenario. Hence, the extreme drought treatment was not realistic concerning the expected future conditions. Nevertheless, it made sense to apply this strong treatment, since it served as a reference contrasting the control treatment with ambient rainfall. It provided valuable additional information and lead to a better process and system understanding.

To compare the intensity of the drought treatments in this experiment with the intensity of the treatments in other drought experiments, it is important to consider the relative share of the
drought treatment period in the growing season duration. I simulated drought in alpine grassland systems, which were situated at c. 2500 m a.s.l. and which were characterised by a growing season lasting from late June to mid-September (75 d, 2.5 months). The moderate drought treatment was applied during 6 weeks, which accounted for c. 50% of the growing season, whereas the extreme drought period lasted for 12 weeks and thus covered c. 100% of the growing season. In drought experiments conducted in temperate grassland systems, the duration of the drought treatment periods reached from 9 weeks (Hofer et al. 2016) to 12 weeks (Gilgen & Buchmann 2009) and hence was comparable to the duration of the treatment periods in this experiment. However, these systems were situated at c. 400 m a.s.l. and therefore were characterised by a much longer growing season, which lasted from mid-April to end of October (200 d, 6.5 months). Thus, the drought treatment periods covered c. 40% of the growing season in the drought experiment of Gilgen & Buchmann (2009) and c. 30% of the growing season in the study of Hofer et al. (2016). In contrast to the alpine systems, the growth was only temporarily affected by the droughts in these temperate systems. In addition, the long growing season allowed for a recovery of the grassland systems in the current season (Hofer et al. 2016). This suggests that a drought period with the same duration may have a lower impact in the temperate systems. But, it has to be mentioned here that the drought treatments in my experiment were not identical to those in the experiments conducted in temperate grassland. The shelters used in temperate grassland excluded precipitation completely from the treatment plots whereas the shelters applied in alpine grassland only to c. 50%.
**Table 4.1** Micro-climatological parameters in alpine grassland during the drought experiment. Measurements were taken during the experimental treatment period in 2009 (late June until mid-September) on an uncovered area with control conditions as well as on an area, which was covered by a rainout shelter used to simulate extreme drought at each of the three experimental sites. LC: low precipitation, calcareous bedrock; HC: high precipitation, calcareous bedrock; HS: high precipitation, siliceous bedrock. CT: control, ambient rainfall; ED: extreme drought, twelve weeks rainfall exclusion. Mean: mean of the daily mean; abs,max: maximal value; mean,max: mean of the daily maxima; abs,min: minimal value; mean,min: mean of the daily minima. The variability is indicated by ± 1 standard deviation.

<table>
<thead>
<tr>
<th>Micro-climatological parameter</th>
<th>Unit</th>
<th>LC site</th>
<th>ED site</th>
<th>HC site</th>
<th>ED site</th>
<th>HS site</th>
<th>ED site</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>CT treatm.</td>
<td>ED treatm.</td>
<td>CT treatm.</td>
<td>ED treatm.</td>
<td>CT treatm.</td>
<td>ED treatm.</td>
</tr>
<tr>
<td>Air temperature Tₐ,mean</td>
<td>°C</td>
<td>11.2±3.5</td>
<td>12.2±3.7</td>
<td>10.1±3.5</td>
<td>11.5±3.9</td>
<td>9.4±3.4</td>
<td>9.3±3.4</td>
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<tr>
<td>Tₐ,abs,max</td>
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<td>28.5</td>
<td>34.0</td>
<td>27.6</td>
<td>33.3</td>
<td>28.8</td>
<td>29.6</td>
</tr>
<tr>
<td>Tₐ,mean,max</td>
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<td>21.1±4.9</td>
<td>23.1±5.2</td>
<td>19.1±5.0</td>
<td>23.0±6.0</td>
<td>20.5±5.2</td>
<td>19.3±5.0</td>
</tr>
<tr>
<td>Tₐ,abs,min</td>
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<td>-4.8</td>
<td>-4.0</td>
<td>-3.8</td>
<td>-3.3</td>
<td>-4.4</td>
<td>-3.0</td>
</tr>
<tr>
<td>Tₐ,mean,min</td>
<td>°C</td>
<td>4.5±3.4</td>
<td>5.0±3.3</td>
<td>4.3±3.1</td>
<td>4.6±3.1</td>
<td>3.2±3.0</td>
<td>4.0±3.0</td>
</tr>
<tr>
<td>Soil temperature Tₛ,mean</td>
<td>°C</td>
<td>11.9±1.9</td>
<td>12.1±1.7</td>
<td>11.7±2.6</td>
<td>12.2±2.4</td>
<td>10.3±2.8</td>
<td>9.9±2.6</td>
</tr>
<tr>
<td>Tₛ,abs,max</td>
<td>°C</td>
<td>19.2</td>
<td>17.4</td>
<td>26.2</td>
<td>24.2</td>
<td>24.2</td>
<td>20.7</td>
</tr>
<tr>
<td>Tₛ,mean,max</td>
<td>°C</td>
<td>15.4±2.7</td>
<td>14.3±2.0</td>
<td>17.2±4.3</td>
<td>16.9±3.7</td>
<td>16.3±4.4</td>
<td>13.7±3.6</td>
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<td>Tₛ,abs,min</td>
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<td>3.4</td>
<td>4.0</td>
<td>2.5</td>
<td>1.6</td>
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<td>Rel. air humidity rH,mean</td>
<td>%</td>
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<td>81.2±8.6</td>
<td>83.8±9.4</td>
<td>79.4±9.8</td>
<td>81.5±11.2</td>
<td>79.7±11.2</td>
</tr>
<tr>
<td>rH,abs,max</td>
<td>%</td>
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<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>rH,mean,max</td>
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<td>97.5±4.5</td>
<td>98.7±4.2</td>
<td>97.9±4.9</td>
<td>98.6±5.6</td>
<td>97.4±6.5</td>
</tr>
<tr>
<td>rH,abs,min</td>
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<td>42.9</td>
<td>42.7</td>
<td>37.3</td>
<td>29.8</td>
<td>30.6</td>
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<tr>
<td>rH,mean,min</td>
<td>%</td>
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<td>58.4±10.5</td>
<td>61.8±11.1</td>
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<td>51.8±13.6</td>
<td>52.8±12.8</td>
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<td>4.2±1.9</td>
<td>1.8±0.9</td>
<td>1.9±0.8</td>
<td>1.6±0.6</td>
</tr>
<tr>
<td>v,abs,max</td>
<td>ms⁻¹</td>
<td>19.8</td>
<td>23.6</td>
<td>36.6</td>
<td>24.9</td>
<td>21.3</td>
<td>21.9</td>
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<tr>
<td>v,mean,max</td>
<td>ms⁻¹</td>
<td>9.5±3.7</td>
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<td>15.0±6.9</td>
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<td>8.9±3.6</td>
<td>8.3±3.1</td>
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<tr>
<td>v,abs,min</td>
<td>ms⁻¹</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
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<tr>
<td>v,mean,min</td>
<td>ms⁻¹</td>
<td>0.0±0.0</td>
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</tbody>
</table>
Figure 4.5  Schematic diagram of the experimental design. The drought experiment was conducted at three sites in the Swiss Central Alps, which represented contrasting conditions in annual precipitation and geology: one site at Albula Pass (LC: low precipitation, calcareous bedrock) and two sites at Furka Pass (HC: high precipitation, calcareous bedrock and HS: high precipitation, siliceous bedrock). The experimental treatments included ambient rainfall (CT: control conditions), six weeks rainfall exclusion (MD: moderate drought) and twelve weeks rainfall exclusion (ED: extreme drought). These treatments were applied during the growing seasons of three consecutive years. Replication of the treatments was n = 4 at each site. At each site, plots were arranged in four replicated units (blocks) with three plots each (control, moderate drought, extreme drought, randomly assigned). This experimental design yielded a total of 3 (sites) × 4 (blocks) × 3 (treatments) = 36 plots.
Figure 4.6 Alpine grassland sites of the drought experiment with rainout shelters to simulate summer drought. LC: low precipitation, calcareous bedrock, HC: high precipitation, calcareous bedrock, HS: high precipitation, siliceous bedrock. The LC site was situated at Albula Pass and both HC and HS sites were located at Furka Pass. The vegetation at the two calcareous sites (LC, HC sites) consisted of a *Sesleria caerulea* sward, the one at the siliceous site (HS site) was formed by a *Carex curvula* sward.
Figure 4.7 Schematic diagram of the area, which was covered by the rainout shelters. 1: 2.4 × 3.0 m base area of the rainout shelter, 2: plastic shield, 3: area for micro-meteorological measurements, 4: 1.0 × 1.0 m sampling plot, 5: positions for soil moisture measurements.
Figure 4.8 Volumetric soil moisture content (VSMC) of the treatment plots of the drought experiment in alpine grassland. Measurements were taken just before the start of the drought simulation (pre trmt, late June), at the end of the moderate drought simulation (early August) and at the end of the extreme drought simulation (mid-September) in both years 2009 and 2010. LC: low precipitation, calcareous bedrock; HC: high precipitation, calcareous bedrock; HS: high precipitation, siliceous bedrock. CT: control, ambient rainfall; MD: moderate drought, six weeks rainfall exclusion; ED: extreme drought, twelve weeks rainfall exclusion. Displayed are means ± 1 standard error, n = 4 per site and treatment.
4.7 Thesis outline

High elevation ecosystems may face considerable changes in the climate. Evidence is accumulating that these changes, in particular higher temperatures, may drastically affect plants in the sub-nival and nival zone, i.e. at the upper limit of plant life. No such evidence is available for the alpine zone and it is unclear how stable these ecosystems are under a changing climate. This doctoral thesis aims at evaluating the impacts of climatic changes (summer droughts and warming) on alpine ecosystems, specifically on alpine grassland. The three studies presented in this thesis contribute to the predictions of the consequences of the most likely climate change scenario for the Swiss Alps. In a field experiment, established at three alpine grassland sites at Albula and Furka Pass, Switzerland, the structural and functional responses (changes in vegetation structure and biomass production) of alpine grassland to several years of summer droughts have been investigated (Studies 1 and 2). These studies were carried out as part of the IMEXCLIME project (Impacts of extreme climatic events on ecosystem functioning in alpine grasslands), which was funded by a PSC-Syngenta Graduate Research Fellowship of the Zurich-Basel Plant Science Center. In an observational study at Furka Pass, Switzerland (Study 3), high-tech infrared thermometry was applied to address habitat heterogeneity and species niche specificity and hence potential responses of alpine plant species to a warmer climate. This work was realised in collaboration with Dr. Daniel Scherrer and Prof. Dr. Christian Körner (Institute of Botany, University of Basel) as part of the EU-funded EC FP6 EcoChange project (Challenges in assessing and forecasting biodiversity and ecosystem changes in Europe, no. 066866 GOCE).

The thesis is structured as follows:

**Study 1** examines the structural responses of alpine grassland to summer droughts and evaluates possible implications on erosion susceptibility. Drought-induced changes in vegetation structure in the canopy layer and on the soil surface are accurately quantified using the grid-point intercept method. The study addresses the following questions: (1) Do alpine grassland sites differ in vegetation structure under the current climate? (2) Is vegetation structure of alpine grassland affected by three years of experimentally-induced summer drought, and if so, does the severity of drought matter? (3) Does summer drought have the same effect at each site? (4) Is the point-intercept method suitable to assess structural responses of alpine grassland to summer drought and can it be used to non-destructively estimate standing above-ground vegetation dry matter?

**Study 2** focusses on the quantification of above- and below-ground biomass responses of alpine grassland to summer droughts. Changes in pools and net production of biomass under drought are sampled by clipping (above-ground) and using a split tube sampler and ingrowth cores (below-ground).
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The biomass responses serve as a basis for estimating the resistance and resilience and thus stability of the grassland ecosystem, when exposed to droughts. The study covers the following questions: (1) Do alpine grassland sites differ in their biomass production under the current precipitation regime? (2) How is the above-ground biomass production of alpine grassland affected by recurring experimental summer droughts? (3) How does the below-ground biomass production respond to drought conditions? (4) To what extent is the overall biomass production of alpine grassland restricted by periodic drought disturbances?

Study 3 assesses thermal surface (plant canopy) and soil (root zone) conditions across topographically rich alpine landscapes with low stature vegetation by thermal imagery techniques and miniature data loggers at different spatial resolution. The recorded actual habitat temperatures allow a precise description of the patterns of current micro-habitats and thus life conditions in alpine terrain. These temperature data are used (1) to partition the surface and soil temperature variation into among-slopes, within-slope and centimetre scale variation, (2) to identify the most influential factors for surface and soil temperature at different spatial scales, (3) to quantify the observed variation in surface temperature dependent on spatial sampling resolution, and (4) to estimate the projected habitat loss under climate warming scenarios and the dependence of predictions on spatial resolution.

4.8 References


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General introduction


General introduction


General introduction


5 Changes in vegetation structure of alpine grassland in response to three years of simulated summer drought are highly site-dependent (Study 1)

5.1 Abstract

Questions  The future summer precipitation in the Swiss Alps is predicted to be reduced as a consequence of climate change, leading to prolonged periods of drought. However, it is unclear how alpine grassland ecosystems will respond to changing precipitation regimes. Is vegetation structure of alpine grassland affected by three years of experimentally-induced summer drought, and if so, does the severity of drought matter? Does summer drought have the same effect at each site? Is the point-intercept method suitable to assess structural responses of alpine grassland to summer drought and can it be used to non-destructively estimate standing above-ground vegetation dry matter?

Location  Swiss Central Alps

Methods  At three sites located at about 2500 m a.s.l. on steep mountain slopes and varying in macroclimate and geology we simulated summer drought with rainout shelters in typical alpine grassland communities. During three consecutive growing seasons, we applied three treatments to the vegetation: (1) ambient rainfall (control), (2) six weeks rainfall exclusion (moderate drought) and (3) twelve weeks rainfall exclusion (extreme drought). After three years of precipitation manipulation, we studied the drought-induced vegetation structural responses by using the grid-point intercept method. To underpin these results, we additionally measured the effect of summer drought on standing above-ground vegetation dry matter. Finally, we investigated the relationship between the non-destructively measured vegetation structural parameters and the destructively quantified dry matter.

Results  Due to varying site conditions and thus different species compositions, the alpine grassland sites clearly differed in initial vegetation structure. Overall, three years of simulated summer drought strongly influenced vegetation structure of alpine grassland by decreasing foliar and basal cover by up to 37% and 54%, respectively, and by increasing the area of bare ground by a factor of up to 8. Summer drought had a gradual effect, meaning that already substantial responses under moderate drought were further intensified under extreme drought. But summer drought had not the same effect at each site since vegetation structure remained unaffected at one of the three sites. Basal
cover highly correlated with standing above-ground vegetation dry matter and therefore can be used as a proxy variable to non-destructively predict vegetation dry matter in alpine grassland stands.

**Conclusions** Our findings reveal that a multi-year summer drought can significantly affect vegetation structure of alpine grassland, but there is no general response to drier conditions. Moreover, our experiment shows that initial structural differences will be further accentuated under a future drier climate in alpine grassland ecosystems.

**Keywords** Albula Pass; bare ground; basal cover; Carex curvula sward; climate change experiment; foliar cover; Furka Pass; ground protection; plant intercepts; point intercept method; Sesleria caerulea sward; vegetation dry matter

**Nomenclature** Lauber et al. (2012)

**Abbreviations** LC = low precipitation, calcareous bedrock; HC = high precipitation, calcareous bedrock; HS = high precipitation, siliceous bedrock; trmt = treatment

### 5.2 Introduction

Human-induced climate change is unequivocal and ongoing, leading to further global warming and changes in the global water cycle (IPCC 2013) as well as higher occurrence of extreme weather events (IPCC 2012). For Switzerland, localised climate change scenarios of mean temperature and precipitation project increased temperatures in all seasons, with a maximum in summer, while precipitation will slightly increase in winter, but strongly decrease in summer towards the end of the 21st century (CH2011 2011, Fischer et al. 2012, Zubler et al. 2014). Furthermore, the future European summer climate might experience a pronounced increase in year-to-year variability so that extreme events such as severe summer droughts will be more likely (Schär et al. 2004).

Slow-growing plant species adapted to low nutrient availability and extreme but stable climatic conditions are dominating alpine ecosystems. Due to these characteristics they are vulnerable to large shifts in air temperature and precipitation. An overall warming and associated changes in precipitation patterns and snow cover will influence alpine vegetation (Theurillat & Guisan 2001). In the European Alps, precipitation increases with increasing elevation (Frei & Schär 1998, Ellenberg & Leuschner 2010, Körner 2003), and at high elevations, vegetation is commonly less constrained by
moisture shortage than at low elevations and only periodically and regionally variable water shortage can occur (Körner 2003). Long-lasting severe summer droughts have been very rare in alpine ecosystems in the last centuries (Van der Schrier et al. 2007). But for the near and long-term future, increases in the frequency and intensity of droughts in Alpine regions are predicted (Gobiet et al. 2014). It is still unclear how alpine grassland ecosystems will respond to altered precipitation regimes and particularly to prolonged summer drought, and thus, whether these ecosystems are susceptible or resistant to such extremes. The response to drought might vary dependent on local environmental conditions such as geology or macroclimate and it is unclear if the severity of drought matters, i.e. if already a moderate drought will have an effect on grassland.

Research on climate change impacts on plant communities mainly follows three approaches: (1) modelling projected species distributions (e.g. Thuiller et al. 2005), (2) document ecosystem changes after natural climate anomalies (e.g. Reichstein et al. 2007), or (3) experimentally manipulating some aspects of predicted atmospheric and subsequent climate change, such as CO₂ enrichment (e.g. Lüschèr et al. 2004), warming (e.g. Harte & Shaw 1995), drought (e.g. Kahmen et al. 2005), or rainfall (e.g. Suttle et al. 2007). But many studies mainly investigated the effects of long-term, gradual changes, while effects of extreme events have rarely been studied (Jentsch et al. 2007). Climate change experiments in alpine ecosystems have focused on CO₂ enrichment (e.g. Körner et al. 1997, Inauen et al. 2012), warming (e.g. Henry & Molau 1997), nitrogen deposition (e.g. Bassin et al. 2012), and snow depth and snowmelt timing (e.g. Wipf et al. 2009). However, the response of alpine vegetation to drought has rarely been investigated. In a short-term experiment, De Boeck et al. (2016) studied the influence of drought and heat waves on alpine grassland. But to our knowledge, no multi-year experiment exists so far, which examined the impact of summer drought with rainout shelters on grassland in the alpine zone, i.e. above the climatic treeline.

Alpine grassland provides several important ecosystem services such as biomass production or conservation of natural habitats with a high plant species diversity. In addition, alpine grassland vegetation enhances the infiltration of water from rainfall, surface runoff and snowmelt, and thus, guarantees the capacity of the site to capture, store and safely release water (hydrologic services). But, the main service of alpine grassland ecosystems is to ensure the protection of alpine soils on steep slopes by preventing erosion and landslides, and thus, to secure slope stability (Körner 2003). On slopes, soils persist only as long as vegetation persists and vegetation integrity rests upon an adequate ground cover and intact root system. For this soil protection service, the vegetation structure of alpine grassland plays a decisive role. Generally, a relatively high natural erosion risk exists in alpine grassland due to the steepness of the terrain, geological conditions, shallow soils and the often sparse vegetation. Summer drought might change structural parameters of the vegetation in such a
way that grassland sites become more susceptible to erosion. As heavy rainfall events are predicted to occur more frequently in the future, erosion is likely to be enhanced at alpine grassland sites, which were damaged by summer drought. Thus, soil protection and slope stability may play a key role at such sites under a future climate. Vegetation cover is an important indicator for the resistance against erosion. To ensure an adequate erosion protection, a threshold value of 75% for the minimum vegetation cover is applied in restoration practice at high elevations (Krautzer et al. 2011). Our detailed measurements of different categories of cover in the canopy layer as well as on the soil surface were used to assess the erosion susceptibility of alpine grassland after a summer drought.

Alpine grassland is mainly composed of graminoids such as grasses and sedges forming tussocks, herbaceous perennials forming rosettes, geophytes with leaves close to the soil surface, prostrate woody shrubs, and cryptogams such as mosses and lichens directly covering the soil surface. All of these growth forms are characterised by a dense basal clustering of vegetation material. Therefore, vegetation dry matter is concentrated close to the soil surface in alpine grassland. To determine standing biomass by destructive harvesting, a cut 0 cm above the ground is necessary to get a representative measurement. Especially in grassland systems with low productivity such as in alpine grassland, removing all above-ground biomass has a very destructive impact and represents a substantial disturbance of the ecosystem. For long-term climate change experiments in alpine grassland, such artefacts could interact with the actual experimental treatment and could lead to unwanted superimposed effects. Also, a repeated measurement of the biomass in the same area is not possible and often experimental plots are too small to use additional area for repeated biomass harvests. Because the estimation of standing biomass is often of interest in environmental studies and in particular in alpine grassland studies, the question arises whether an appropriate non-destructive method exists. In this study, we examined whether the grid-point intercept method is suitable for a non-destructive determination of the biomass.

In the work presented here, we investigated the structural responses at community level of alpine grassland to summer drought, which is predicted as a consequence of climate change for the Swiss Alps. For this, we simulated summer drought with rainout shelters in typical alpine grassland communities (Sesleria caerulea and Carex curvula swards) at three sites located at about 2500 m a.s.l. on steep mountain slopes and varying in macroclimate (low vs. high precipitation) and geology (calcareous vs. siliceous bedrock). An important aspect of the experimental design was that the three swards differed in their initial vegetation structure to test for its role in the structural responses of the vegetation to drought. During three consecutive growing seasons we applied three treatments to the vegetation: (1) ambient rainfall (control), (2) six weeks rainfall exclusion (moderate drought), and (3) twelve weeks rainfall exclusion (extreme drought). After three years of precipitation manipu-
We studied the drought-induced vegetation structural responses both in the canopy layer and on the soil surface by using the grid-point intercept method. Furthermore, we assessed whether changes in vegetation structure affected ground protection against erosion. To underpin the structural responses, we measured standing above-ground vegetation material by harvesting it and determining dry matter. Finally, we investigated the relationship between the non-destructively measured vegetation structural parameters and the destructively measured dry matter. Our study addressed three main questions: (1) Is vegetation structure of alpine grassland affected by three years of experimentally-induced summer drought, and if so, does the severity of drought matter? (2) Does summer drought have the same effect at each site? (3) Is the point-intercept method suitable to assess structural responses of alpine grassland to summer drought and can it be used to non-destructively estimate standing above-ground vegetation dry matter?

5.3 Methods

5.3.1 Study sites

Our study was conducted in the alpine zone in the regions of the Albula Pass, Grisons (46°35’ N, 9°50’ E) and Furka Pass, Valais (46°34’ N, 8°25’ E) in the Swiss Central Alps. The climate at this elevation is characterised by cold winters with permanent snow cover and short summers limiting the growing season to about 75 days (from late June to mid-September). The two regions had a similar mean annual temperature (-2.2 °C at Albula Pass and -2.1 °C at Furka Pass, ETH Zurich et al. 2004), but significantly differed in the mean annual precipitation (845 mm at Albula Pass and 1920 mm at Furka Pass, ETH Zurich et al. 2004). We established our experiment at three grassland sites representing contrasting conditions in macroclimate and geology: (1) a site at Albula Pass with low precipitation and calcareous bedrock (referred to as LC site), (2) a site at Furka Pass with high precipitation and calcareous bedrock (HC site), and (3) a site at Furka Pass with high precipitation and siliceous bedrock (HS site). The sites were located at about 2500 m a.s.l. on steep mountain slopes. At LC and HC sites, the slopes were characterised by a 30° inclination and a southern aspect, and at HS site by a 40° inclination and a western aspect. The vegetation at the three sites represented typical alpine grassland communities: two Sesleria caerulea-dominated swards (Seslerio-Caricetum sempervirentis) on calcareous bedrock with Sesleria caerulea, Carex sempervirens, Anthyllis vulneraria ssp. alpestris, Aster alpinus and Helianthemum nummularium ssp. grandiflorum as characteristic species, and a Carex curvula-dominated sward (Caricetum curvulae) on siliceous bedrock with Carex curvula, Helictotrichon versicolor, Trifolium alpinum, Leontodon helveticus and Homogyne alpina as characteristic species. Sesleria caerulea and Carex curvula swards are the prevailing grassland communities.
in the alpine zone and form widespread natural grassland vegetation (Ellenberg & Leuschner 2010). Most of the plant species at the three grassland sites were perennial. The grassland at the sites was very extensively grazed by domestic and wild herbivores.

5.3.2 Experimental design and drought simulation

During the summers of 2008, 2009 and 2010 (from late June to mid-September), summer drought was simulated with rainout shelters. The treatments included (1) a control (ambient rainfall), (2) moderate drought (six weeks rainfall exclusion), and (3) extreme drought (twelve weeks rainfall exclusion). Replication of the experimental treatments was $n = 4$. At each site, plots were arranged in four replicated units (blocks) with three plots each. The three treatments (control, moderate drought, extreme drought) were randomly assigned to the three plots of each replicated unit. This design yielded a total of $3 \times 3 \times 4 = 36$ plots, equivalent to a total of 24 rainout shelters installed.

Drought was simulated by covering the treatment plots with rainout shelters during approximately six weeks (moderate drought) and twelve weeks (extreme drought) in early summer. We used a template of rainout shelter design that had been proven to be suitable for realistic drought simulations (Kahmen et al. 2005) and modified it for alpine conditions (e.g. lower height to provide stability to withstand strong winds, roof slope of 45° to facilitate the gliding of snow). The shelter consisted of an aluminium basic construction covered by an UV-B transmissible greenhouse film (Luminance AF Window, Folitec, Germany). The base area was $2.4 \times 3.0$ m, the height 1.2 m. In essence, the shelter was tunnel-shaped with larger openings parallel to the main wind direction, allowing for constant wind through-flow which prevented warming beneath the shelters. To minimise edge effects, the covered base area was six times larger than the central 1 m$^2$ sampling plot, and plastic shields were inserted into the soil upslope of the plots to interrupt surface and sub-surface water flow at the HS site. Control plots remained uncovered and thus received ambient rainfall. Herbivores were excluded from the experimental plots by fencing during the drought simulation period.

We applied soil moisture measurements (ThetaProbe type ML2x, Delta-T Devices Ltd, Cambridge, UK) to ensure significant differences in water availability between covered drought plots and uncovered control plots. Soil moisture data have been collected just before the start of the drought simulation (late June), at the end of the moderate drought simulation (early August) and at the end of the extreme drought simulation (mid-September). The measurements revealed that the drought simulation was successful, as the desired drying-out under the shelters was observed and the two drought treatments (moderate and extreme drought) actually led to droughts differing in severity (Fig. 5.1).
5.3.3 Data collection

After three years of summer drought simulation, in September 2010, vegetation structure measurements were taken using a grid-point intercept method applied to each $1 \times 1$ m sampling plot. The measurement procedure was modified from Herrick et al. (2009) and was based on the point intercept method described by Wilson (2011). We used a $0.5 \times 0.5$ m recording frame with 72 regularly arranged points on a fixed grid. To sample the entire area of the $1 \times 1$ m sampling plot, the frame was positioned four times above the vegetation, resulting in 288 points per plot. At each of the 288 points, a rigid pin with a diameter of 0.5 mm and a length of 20 cm was inserted perpendicularly to the grid plane into the vegetation and lowered through the canopy layer down to the soil surface. At each point, the intercepts of the pin with living or dead plant foliage in the canopy layer and with plant bases, mosses, lichens, litter, rocks or bare soil on the soil surface were recorded. We allowed for a maximum of three intercepts in the canopy layer (i.e. no, one, two or three intercepts with living or dead plant foliage) and one intercept on the soil surface (i.e. one intercept with any of the above-mentioned materials or bare soil). The intercepts in the canopy layer were recorded from top to bottom and if there were more than three intercepts, those in the lower part of the canopy layer were ignored. The plant foliage included all above-ground plant organs such as leaves, stems and flowers. In the canopy layer, we distinguished between intercepts with living and dead plant material, where an intercept with living or dead material meant that only the intercepted plant part and not the entire plant was living or dead. For the plant bases, no distinction between living and dead could be made. Bare soil occurred when mineral soil was visibly unprotected by any of the above-mentioned materials.

Also in 2010, standing above-ground vegetation material was harvested at the time of peak standing biomass (early August) and at the end of the growing season (mid-September). On each of the $1 \times 1$ m sampling plots we collected six subsamples at fixed and regularly arranged positions on $4 \times 24$ cm rectangular sampling areas. These were aligned with the longer side in slope direction and distributed in two rows of three perpendicular to slope direction. After installing a small harvesting frame, we clipped and collected all above-ground vegetation material 0 cm above the ground, representing standing phytomass and litter, including a high proportion of phytomass produced in previous years. The six subsamples were pooled, resulting in one sample per sampling plot and corresponding to an area of $576$ cm$^2$ and accordingly $5.76\%$ of the entire area of the $1 \times 1$ m plot. The second sampling was carried out at slightly offset positions with the same arrangement pattern as in the first sampling. For a maximum of one week, vegetation material samples were stored in paper bags at 4 °C before being separated into living plant material (biomass), dead plant material (necromass) combined with litter, mosses and lichens. Litter, i.e. detached senescent plant material, could not be col-
lected separately and therefore was combined with dead plant material. Finally, vegetation material was dried at 70 °C for at least 48 h to constant weight, and thereafter dry matter was determined by weighing each sample.

5.3.4 Data analysis

The grid-point intercept data were used to calculate several vegetation structural parameters (see Table 5.1).

Our approach to assess the ground protection and thus the erosion susceptibility in alpine grassland is based on a separate consideration of the canopy layer and the soil surface (Table 5.1). In the canopy layer as well as on the soil surface, the presence of protective material (plant foliage, plant bases, mosses, lichens, litter and rocks) can mitigate the erosive effect of water (raindrops and surface runoff) or wind. The combination of the cover pattern in the canopy layer with the one on the soil surface results in a classification with four ground protection classes: (1) “high protection”, canopy over protected soil (cover both in the canopy layer and on the soil surface), (2) “medium protection”, protected soil (no cover in the canopy layer, but cover on the soil surface), (3) “low protection”, canopy over bare soil (cover in the canopy layer, but no cover on the soil surface) and (4) “no protection”, bare ground (both no cover in the canopy layer and on the soil surface). Each protection class represents a certain degree of protection of the ground and a change in the protection class pattern of a representative ground area indicates a change in the erosion susceptibility at the grassland site. As long as the ground area is directly protected on the soil surface, as this is the case for the two above-mentioned protection classes (1) and (2), the erosion risk is negligible and the protection of the ground is ensured. The ground area with a protection in the canopy layer, but not on the soil surface, which is rated as protection class (3), is relevant for surface runoff erosion. And finally, bare ground, the area with neither a protection in the canopy layer nor on the soil surface, which is rated as protection class (4), is important for rainfall, wind and surface runoff erosion. The sum of the areas with the ground protection classes (3) and (4) corresponds to the structural parameter bare soil.

Statistical analyses were performed using IBM SPSS Statistics 20. Data were analysed with a two-way analysis of variance (ANOVA) to test for main effects of site and treatment and interactions between these two factors. A Tukey HSD test was used for multiple comparisons of means.
**Table 5.1** Vegetation structural parameters used to describe the canopy layer and the soil surface in alpine grassland. The calculation of the parameters is based on data measured by the grid-point intercept method using a grid with 288 points. C1, C2, C3: potential intercept positions 1, 2 and 3 in the canopy layer; S: intercept position on the soil surface.

<table>
<thead>
<tr>
<th>Category</th>
<th>Name</th>
<th>Definition</th>
<th>Calculation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy layer</td>
<td>Foliar cover</td>
<td>Percentage of ground covered by the vertical projection of the foliage of living and dead plants</td>
<td>Number of points with at least 1 living or dead plant intercept for C1 to C3 *100/288</td>
</tr>
<tr>
<td></td>
<td>Living plant</td>
<td>Proportion of the number of living plant intercepts to the maximum possible number of intercepts in the canopy layer multiplied by 100</td>
<td>Number of living plant intercepts for C1 to C3 of all points *100/864</td>
</tr>
<tr>
<td></td>
<td>Dead plant</td>
<td>Proportion of the number of dead plant intercepts to the maximum possible number of intercepts in the canopy layer multiplied by 100</td>
<td>Number of dead plant intercepts for C1 to C3 of all points *100/864</td>
</tr>
<tr>
<td></td>
<td>Total plant</td>
<td>Proportion of the number of living and dead plant intercepts to the maximum possible number of intercepts in the canopy layer multiplied by 100</td>
<td>Number of living and dead plant intercepts for C1 to C3 of all points *100/864</td>
</tr>
<tr>
<td></td>
<td>Basal cover</td>
<td>Percentage of soil surface covered by plant bases</td>
<td>Number of points with a living or dead plant intercept for S *100/288</td>
</tr>
<tr>
<td></td>
<td>Moss cover</td>
<td>Percentage of soil surface covered by mosses</td>
<td>Number of points with a moss intercept for S *100/288</td>
</tr>
<tr>
<td></td>
<td>Lichen cover</td>
<td>Percentage of soil surface covered by lichens</td>
<td>Number of points with a lichen intercept for S *100/288</td>
</tr>
<tr>
<td></td>
<td>Litter cover</td>
<td>Percentage of soil surface covered by litter</td>
<td>Number of points with a litter intercept for S *100/288</td>
</tr>
<tr>
<td></td>
<td>Rock cover</td>
<td>Percentage of soil surface covered by rocks</td>
<td>Number of points with a rock intercept for S *100/288</td>
</tr>
<tr>
<td></td>
<td>Bare soil</td>
<td>Percentage of soil surface not covered by plant bases, mosses, lichens, litter and rocks on the soil surface but possibly covered by living and dead plants in the canopy layer</td>
<td>Number of points with a bare soil intercept for S *100/288</td>
</tr>
<tr>
<td>Overlay canopy layer, soil surface</td>
<td>Total ground cover</td>
<td>Percentage of ground covered by living and dead plants in the canopy layer and/or by plant bases, mosses, lichens, litter and rocks on the soil surface</td>
<td>Number of points with at least 1 living or dead plant intercept for C1 to C3 or with no intercept for C1 to C3 but with an intercept with any material excluding bare soil for S *100/288</td>
</tr>
<tr>
<td></td>
<td>Bare ground</td>
<td>Percentage of ground not covered by living and dead plants in the canopy layer as well as by plant bases, mosses, lichens, litter and rocks on the soil surface (unvegetated bare soil)</td>
<td>Number of points with no intercept for C1 to C3 and with a bare soil intercept for S *100/288</td>
</tr>
</tbody>
</table>
Study 1

Figure 5.1 Volumetric soil moisture content (VSMC) of the treatment plots of the drought experiment in alpine grassland. Measurements were taken just before the start of the drought simulation (pre trmt, late June), at the end of the moderate drought simulation (early August) and at the end of the extreme drought simulation (mid-September) in both years 2009 and 2010. LC: low precipitation, calcareous bedrock; HC: high precipitation, calcareous bedrock; HS: high precipitation, siliceous bedrock. CT: control, ambient rainfall; MD: moderate drought, six weeks rainfall exclusion; ED: extreme drought, twelve weeks rainfall exclusion. Displayed are means ± 1 standard error, n = 4 per site and treatment.
5.4 Results

We present our results on vegetation structure at the grassland sites by first focussing on the canopy layer, then on the soil surface, and finally on the overlay of the canopy layer and the soil surface to quantify ground protection. In addition, we show results on standing vegetation dry matter. To enhance clarity, in each result section we first report on initial structural differences between the three grassland sites under control conditions (i.e. ambient rainfall) and then on structural responses to simulated summer drought.

5.4.1 Canopy structure

The swards at the three sites differed strongly in living plant intercepts ($p_{site} < 0.01$), dead plant intercepts ($p_{site} < 0.001$), total plant intercepts ($p_{site} < 0.001$) and foliar cover ($p_{site} < 0.001$) under ambient rainfall (Fig. 5.2, Table 5.2). At LC site, the sward was characterised by a very dense (90% of total plant intercepts), vital (more than 60% of living plant intercepts) and closed (almost 100% foliar cover) canopy, whereas the swards at HC and HS sites showed a more sparse and open canopy, with the least dense canopy (55% total plant intercepts) at HS site.

Overall, three years of simulated summer drought significantly affected canopy density, measured by total plant intercepts ($p_{trmt} < 0.001$), but summer drought had not the same effect at each site ($p_{site \times trmt} < 0.05$, Fig. 5.2, Table 5.2). At LC site, total plant intercepts did not substantially change with increasing drought ($p_{trmt} = n.s.$ in an ANOVA for each site separately), but there was a clear and gradual reduction with increasing drought from 64% under ambient rainfall to 55% (-14%) under moderate drought to 30% (-53%) under extreme drought ($p_{trmt} < 0.01$) at HC site and from 56% to 43% (-23%) to 29% (-48%, $p_{trmt} < 0.001$) at HS site, respectively. The reduction in total plant intercepts at the HC and HS sites with increasing drought was exclusively caused by the decrease in living plant intercepts, since the dead plant intercepts remained constant. Additionally, foliar cover changed significantly under summer drought ($p_{trmt} < 0.001$). However, the effect of drought was again depending on the site ($p_{site \times trmt} < 0.001$). Foliar cover did not significantly change with increasing drought at LC site ($p_{trmt} = n.s.$ in an ANOVA for each site separately), but it gradually and significantly decreased from 86% under ambient rainfall to 82% (-5%) under moderate drought to 54% (-37%) under extreme drought at HC site ($p_{trmt} < 0.001$) and from 87% to 74% (-15%) to 56% (-36%) at HS site ($p_{trmt} < 0.001$).
Due to the varying site conditions and the different drought treatments, foliar cover and total plant intercepts clearly differed on the 36 plots, ranging from 55 to almost 100% and from 30 to 90%, respectively.

### 5.4.2 Soil surface structure

The differences in soil surface structure between the sites under ambient rainfall could be explained mainly by basal cover ($p_{\text{site}} < 0.001$) and litter cover ($p_{\text{site}} < 0.001$, Fig. 5.3, Table 5.2). On calcareous bedrock, we observed a very high basal cover (93% at LC site and 82% at HC site, respectively), while in contrast, the basal cover on siliceous bedrock was low (39% at HS site). Litter cover was quite low on calcareous bedrock (5% at LC site and 8% at HC site, respectively) and comparatively high on siliceous bedrock (43% at HS site).

Summer drought had a significant effect on percent basal cover ($p_{\text{trmt}} < 0.001$), but had not the same effect at each site ($p_{\text{site} \times \text{trmt}} < 0.001$, Fig. 5.3, Table 5.2). There was a significant influence of increasing drought but no consistent response at LC site (93% under ambient rainfall, 85% under moderate drought and 87% under extreme drought, $p_{\text{trmt}} < 0.05$), but percent basal cover was gradually and considerably reduced with increasing drought from 82% under ambient rainfall to 73% (-11%) under moderate drought to 59% (-28%) under extreme drought at HC site and from 39% to 24% (-38%) to 18% (-54%) at HS site ($p_{\text{trmt}} < 0.001$ for both sites). Additionally, summer drought led to significant changes in percent bare soil ($p_{\text{trmt}} < 0.001$), but again had not the same effect at each site ($p_{\text{site} \times \text{trmt}} < 0.001$). Percent bare soil did not change at LC site ($p_{\text{trmt}} = \text{n.s.}$) but clearly increased from ambient rainfall to moderate drought to extreme drought from 5% to 12% (+140%) to 20% (+300%) at HC site ($p_{\text{trmt}} < 0.01$) and from 8% to 21% (+163%) to 35% (+338%) at HS site ($p_{\text{trmt}} < 0.001$).

### 5.4.3 Ground protection (overlay canopy layer, soil surface)

The three sites differed in the percentage of ground area with high, medium, low and no protection under control conditions ($p_{\text{site}} < 0.001$ for all protection categories, Fig. 5.4, Table 5.2). The LC site had an extremely high percentage of ground area with high protection (97%), while the highly protected areas were lower at the HC and HS sites (84 and 83%, respectively).

The percentage of ground area with high protection was significantly influenced by summer drought ($p_{\text{trmt}} < 0.001$, Fig. 5.4, Table 5.2). However, summer drought had not the same effect at each site ($p_{\text{site} \times \text{trmt}} < 0.001$). At LC site, it did not influence the percentage of highly protected area ($p_{\text{trmt}} = \text{n.s.}$), whereas this area gradually and drastically decreased with increasing drought from 84% under am-
bient rainfall to 76% under moderate drought to 49% under extreme drought at HC site ($p_{\text{trmt}} < 0.001$) and from 83 to 63 to 45% at HS site ($p_{\text{trmt}} < 0.001$). Summer drought also affected the percentage of area with medium protection ($p_{\text{trmt}} < 0.001$), but again the treatment interacted with the site ($p_{\text{site} \times \text{trmt}} < 0.001$). Drought had no effect at LC site ($p_{\text{trmt}} = \text{n.s.}$), but led to an increase in the area with medium protection at the HC and HS sites (11, 12, 31% at HC site, $p_{\text{trmt}} < 0.01$ and 9, 16, 20% at HS site, $p_{\text{trmt}} < 0.01$). Summer drought also had an effect on the percentage of area with low protection ($p_{\text{trmt}} < 0.01$, no interaction with site) – it led to an increase at each site. But this increase was only relevant at the HC and HS sites. Finally, there also was an effect of drought on the percentage of area with no protection ($p_{\text{trmt}} < 0.001$), but again not the same effect at each site ($p_{\text{site} \times \text{trmt}} < 0.001$). Drought had no effect at LC site ($p_{\text{trmt}} = \text{n.s.}$), however it gradually and considerably enlarged the unprotected area under increasing drought from 2 to 6 to 15% at HC site ($p_{\text{trmt}} < 0.01$) and from 4 to 11 to 24% at HS site ($p_{\text{trmt}} < 0.001$).

### 5.4.4 Vegetation dry matter

The three sites differed in standing above-ground dry matter of living plants, mosses, lichens and dead plants under ambient rainfall ($p_{\text{site}} < 0.001$ for all components, Fig. 5.5, Table 5.2). The total dry matter ranged from 434 g m$^{-2}$ at HS site to 707 g m$^{-2}$ at HC site to 920 g m$^{-2}$ at LC site. Similar patterns were also found for living and dead plant dry matter: The sward at HS site consisted of 158 g m$^{-2}$ living plant dry matter and 205 g m$^{-2}$ dead plant dry matter, the one at HC site of 232 and 375 g m$^{-2}$, respectively, and the one at LC site of 397 and 510 g m$^{-2}$, respectively. The proportion of living plants in total dry matter was highest at LC site (43%), followed by HS site (36%) and HC site (33%).

Summer drought affected only standing living plant dry matter ($p_{\text{trmt}} < 0.001$) – moss and lichen dry matter as well as dead plant dry matter did not change under drought ($p_{\text{trmt}} = \text{n.s.}$). The impact of summer drought on living plant dry matter was the same at each of the three sites ($p_{\text{site} \times \text{trmt}} = \text{n.s.}$), drought led to a reduction of living plant dry matter.

### 5.4.5 Methods comparison

Simple linear regressions of total plant dry matter against both plant foliar cover ($R^2 = 0.290$) and total plant intercepts (considering four intercepts in the canopy layer and on the soil surface, $R^2 = 0.532$) revealed rather weak correlations. However, we found a strong relationship when total plant dry matter was regressed on plant basal cover ($R^2 = 0.732$, Fig. 5.6). This relationship could not be
Study 1

significantly improved with a multiple linear regression of total plant dry matter against plant basal cover and total plant intercepts (considering three intercepts in the canopy layer, $R^2 = 0.741$).
Table 5.2 Significance levels (P-values) of the two-way analyses of variance (ANOVA) testing for the main effects of site and treatment and their interaction on vegetation structure, ground protection and vegetation dry matter response variables. Factors are site (LC, HC and HS) and treatment (ambient rainfall, moderate drought and extreme drought). Data were collected in alpine grassland in 2010. Significant test results are given in bold face; \( n = 4 \) per site and treatment.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Significance level (P-value)</th>
<th>Site d.f. = 2</th>
<th>Treatment d.f. = 2</th>
<th>Site × treatment d.f. = 4</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Structural parameter canopy layer</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Foliar cover</td>
<td>(&lt; 0.001)</td>
<td>(&lt; 0.001)</td>
<td>(&lt; 0.001)</td>
<td></td>
</tr>
<tr>
<td>Living plant intercepts</td>
<td>(0.009)</td>
<td>(&lt; 0.001)</td>
<td>0.194</td>
<td></td>
</tr>
<tr>
<td>Dead plant intercepts</td>
<td>(&lt; 0.001)</td>
<td>0.288</td>
<td>0.075</td>
<td></td>
</tr>
<tr>
<td>Total plant intercepts</td>
<td>(&lt; 0.001)</td>
<td>(&lt; 0.001)</td>
<td>(0.034)</td>
<td></td>
</tr>
<tr>
<td><strong>Structural parameter soil surface</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal cover</td>
<td>(&lt; 0.001)</td>
<td>(&lt; 0.001)</td>
<td>(&lt; 0.001)</td>
<td></td>
</tr>
<tr>
<td>Moss cover</td>
<td>(&lt; 0.001)</td>
<td>0.318</td>
<td>0.336</td>
<td></td>
</tr>
<tr>
<td>Lichen cover</td>
<td>(&lt; 0.001)</td>
<td>0.695</td>
<td>0.561</td>
<td></td>
</tr>
<tr>
<td>Litter cover</td>
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<td>0.115</td>
<td></td>
</tr>
<tr>
<td>Rock cover</td>
<td>0.158</td>
<td>0.444</td>
<td>0.332</td>
<td></td>
</tr>
<tr>
<td>Bare soil</td>
<td>(&lt; 0.001)</td>
<td>(&lt; 0.001)</td>
<td>(&lt; 0.001)</td>
<td></td>
</tr>
<tr>
<td><strong>Ground protection</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High protection</td>
<td>(&lt; 0.001)</td>
<td>(&lt; 0.001)</td>
<td>(&lt; 0.001)</td>
<td></td>
</tr>
<tr>
<td>Medium protection</td>
<td>(&lt; 0.001)</td>
<td>(&lt; 0.001)</td>
<td>(0.001)</td>
<td></td>
</tr>
<tr>
<td>Low protection</td>
<td>(&lt; 0.001)</td>
<td>(0.007)</td>
<td>0.199</td>
<td></td>
</tr>
<tr>
<td>No protection</td>
<td>(&lt; 0.001)</td>
<td>(&lt; 0.001)</td>
<td>(&lt; 0.001)</td>
<td></td>
</tr>
<tr>
<td><strong>Dry matter</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Living plant dry matter</td>
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<td>(&lt; 0.001)</td>
<td>0.063</td>
<td></td>
</tr>
<tr>
<td>Moss dry matter</td>
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<td>0.562</td>
<td>0.478</td>
<td></td>
</tr>
<tr>
<td>Lichen dry matter</td>
<td>(&lt; 0.001)</td>
<td>0.690</td>
<td>0.511</td>
<td></td>
</tr>
<tr>
<td>Dead plant dry matter</td>
<td>(&lt; 0.001)</td>
<td>0.406</td>
<td>0.679</td>
<td></td>
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</tbody>
</table>
Figure 5.2 Percent foliar cover as well as percent living and dead plant intercepts summed up to percent total plant intercepts at three alpine grassland sites treated with ambient rainfall, moderate drought and extreme drought. LC: low precipitation, calcareous bedrock, HC: high precipitation, calcareous bedrock, HS: high precipitation, siliceous bedrock. Data were collected in 2010 after three years of drought simulation. Displayed are means ± 1 standard error, n = 4 per site and treatment.
Figure 5.3 Percent soil surface covered with plant bases (basal cover, a), mosses (b), lichens (c), litter (d) and rocks (e) plus percent bare soil (f) at three alpine grassland sites treated with ambient rainfall, moderate drought and extreme drought. LC: low precipitation, calcareous bedrock, HC: high precipitation, calcareous bedrock, HS: high precipitation, siliceous bedrock. Data were collected in 2010 after three years of drought simulation. The slices of the pie chart are labelled with means ± 1 standard error, n = 4 per site and treatment.
Figure 5.4 Cover patterns in the canopy layer and on the soil surface as well as ground protection at three alpine grassland sites treated with ambient rainfall, moderate drought and extreme drought. Percent cover in the canopy layer and on the soil surface is shown with two narrow bars and percent ground area with a certain protection with a wide bar. a: high protection (cover in the canopy layer and on the soil surface), b: medium protection (no cover in the canopy layer but cover on the soil surface), c: low protection (cover in the canopy layer but no cover on the soil surface), d: no protection (no cover in the canopy layer and on the soil surface). LC: low precipitation, calcareous bedrock, HC: high precipitation, calcareous bedrock, HS: high precipitation, siliceous bedrock. Data were collected in 2010 after three years of drought simulation. The segments of the wide bar are labelled with means ± 1 standard error, n = 4 per site and treatment.
Figure 5.5 Standing above-ground dry matter of dead plants, lichens, mosses and living plants at three alpine grassland sites treated with ambient rainfall, moderate drought and extreme drought. LC: low precipitation, calcareous bedrock, HC: high precipitation, calcareous bedrock, HS: high precipitation, siliceous bedrock. Standing above-ground dry matter was measured in 2010, at the time of maximum biomass and at the end of the growing season and averaged. Displayed are means ± 1 standard error, n = 4 per site and treatment.
Figure 5.6  Linear regression of plant dry matter vs. plant basal cover of all plots at the three alpine grassland sites treated with ambient rainfall, moderate drought and extreme drought. Data were collected in 2010 after three years of drought simulation. Regression line, 95% confidence band and 95% prediction band are shown.
5.5 Discussion

5.5.1 Structural variability in alpine grassland

Alpine ecosystems are characterised by spatially strongly varying site conditions (Körner 2003), resulting in a multitude of different plant communities with characteristic species composition (Braun-Blanquet 1948/1949, Reisigl & Keller 1994, Ellenberg & Leuschner 2010). Not one single factor, but the interplay of several environmental factors, namely micro-climatological, pedological, geomorphological and other factors are responsible for the presence of a specific plant community at a particular location (Vonlanthen et al. 2006, Gigon 1987). The bedrock type, i.e. calcareous versus siliceous, determines the substrate type and plays an important role in the assembly of alpine plant communities (Michalet et al. 2002, Gigon 1987). Each plant community exhibits its own characteristic vegetation structure and thus contributes to a pronounced structural variability in the European Alps. In our experiment, three sites were chosen which basically varied in geology and annual precipitation to broadly cover the alpine site conditions. This experimental setup made it possible to examine how summer drought affects vegetation under different site conditions, and thus how summer drought interacts with the site. Therefore, this setup allows to draw general conclusions about the effect of summer drought on grassland in the entire Alpine region.

Our study showed that the vegetation structure at the three alpine grassland sites differed widely under current conditions, i.e. in the natural, undisturbed state of the ecosystem. These differences were evident both in the canopy layer and on the soil surface but were not consistent on both levels. A comparison of the canopy structure under ambient rainfall revealed a clear separation of the LC site characterised by a very closed and dense canopy with a high proportion of living plant material from the HC and HS sites with a more open and less dense canopy containing a lower proportion of living plant material (Fig. 5.2). It is striking that despite an almost identical species composition at the two sites on calcareous bedrock (LC and HC sites) the canopy structure differed substantially, whereas the canopies composed of completely different species at the two sites on contrasting bedrock (HC and HS sites) were structurally very similar. By contrast, a comparison of the soil surface structure resulted in a grouping corresponding to the geology: the two LC and HC sites on calcareous bedrock differed from the HS site on siliceous bedrock by a much higher percentage of basal cover (Fig. 5.3). However, irrespective of the structural dissimilarities under current conditions, the percentage of bare ground was generally very low and thus, the slopes at the three sites had a high level of ground protection in the undisturbed state (Fig. 5.4). Furthermore, we found that the variation in closeness and compactness of the vegetation under current conditions was directly reflected in the standing above-ground vegetation material. The LC site with a very closed and compact vegetation...
had the highest amount of standing vegetation material followed by the HC and HS sites, respectively (Fig. 5.5).

5.5.2 Alpine grassland structural responses to summer drought

Impact of summer drought on vegetation structure (compactness and closeness)

With this study, we provide direct evidence that an experimentally-induced multi-year summer drought can substantially alter the vegetation structure of alpine grassland. Our findings demonstrate that three years of summer drought disturbance led to obvious and consistent structural changes in the canopy layer as well as on the soil surface at two of the three investigated grassland sites (HC and HS sites). In the canopy layer, drought caused a significant reduction in the percentage of foliar cover, i.e. a reduction in the closeness of the foliage (Fig. 5.2). In addition, the percentage of total plant intercepts, which measures the compactness of the foliage, declined clearly due to the drought disturbance. Finally, on the soil surface, the percentage of basal cover has severely dropped under drier conditions and as a result, bare soil has increased accordingly (Fig. 5.3). The overall effect of drought on vegetation corresponds to a “thinning”, which can be attributed to a drought-induced progressive dieback of the vegetation during the three summers of the experiment. The thinning of the vegetation was reflected in fewer intercepts with plant material in the canopy layer as well as on the soil surface, detected by the point intercept method. A decrease in the number of plant intercepts can be attributed to the following two mechanisms: (1) a reduced density of plant individuals due to a drought-induced increase in mortality, i.e. a decreased number of plant individuals per plot or (2) a changed morphology of surviving plant individuals due to a shortened vigour under drought (decreased individual productivity), i.e. plant individuals with reduced shoot or leaf length, leaf area, number of leaves etc. It is unclear whether the recurring summer drought disturbance led to an extinction of individual drought-susceptible plant species and thus to changes in species composition on the plots after three years. To get a clearer picture about the species-specific responses further analysis of our data at the species level is required.

A striking finding was that only phanerogams, but not cryptogams (mosses and lichens) responded to drought, which was reflected in the soil surface structure (Fig. 5.3) as well as in the standing above-ground dry matter (Fig. 5.5). Furthermore, summer drought has affected only the living components of the vegetation, which was evident on the basis of the plant intercepts in the canopy layer (Fig. 5.2) and the standing above-ground dry matter (Fig. 5.5). The percentage of living plant intercepts can be used as an indicator to assess the health and vigour of alpine grassland in response to drought. Our data show that this indicator significantly dropped at two of the three investigated
grassland sites (HC and HS sites, Fig. 5.2). Contrary to our expectations, the dead components did not accumulate during the drought periods (Figs. 5.1 and 5.5). In particular, the litter pool has not changed after three years of summer drought (Fig. 5.3). The amount of litter on the soil surface is determined by an interplay of litter production and litter decomposition, while both processes may be influenced by drought. Under the assumption that the litter decomposition had been restricted under drought, the litter production must also have been restricted, otherwise the pool would have increased. To better understand these processes under drought conditions, additional research should be carried out.

Vegetation structural changes in response to summer drought have, to our knowledge, never been investigated in alpine grassland systems and rarely in temperate ones. Gilgen & Buchmann (2009) used the LAI and the vegetation height to examine the impact of drought on vegetation structure of temperate grassland. As in our study, drought led to a thinning of the grassland stands, reported by a reduction in LAI and vegetation height, with the extent of the reduction depending on site and year. Responses of grassland to simulated drought disturbance are often quantified by changes in the biomass production. The extent of the reduction of biomass production under dry conditions compared to control conditions can be used to quantify the resistance of the grassland to the drought disturbance. No or a weak decrease in biomass production indicates a high resistance, whereas a significant decrease points to a reduced resistance. In temperate grassland ecosystems, it is a general phenomenon that summer drought decreases the above-ground biomass production (Kahmen et al. 2005, Gilgen & Buchmann 2009, Hartmann & Niklaus 2012, Vogel et al. 2012, Cantarel et al. 2013, Hoekstra et al. 2014, Deléglise et al. 2015, Prechsl et al. 2015). A study that focused on alpine grassland at Furka Pass found that a short-term drought exposure of 17 days is sufficient to negatively affect biomass production (De Boeck et al. 2016). Our multi-year experiment in alpine grassland revealed that primary production was reduced already at moderate drought levels in the second year of drought simulation (Schmid et al. 2011) and this response clearly persisted in the third year (Fig. 5.5).

**Gradual effect of summer drought in alpine grassland**

As expected, the duration of the drought period, and hence the severity of drought, played an important role in the response of the alpine grassland systems to summer drought at the HC and HS sites. Already moderate drought, simulated by six weeks of rainfall exclusion during three consecutive summers, resulted in structural changes (Figs. 5.2 and 5.3). But these changes have been significantly intensified under the extreme drought treatment with twelve weeks of rainfall exclusion eve-
ry summer. This important finding clearly shows that increasing summer drought affected vegetation structure gradually. Thus, this gradual response to drought suggests that drought affects alpine grassland systems progressively rather than via thresholds meaning that the system is flexible over a wider range of drought stress and does not abruptly collapse when a threshold is exceeded at a certain severity of drought. The alleviated effect of the moderate drought treatment can be explained by the shorter duration of the drought simulation and thus drought stress, but could also be traced back to a recovery during the 6 weeks after the drought simulation in the ending growth period. Under moderate drought, the grassland system seemed to be in a transition state, which was visible in the medium level and the greater variation of the canopy structure parameter values under moderate drought compared to control and extreme drought conditions, respectively (Fig. 5.2).

**Extent of the drought disturbance and ability for regeneration in alpine ecosystems**

None of the three swards has been destroyed completely during the three years of drought simulation, not even under the extreme drought treatment. But the reductions of the percentages of foliar cover by up to 37% and basal cover by up to 54%, respectively, and the increase of the area of bare ground by a factor of up to 8 strongly suggest that the swards at the HC and HS sites were intensely affected by three years of summer drought disturbance. These short-term irreversible structural changes show that the swards could not maintain structural stability at these sites and thus, the long-term vegetation integrity may be endangered. The degree of the drought-induced damage appears even more evident when considering the stability and persistence of undisturbed alpine grassland under the harsh alpine conditions. Alpine plant species are characterised by a pronounced longevity, some have been shown to be thousands of years old (De Witte et al. 2012).

In alpine ecosystems, the timing and duration of a summer drought may play an important role, since the already short growing season, which limits the time period for growth and reproduction to 2–3 months (Körner 2003), is shortened even more when a drought occurs. The duration of the drought treatment periods in this experiment (6 weeks for moderate drought or 12 weeks for extreme drought) was comparable to the duration in other drought experiments, which were conducted in temperate grassland systems. For example, Hofer et al. (2016) simulated drought during 9 weeks and Gilgen & Buchmann (2009) during 12 weeks. But in contrast to these temperate grassland systems, the alpine system was characterised by a much shorter growing season (2.5 instead of 6.5 months) and thus the simulated droughts covered the half or full growing season. This suggests that a drought with the same duration may more strongly affect the alpine system. However, the shelters used in alpine grassland excluded rainfall only to c. 50% during the drought treatment periods,
whereas the shelters applied in temperate grassland completely excluded rainfall from the experimen-
tal treatment plots.

Our study shows that alpine grassland systems are characterised by a similar resistance to summer
drought as temperate systems (e.g. Gilgen & Buchmann 2009, Hofer et al. 2016). However, the long-
term stability of the alpine system may be lower because its resilience is most likely reduced com-
pared to non-alpine systems. This can be explained by the limited possibility of recovery by short-
term regrowth due to the short growing seasons. In particular, a direct recovery after a drought
event during the current growing season, as it has been observed in temperate grassland systems
(Hofer et al. 2016), is severely restricted in alpine grassland. In addition, alpine vegetation generally
has a lower regeneration potential after disturbances than vegetation at low elevation due to the
extreme site conditions and the slow-running ecosystem processes under the harsh climate in these
ecosystems.

To ensure the long-term vegetation integrity, the affected grassland systems must regain their origi-
nal vegetation structure. For this, a recolonisation of the bare soil by plants is essential. Open gaps
can be colonised either by clonally growing local plant species or by seedlings from the local seed
bank, whereas the recruitment by seeds plays a minor role in alpine ecosystems. However, the re-
colonisation of open gaps by local plant species takes a very long time due to the extremely low an-
nual growth rates of these species. Investigations on Carex curvula, the dominant plant species in
the sward at the HS site, have shown that this plant spreads very slowly into open gaps, with an ex-
pansion rate of only one millimetre per year (Grabherr et al. 1978). According to this study, the natu-
ral regeneration of 1 m² bare soil would take roughly 500 years. This fact considerably limits the abil-
ity for regeneration in alpine grassland ecosystems.

Site dependence of drought-induced structural changes in alpine grassland

Our experiment revealed significant interactions between site and treatment for several vegetation
structural parameters, meaning that summer drought had not the same effect on vegetation struc-
ture at each grassland site (Table 5.2). While summer drought led to significant responses at the HC
and HS sites, showing that these sites are susceptible to drought, surprisingly, the LC site could suc-
cessfully resist the drought disturbance (Figs. 5.2 and 5.3). This implies that the resistance of alpine
grassland to summer drought is highly site-dependent. This important finding clearly demonstrates
that there will be no general response to future drier conditions in alpine grassland meaning that not
all sites will be equally affected by a prolonged summer drought under a future climate in the Swiss
Alps. Because the majority of drought experiments in grassland were conducted at only one location
so far, the interaction of drought with the site was rarely investigated. However, in addition to our study, a similar multi-site study in non-alpine grassland does exist (Gilgen & Buchmann 2009). This study examined the effect of summer drought in managed temperate grassland at three sites along an elevational gradient from the Swiss Plateau to the subalpine zone of the Swiss Central Alps. In line with our study, an interaction of drought with the site was detected, indicating that there may be no general response to future summer droughts also in non-alpine grassland systems in Switzerland.

Grassland micro-climate dampening the effect of less precipitation

The canopy and soil surface structure of alpine grassland influences the micro-climate in the sward, particularly near the soil surface (Körner 2003). A favourable micro-climate, in turn, enables the sward to cope with less precipitation, and thus, can dampen the effect of drought.

The sward at LC site was characterised by a compact and closed canopy and a highly covered soil surface and thereby clearly differed structurally from the two other swards. The compact canopy layer and the protective material on the soil surface in this sward decoupled the ground from atmospheric conditions resulting in an own micro-climate near the soil surface. A low percentage of bare soil means first that the evaporation from the soil surface can be effectively impeded, and thus, water losses prevented. In addition, a heating by radiation is limited, because there is not enough dark absorption area on the soil surface exposed to sunlight. So, the covering vegetation serves as a protection against evaporation and heating in the sward. The limitation of water losses as well as a controlled heating lead to moist and cool conditions in the canopy layer and especially on the soil surface. Thus, with these conditions, possible drought stress caused by excluded rainfall can be mitigated or even prevented.

In contrast, the swards at HC and HS sites with a sparse and open canopy and a poorly covered soil surface were strongly coupled to the free atmosphere. Due to a high percentage of bare soil, the evaporation from the soil surface is unrestricted and can be very strong under promotive conditions leading to high water losses. The heating of the dark-coloured soil surface by solar radiation strongly enhances evaporation. Körner & Cochrane (1983) report soil surface temperatures on bare spots as high as 80 °C in alpine vegetation. Besides heating, also wind-induced turbulences reaching the ground in a sparse canopy and increasing the vapour pressure deficit can raise evaporation from the soil surface. Both warming and a high vapour pressure deficit in the canopy layer enhance the leaf transpiration of the plants. To compensate for strong warming during full sunlight, the vegetation might actively cool down by upregulating transpiration, resulting in a further loss of water. Taken all together, the enhanced evapotranspiration leads in the long term to a desiccation of the topsoil.
Since grassland plants absorb water mainly in the uppermost centimetres of the soil (Prechsl et al. 2015), topsoil desiccation strongly affect the water balance of plants and can cause drought stress. Depleted water reserves lead to a higher probability of high-temperature stress as heat mitigation through transpiration fails (De Boeck et al. 2011). A climate change experiment by De Boeck et al. (2016) revealed that the interplay of drought and heat stress plays an important role in alpine grassland ecosystems. Their findings show that alpine grassland that is exposed to drought stress, is more susceptible to heat stress, meaning that high temperatures have much more potential for immediate, significant effects on vegetation when coinciding with water limitation. Exactly this situation arises in alpine grassland that is subjected to summer drought and exposed to a stronger warming due to its vegetation structure.

In summary, our data suggest that initial vegetation structure plays a key role in the resistance of alpine grassland to prolonged summer drought. On the one hand, initial vegetation structure may determine the ability to exploit alternative water sources, and on the other hand, it may influence the micro-climate in the sward, which in turn affects the water losses. Our study clearly demonstrates that sparse and open vegetation seems to be more susceptible, whereas compact and closed vegetation seems to be resistant to a multi-year summer drought.

### 5.5.3 Erosion susceptibility in alpine grassland

#### Impact of summer drought on ground protection

Structurally intact grassland vegetation ensures the stability of slopes in alpine ecosystems. After a disturbance, such as a multi-year summer drought, the integrity of the vegetation is essential to maintain this important function. As a consequence of a modified vegetation structure, erosion susceptibility could be raised after a drought disturbance in alpine grassland, which may lead to erosion damage and endanger slope stability. A reduced slope stability in turn can lead to an increase in landslides and trampling damage caused by pasture livestock. Once, erosion processes have been triggered in alpine vegetation, and erosion generated damage, a re-establishment of the vegetation is limited or even prevented at high elevation (Mosimann 1985).

In addition to other factors (such as rainfall intensity, amount of surface runoff, soil characteristics or steepness of the slope, etc.), vegetation cover plays an important role in determining the extent of soil erosion (Stocking & Elwell 1976). There is experimental evidence that vegetation cover limits the surface runoff intensity (Huang et al. 2013). Based on observations in the Swiss Central Alps, Mosimann (1985) developed two non-linear relationships between an erosion intensity index and vegetation cover, dependent on elevation. Up to elevations of about 2000 m a.s.l., erosion intensity
is negligible if a minimum of 70% vegetation cover is achieved. Above 2000 m a.s.l., i.e. in the alpine zone, erosion phenomena existed even at about 80% vegetation cover. Direct measurements of sediment yield during the simulation of heavy rainfall in alpine grassland revealed that the quantity of the eroded soil is clearly negatively related to vegetation cover (Martin et al. 2010, Bunza 1989). The irrigation study of Bunza (1989) indicated that at values of at least 70% vegetation cover, soil erosion became acceptable, but an increasing cover up to 80% resulted in further erosion decline. So, these studies show that in alpine grassland, only a sufficient vegetation development with more than 70% cover stabilises the topsoil in the long term and reduces soil erosion to an acceptable degree. Thus, to ensure an adequate erosion protection, a threshold value of 75% for the minimum cover is applied in restoration practice at high elevations (Krautzer et al. 2011).

Our study showed that the structural changes of the drought-disturbed grassland stands at the HC and HS sites resulted in decreases of the cover in the canopy layer as well as on the soil surface (Fig. 5.4). This reduction in the closeness of the stands led to a clear increase in percent bare ground and percent ground area, which is covered in the canopy layer, but not on the soil surface (ground protection class “low protection”). Therefore, the area of ground protected against erosion decreased substantially at the affected grassland sites after three years of summer drought meaning that the erosion risk could be raised after the drought disturbance. The reduced vegetation integrity at HC and HS sites indicates that these sites may be more susceptible to erosion during a heavy rainfall coinciding or following a longer summer drought period and the slope stability may no more be guaranteed. In contrast, the sward at LC site was sufficiently stable and could maintain vegetation integrity during the drought disturbance. These contrasting responses in structural stability suggest that erosion events may occur only at certain locations in the Alps under a future climate.

Our study demonstrated that the above-mentioned threshold value of 75% for the minimum ground cover was reached at the HS site under the extreme drought treatment (Fig. 5.4). At this site, percent bare ground increased from 4±1% to 24±3% with increasing drought. At HC site this threshold value was not reached under extreme drought. Nevertheless, bare ground has increased at this site from 2±0% to 15±2% with increasing drought. Percent bare ground remained constant at 1% with increasing drought at LC site, which clearly shows that this site is not at all prone to erosion. Reaching the threshold value at HS site shows that this sward is in a critical state concerning the risk of erosion after the multi-year extreme summer drought, just in a transition from invulnerable to endangered. Continuing drought could intensify the risk of erosion at this site. Considering bare soil (area with ground protection classes (3) and (4)) as the area that is exposed to erosion rather than bare ground (area with protection class (4)) results in a more stringent assessment and thus an aggravated risk for erosion. Percent bare soil increased from 8±1% to 35±1% with increasing drought at
Study 1

HS site and from 5±0% to 20±3% at HC site. So, at HS site, the protected area has dropped to no more than 65% after extreme drought when considering bare soil as unprotected area, indicating a high erosion risk.

Assessment of the erosion susceptibility in alpine grassland

Soil and site stability is an important attribute of alpine grassland ecosystems. It is defined as the capacity of the site to limit redistribution and loss of soil resources (including nutrients and organic matter) by wind and water (Herrick et al. 2009). Total ground cover, the percentage of ground covered by plant foliage and bases, mosses, lichens, litter and rocks, is related to wind and water erosion, water infiltration and the ability of the site to resist and recover from degradation. Alpine grassland on steep slopes is affected mainly by water erosion, whereas wind erosion plays a minor role. On slopes, water can cause damage to soils either by the impact of raindrops or surface runoff water. Material covering the ground in the canopy layer (plant foliage) and on the soil surface (plant bases, mosses, lichens, litter and rocks) protects the soil against raindrop impact by interception and absorption of kinetic energy. This inhibits the detachment process and therefore reduces the amount of soil splashed from the soil surface. This also prevents a damage to the soil aggregates by raindrops reaching the soil surface unimpeded and therefore secures the infiltration of water into the soil, which in turn reduces the surface runoff. In addition, material on the soil surface protects the soil against surface runoff water impact by obstructing the water flow and reducing its kinetic energy.

Bare ground, the percentage of ground not protected by any material in the canopy layer and on the soil surface, is generally used as an indicator to estimate the risk of erosion in grassland. Increases in bare ground indicate a higher risk of erosion (Herrick et al. 2009). But with this indicator, the erosion risk in alpine grassland may be underestimated. During heavy rainfall events, surface runoff occurs regularly in alpine grassland due to the steepness of the slopes and the limited water storage capacity in the shallow soils. Especially at the HS site, this phenomenon was often observed during the experiment (personal observation). Damage of surface runoff is created regardless of whether or not plant material is present in the canopy layer. Therefore, bare soil instead of bare ground is the crucial indicator when runoff is involved. And bare soil is, not theoretical, but in reality, always larger than bare ground (see our data). Here, the question arises, which indicator is more suitable for assessing the susceptibility to erosion on vegetated alpine slopes. Is it bare ground, incorporating the protection in the canopy layer and on the soil surface or bare soil, taking into account only the protection on the soil surface? In our opinion, both indicators should be considered, whereas at a site
with an increased risk of surface runoff, bare soil may have more explanatory power. To confirm this, experimental evidence should be provided with on-site erosion measurements during rainfall simulation on structurally differing grassland plots.

5.5.4 Non-destructive assessment of structural responses to summer drought in alpine grassland vegetation

Suitability of the point intercept method

Often, vegetation structural parameters, and in particular cover, is sampled using visual estimates. In experiments, where the recorded values are analysed directly to quantify the response of the vegetation, subjective sampling is quite inappropriate (Wilson 2011). The point intercept method, however, is a quantitative method yielding objective, repeatable measurements that are only minimally biased by the observer. We applied this accurate method to quantify structural changes in alpine grassland in response to a multi-year summer drought in alpine grassland. At three different sites and under three different treatments both the canopy and soil surface structure could be described precisely by using multiple structural parameters on the basis of the point intercept method.

A major benefit of the method is that it is non-destructive and therefore suitable for the use on permanent plots in climate change studies. In contrast to a destructive harvesting the point intercept measuring procedure does not adversely affect vegetation. Therefore, a possible interference with the climate change treatment and thus, undesirable effects on the responses to be measured, are thereby avoided. Another advantage of the point intercept method is that it is sensitive to both changes in the number (mortality and recruitment) and in the vigour (annual biomass production) of plant individuals in a community. So, it integrates the changes in density and production of a plant community and is therefore suitable to comprehensively determine the response of alpine grassland to climate change. The point intercept method was also applied in other climate change studies. Rötzel et al. (1997) used the method to non-destructively assess the effects of elevated CO$_2$ on plant community structure in a calcareous grassland in the Jura mountains of Northwest Switzerland.

Due to the small-scale variation of growth conditions (e.g. locally shallow soil, scree or rocks) and the special growth forms of alpine grassland species characterised by an aggregation of leaves, alpine grassland vegetation is clumped to a certain extent. To meet this heterogeneity we used a relatively high number of sampling points per 1 m$^2$ grassland plot, namely 288 points. Furthermore, we inserted the pin at regularly arranged grid points. With this sampling design, it was possible to representatively sample the grassland plots. With these modifications, the point intercept method has proven
to be highly suitable to precisely measure the responses of alpine grassland to summer drought and can be recommended for further climate change impact research in alpine ecosystems.

**Comparison with the concepts of Wilson (2011)**

The concepts to analyse the foliage of a plant community of Wilson (2011) are based on the measurement of a theoretically infinite number of plant intercepts in one layer, the canopy layer. This layer reaches right down to the ground, including the soil surface. In our concepts, we considered the soil surface as a separate level with one possible intercept. In addition, we limited the possible number of intercepts in the canopy layer to three intercepts. Thus, both the canopy layer and the soil surface could be analysed separately. This allowed for example the separate quantification of plant cover in the canopy layer (foliar cover) and on the soil surface (basal cover) or the quantification of uncovered soil surface (bare soil, cf. Table 5.1). Furthermore, both levels could be overlayed to quantify total ground cover or bare ground, respectively. The separate consideration of the soil surface is important especially in alpine grassland, because there, vegetation material is not evenly distributed over the height profile of the stand, but concentrated close to the soil surface. Thus, a consideration of two levels allows a much more detailed description of the vegetation structure. In particular, a separate consideration of the soil surface is useful when assessing the risk of erosion in inclined alpine grassland.

**Non-destructive estimation of standing above-ground vegetation dry matter**

To estimate above-ground vegetation material in grassland, several non-destructive methods exist (Byrne et al. 2011, Redjadj et al. 2012). In methodological studies, the point intercept method was evaluated for the estimation of vegetation dry matter (Jonasson 1988, Brathen & Hagberg 2004). These studies show that parameters, resulting from point intercept measurements, correlate highly with standing above-ground vegetation material, and therefore, can be used as regression variables to predict vegetation material in plant stands.

To identify the point intercept parameters that best estimate standing above-ground vegetation dry matter in alpine grassland, we performed several simple and multiple linear regressions. Our findings show that a simple linear regression model yielded the highest explained variance for total plant dry matter on the 1 m² plots when regressed on plant basal cover ($R^2 = 0.732$). Thus, basal cover, recorded by the point intercept measurement on the soil surface, represented the most precise estimate of total plant dry matter in alpine grassland. Surprisingly, we found the closest relationship
with a parameter, which is a two-dimensional measurement (intercepts on the soil surface) and not, as expected, a three-dimensional measurement such as the total plant intercepts (intercepts in the canopy layer and on the soil surface). It is striking that a measurement on the soil surface alone, with the canopy layer being unconsidered, is sufficient to make a good estimate of the standing vegetation material in alpine grassland. One reason for this could be that in alpine grassland a large pool of plant material, composed of long-lived and dead plant parts, is located very close to the soil surface. An intercept with plant material on the soil surface therefore corresponds to a multiple of the plant material of an intercept in the canopy layer and thus, contributes to a more precise estimate of total plant dry matter.

The relationship between harvest and point intercept measurements was also studied by Rötzel et al. (1997) in calcareous grassland. In contrast to our findings, they identified a close relationship by regressing plant dry matter on a three-dimensional point intercept parameter. In contrast to alpine grassland, calcareous grassland is characterised by a less pronounced concentration of plant material at ground level. Therefore, a three-dimensional point intercept parameter might be more appropriate in this grassland type.

Our study clearly shows that in alpine grassland, where the main vegetation material is concentrated close to the soil surface, basal cover highly correlates with standing above-ground vegetation dry matter. Thus, it is the best estimate for vegetation dry matter, better than canopy measures. Therefore, basal cover can be used as a regression variable to non-destructively predict standing above-ground vegetation dry matter in alpine grassland stands.

5.6 Conclusions

To our knowledge, this is the first climate change experiment investigating the impact of a multi-year summer drought simulated with rainout shelters on vegetation above the climatic treeline, i.e. in the alpine zone. Our results impressively show that a prolonged and recurring summer drought can affect above-ground vegetation integrity of alpine grassland. More precisely, summer drought can have a pronounced thinning effect on above-ground vegetation, detectable by a decreased plant cover in the canopy layer and on the soil surface, a reduced canopy compactness, as well as a decreased amount of standing above-ground vegetation material. The drought-induced structural changes, namely the increased area of bare ground, might restrict the important function of alpine grassland to protect soil against erosion and, thus, to maintain slope stability. But surprisingly, our study also demonstrates that the resistance of alpine grassland to summer drought, assessed on the
basis of structural stability, is clearly site-dependent. This means that some sites can strongly counterbalance the effect of drought and maintain vegetation integrity. We conclude that there will be no general response to future drier conditions in alpine grassland. Moreover, we predict that the presently existing high structural variability in alpine grassland ecosystems will be further accentuated under a future drier climate.

5.7 References


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Study 1


6 Shift from above- to below-ground biomass production in alpine grassland to resist recurring experimental summer droughts (Study 2)

6.1 Abstract

Questions The future summer climate in the Swiss Alps is predicted to be drier and warmer, with an increased probability of extreme events such as prolonged periods of drought. However, it is unclear how recurring summer droughts of different severity will affect alpine grassland ecosystems. Do alpine grassland sites differ in their biomass production under the current precipitation regime? How is the above-ground biomass production of alpine grassland affected by recurring experimental summer droughts? How does the below-ground biomass production respond to drought conditions? To what extent is the overall biomass production of alpine grassland restricted by periodic drought disturbances?

Location Swiss Central Alps.

Methods We simulated recurring summer droughts with rainout shelters at three grassland sites, located on steep mountain slopes at about 2500 m a.s.l. and varying in macroclimate and geology. During three consecutive growing seasons, the alpine swards were exposed to three treatments: (1) ambient rainfall (control), (2) six weeks rainfall exclusion (moderate drought) and (3) twelve weeks rainfall exclusion (extreme drought). To study the drought-induced responses in biomass production, we sampled standing above- and below-ground biomass by clipping and using a split tube sampler, respectively. To measure the effect of summer drought on below-ground biomass productivity, we used the ingrowth core method.

Results Contrasting site conditions and thus diverging species compositions resulted in a considerably different biomass production of the three swards under the current precipitation regime. Recurring simulated summer droughts strongly influenced the swards by decreasing standing above-ground biomass, while increasing standing below-ground biomass, thereby leading to significantly increased root-shoot ratios. The gradual responses to increasing drought severity were already visible in the second year of drought simulation and were further intensified in the third year of the experiment, indicating carry-over effects. The changes in the biomass pools could be primarily explained by a drought-induced modification of the biomass productivity in the respective compart-
ments and by a changed root biomass loss. However, three years of recurring summer droughts did not affect the overall biomass production in the alpine swards.

**Conclusions** Our findings clearly show that recurring summer droughts affect the resource allocation in alpine grassland by inducing a significant shift from above- to below-ground biomass production. This response emphasises the key role of roots and storage organs for the resistance and resilience of alpine grassland ecosystems when subjected to drier conditions. The fact that the overall production was not restricted during the experimental drought periods suggests a high stability of these ecosystems in a future drier climate.

**Keywords** Albula Pass, biomass productivity, *Carex curvula* sward, climate change experiment, dry matter, Furka Pass, ingrowth core method, resource allocation, root-shoot ratio, *Sesleria caerulea* sward, standing biomass, storage organ

**Nomenclature** Lauber et al. (2012)

**Abbreviations** LC = low precipitation, calcareous bedrock; HC = high precipitation, calcareous bedrock; HS = high precipitation, siliceous bedrock; CT = control; MD = moderate drought; ED = extreme drought; trmt = treatment

### 6.2 Introduction

Primary production is one of the most essential ecosystem processes, since almost all life on Earth is directly or indirectly reliant on it. Plant growth and thus biomass productivity of terrestrial ecosystems rests upon favourable climatic and edaphic conditions. Temperature, radiation, and water impose climatic constraints on productivity, while water availability most strongly limits vegetation growth globally (Nemani et al. 2003). The major edaphic constraint arises from mineral nutrients, with nitrogen limitation being globally distributed (LeBauer & Treseder 2008). In alpine ecosystems, plant growth is primarily limited by low temperatures, but also by the absence of nitrogen, whereas water shortage plays a less decisive role (Körner 2003). Primary production integrates plant responses to changing growing conditions and thus is suitable to assess the stability of ecosystems under changing environmental conditions.

Climate change as a consequence of human activities is evident and progressing, with a further increase of global air temperatures and changes in the global water cycle (IPCC 2013) as well as a
Study 2

higher occurrence of extreme weather events (IPCC 2012). Based on localised climate change scenarios of mean temperature and precipitation, Switzerland is projected to experience increased temperatures in all seasons, with a maximum in summer, while precipitation will slightly increase in winter, but strongly decrease in summer towards the end of the 21st century (CH2011 2011, Fischer et al. 2012, Zubler et al. 2014). In addition, Switzerland is predicted to be subjected to an increased year-to-year variability of the summer climate, so that extreme events such as severe summer droughts might occur more frequently in the future (Schär et al. 2004). It is expected that an overall warming and associated changes in precipitation patterns and snow cover will influence alpine vegetation (Theurillat & Guisan 2001).

With increasing elevation, precipitation inputs rise in the European Alps (Frei & Schär 1998, Ellenberg & Leuschner 2010). Hence, moisture deficiency is uncommon in alpine vegetation and local water shortages occur only temporarily (Körner 2003). In the last centuries, long-lasting severe summer droughts occurred very rarely in alpine ecosystems (Van der Schrier et al. 2007), however an increased frequency and intensity of droughts in alpine regions is predicted for the near and long-term future (Gobiet et al. 2014). It is unclear how alpine grassland ecosystems will respond to altered precipitation regimes, and particularly to prolonged summer droughts. Little is known about the stability of these ecosystems, when exposed to such climate extremes, which did not occur so far. During the growing season, alpine grassland biomass productivity is limited mainly by the availability of nutrients, in particular by the supply of enough plant-available nitrogen. If summer droughts will become more frequent, water availability may be restricted temporarily leading to a water shortage. A water deficiency can directly cause physiological drought stress, but may affect alpine grassland also indirectly by restricting the nitrogen availability (through reduced decomposition and mineralisation) or reducing the transpirative cooling capacity, leading to nutrient and heat stress, respectively. All these drought-induced effects may co-limit plant growth and thereby reduce the biomass production of alpine grassland. It is unclear how recurring summer drought events of different severity affect alpine grassland biomass production above and below the ground. The biomass responses to drought might vary dependent on local environmental conditions such as geology or macroclimate and might change over time.

To study the impacts of droughts on grassland ecosystems, mainly two approaches are followed: (1) monitoring the effect of naturally occurring droughts on grassland systems in observational field studies (e.g. Weaver et al. 1935, Gibbens & Beck 1988, Stampfli & Zeiter 2004) or (2) measuring the responses of grassland systems to simulated droughts in field experiments manipulating rainfall amounts. Such experimental field studies were conducted in arid or semi-arid regions, which are regularly exposed to drought conditions (e.g. Sternberg et al. 1999, Köchy & Wilson 2004, English et
al. 2005, Schwinning et al. 2005, Yahdjian & Sala 2006, Arredondo et al. 2016), but also in temperate regions, where droughts did not occur frequently so far (e.g. Morecroft et al. 2004, Kahmen et al. 2005, Gilgen & Buchmann 2009, Hartmann & Niklaus 2012, Vogel et al. 2012, Cantarel et al. 2013, Prechsl et al. 2015, Deléglise et al. 2015, Hofer et al. 2016). However, there is a significant lack of experiments simulating droughts in alpine regions and thus, the response of alpine grassland systems to drier conditions has been poorly investigated so far. A short-term experiment by De Boeck et al. (2016) investigated the influence of both drought and heat waves on alpine grassland. But to our knowledge, no multi-year experiment exists so far, which examined the impact of recurring summer droughts on grassland in the alpine zone, i.e. above the climatic treeline.

Alpine grassland ecosystems deliver several ecosystem services such as slope stability, water provision and quality, forage quantity and quality, carbon sequestration, conservation of botanical diversity and aesthetic value of landscape (Lamarque et al. 2011). For most of these services, plant growth and thus biomass productivity plays a key role. Therefore, a drought-induced decrease of the biomass productivity could compromise the provision of these services. Slope stability for example, one of the most important ecosystem services of alpine grassland, rests upon an adequate ground cover and intact root system (Körner 2003). Hence, both above- and below-ground biomass pools are relevant to ensure slope stability. A reduction in the above-ground pool results in an increased area of bare ground and consequently a decreased ground protection and higher erosion risk (see Study 1 of this thesis), whereas a reduction in the below-ground pool leads to a decreased rooting density involving a decreased soil stability and higher landslide risk, both changes negatively influencing the slope stability. Summer droughts may change the biomass pools of the swards in such a way that the alpine grassland sites become more susceptible to erosion and landslides. As heavy rainfall events are predicted to occur more frequently in the future, slope stability could be jeopardised after prolonged summer droughts.

A plant consists of different organs, which either belong to the above-ground biomass compartment (leaves, stems and reproductive organs) or to the below-ground compartment (roots and storage organs, Körner & Renhardt 1987). The biomass allocation to these different organs and thus the relative size of the above- and below-ground compartments of a given plant species is largely genetically determined and thus, biomass partitioning within a species results in rather conservative patterns (Körner 1991). However, environmental influences can trigger significant shifts in investments towards needed structures (de Kroon et al. 2009). The above- and below-ground biomass compartments in grassland ecosystems perform various functions. The main function of above-ground biomass is carbon assimilation by photosynthesis, while below-ground biomass is responsible for water and nutrient uptake from the soil. Carbohydrates, water and nutrients are exchanged between the
two compartments and their fluxes determine the coupling of the roots and shoots in the grassland system. Scheiter & Higgins (2013) showed that the behaviour of a disturbed grassland system is strongly influenced by the strength of coupling between the above- and below-ground biomass compartments. Intermediate levels of coupling between roots and shoots optimised the trade-off between productivity and persistence of the grassland system. Thus, root-shoot interactions resulting in a changed biomass partitioning may play a key role in alpine grassland, when exposed to summer droughts and may maintain the persistence of the system.

The biomass responses of temperate grassland systems to experimental droughts have been widely studied. In general, the studies yielded consistent results and revealed that drought conditions clearly reduced above-ground productivity, while the allocation of carbon to below-ground organs was enhanced. Alpine grassland systems differ fundamentally from temperate systems by a comparatively low overall annual biomass production and a proportionately large below-ground biomass compartment, with possible implications on the drought responses. In contrast to temperate grassland systems with a growing season of up to six months (Gilgen & Buchmann 2009), the period with favourable growth conditions in alpine systems lasts only a few months (2.5 months at our study sites). If expressed per unit of growing period duration rather than per year, alpine grassland productivity is in fact not necessarily low (Körner 2003). The low annual biomass production in alpine grassland compared to temperate grassland systems can be explained mainly by the short growing season. This suggests that a drought period of equal duration, taking place during the growing season, may have a stronger impact on the alpine system than on the temperate one. In the alpine system, a drought-induced production loss is proportionately bigger and may hardly be compensated in the current season due to time constraints. In contrast, a temperate grassland system with a much longer growing season is able to largely compensate a production loss after a drought in the ongoing season (Hofer et al. 2016). The below-ground biomass compartment, consisting of roots and storage organs, plays a major role in high elevation ecosystems and especially in alpine grassland systems (Körner & Renhardt 1987, Hitz et al. 2001). This large below-ground biomass compartment may have the capacity to better buffer the drought-induced dieback of above-ground biomass in alpine grassland compared to temperate grassland. This allocation pattern suggests that alpine grassland vegetation is able to survive a drought period in the soil and quickly recover thereafter from below the ground. Both resistance and resilience of grassland vegetation are basic requirements to maintain ecosystem stability when subjected to drought disturbances.

The objective of this multi-year study was to quantify alpine grassland above- and below-ground biomass responses (biomass pools and productivity) at community level to summer droughts, which are predicted to increase in frequency and severity due to climate change. For this, we simulated
recurring summer droughts with rainout shelters at three sites in the Swiss Central Alps with typical alpine grassland communities (Sesleria caerulea and Carex curvula swards). The experimental sites were located on steep mountain slopes at about 2500 m a.s.l. and varying in macroclimate (low vs. high precipitation) and geology (calcareous vs. siliceous bedrock). During three consecutive growing seasons, the alpine swards were exposed to three treatments: (1) ambient rainfall (control), (2) six weeks rainfall exclusion (moderate drought) and (3) twelve weeks rainfall exclusion (extreme drought). To study the drought-induced responses in biomass production we sampled standing above- and below-ground biomass in the second and third year of the experiment by clipping and using a split tube sampler, respectively. To specifically measure the effect of summer drought on below-ground biomass productivity, we applied the ingrowth core method in the third year of rainfall manipulation. We hypothesised that summer droughts adversely affect the overall productivity of alpine grassland, which should result in reduced above- and below-ground biomass production during the drought periods as well as reduced above- and below-ground biomass pools after the drought periods. We addressed the following questions: (1) Do alpine grassland sites differ in their biomass production under the current precipitation regime? (2) How is the above-ground biomass production of alpine grassland affected by recurring experimental summer droughts? (3) How does the below-ground biomass production respond to drought conditions? (4) To what extent is the overall biomass production of alpine grassland restricted by periodic drought disturbances?

6.3 Methods

6.3.1 Study sites

Our climate change study was conducted in the alpine zone at about 2500 m a.s.l. at Albula Pass, Grisons (46°35’ N, 9°50’ E) and Furka Pass, Valais (46°34’ N, 8°25’ E). The two regions are situated in the Swiss Central Alps. The climate at this elevation is characterised by cold winters with permanent snow cover followed by short summers, limiting the growing season to about 75 days (from late June to mid-September). Both regions had a similar mean annual temperature (-2.2 °C at Albula Pass and -2.1 °C at Furka Pass, ETH Zurich et al. 2004), but differed significantly in the mean annual precipitation (845 mm at Albula Pass and 1920 mm at Furka Pass, ETH Zurich et al. 2004). The experiment was established at three grassland sites with contrasting conditions in macroclimate and geology: (1) a site at Albula Pass with low precipitation and calcareous bedrock (referred to as LC site), (2) a site at Furka Pass with high precipitation and calcareous bedrock (HC site), and (3) a site at Furka Pass with high precipitation and siliceous bedrock (HS site). The sites were located on steep mountain slopes representing the predominant landform at this elevation. The slopes at LC and HC sites were
characterised by a 30° inclination and a southern aspect, and the one at HS site by a 40° inclination and a western aspect. The vegetation at the three sites consisted of typical alpine grassland communities: two *Sesleria caerulea*-dominated swards (*Seslerio-Caricetum sempervirentis*) on calcareous bedrock with *Sesleria caerulea*, *Carex sempervirens*, *Anthyllis vulneraria ssp. alpestris*, *Aster alpinus* and *Helianthemum nummularium ssp. grandiflorum* as characteristic plant species and a *Carex curvula*-dominated sward (*Caricetum curvulae*) on siliceous bedrock with *Carex curvula*, *Helictotrichon versicolor*, *Trifolium alpinum*, *Leontodon helveticus* and *Homogyne alpina* as characteristic plant species. *Sesleria caerulea* and *Carex curvula* swards form widespread natural grassland vegetation and therefore represent the prevailing grassland communities in the alpine zone (Ellenberg & Leuschner 2010). Most of the plant species at the three grassland sites were perennial, and many of them were able to form below-ground storage organs. Grazing by domestic and wild herbivores played only a minor role and thus, grazing intensity was very low at the three grassland sites.

### 6.3.2 Experimental design and drought simulation

At each of the three sites, twelve 1 × 1 m experimental plots were arranged in four replicated units (blocks) with three plots each. The sward plots have been selected such as to achieve homogeneity in species composition, vegetation structure, micro-topography and rock cover preferably within each site, but necessarily within each block. The experimental treatments included (1) a control (referred to as CT), (2) moderate drought (MD) and (3) extreme drought (ED). The three treatments were randomly assigned to the three plots of each block. Hence, the application of each treatment was replicated four times at each site. This experimental set-up yielded a total of 3 (sites) × 4 (blocks) × 3 (treatments) = 36 plots, equivalent to a total of 24 rainout shelters installed. It corresponds to a locally reproduced randomised complete block design.

We simulated recurring summer droughts at the three grassland sites by covering the experimental plots with rainout shelters and thereby excluding the ambient rainfall in the summers of 2008, 2009 and 2010. In order to create drought at different severity levels, we manipulated rainfall during periods varying in length. After installing the shelters at the beginning of each growing season (late June), we excluded rainfall during approximately six weeks to simulate moderate drought (MD treatment) and during approximately twelve weeks to simulate extreme drought (ED treatment). Control plots remained uncovered and thus received ambient rainfall (CT treatment). Our rainout shelter design was based on a shelter template that had been proven to be suitable for realistic drought simulations (Kahmen et al. 2005, Gilgen & Buchmann 2009), but was modified for alpine conditions (e.g. lower height to provide stability to withstand strong winds, roof slope of 45° to facil-
Study 2

itate the gliding of snow). The shelter consisted of a triangular aluminium construction that was covered by an UV-B-transmissible greenhouse film (Luminance AF Window, Folitec, Germany). The base area of the shelter was $2.4 \times 3.0$ m and the height 1.2 m. In essence, the shelter was tunnel-shaped with large openings parallel to the main wind direction, allowing for constant wind through-flow preventing warming beneath the shelters. To minimise edge effects of the shelter, the covered base area was six times larger than the central $1 \times 1$ m sampling plot. Plastic shields were inserted into the soil upslope of the plots to interrupt surface and sub-surface water flow at the HS site with the steepest slope. During the drought simulation period, herbivores were excluded from the experimental plots by fencing. At the end of each growing season (mid-September), rainout shelters were removed and plants overwintered under snow.

To ensure significant differences in water availability between covered plots (MD, ED treatment) and uncovered plots (CT treatment), soil moisture measurements (ThetaProbe type ML2x, Delta-T Devices Ltd, Cambridge, UK) were carried out. Soil moisture was determined just before the start of the drought simulation (late June), at the end of the MD simulation (early August) and at the end of the ED simulation (mid-September). The measurements revealed that the drought simulation was successful, as the desired drying-out under the shelters was observed and the two drought treatments (MD and ED) actually led to droughts differing in severity (Fig. 6.1).

6.3.3 Data collection

In both years 2009 and 2010, i.e. in the second and third year of the experiment, all standing above-ground plant material was harvested at the time of peak standing above-ground biomass (early August, referred to as harvest date H1) and at the end of the growing season (mid-September, harvest date H2) at each of the three sites. At each harvest, we collected six subsamples at fixed and regularly arranged positions on each of the $1 \times 1$ m sampling plots. The $4 \times 24$ cm rectangular subsampling areas were aligned with the longer side in slope direction and distributed in two rows of three perpendicular to the slope direction. The total subsampling area corresponded to an area of $576$ cm$^2$ and accordingly 5.76% of the entire area of the $1 \times 1$ m plot. We clipped all above-ground plant material 0 cm above the ground by using a small harvesting frame and scissors. The collected material represented standing phytomass and litter, including a high proportion of necromass and litter produced in previous years (see Table 6.1 for terminology of plant material fractions). The six subsamples were pooled, resulting in one representative sample per sampling plot. Any following harvesting was carried out at slightly offset positions with the same arrangement pattern as in the first sampling. Plant material samples were stored in paper bags at 4 °C for a maximum of one week before
being separated into biomass, cryptogam mass and dead plant mass (see Table 6.1 for terminology of plant material fractions). Since litter could not be collected separately during the harvesting, it was combined with necromass, representing the fraction of dead plant mass. All samples were dried at 70 °C for at least 48 h to constant weight and thereafter dry matter (d.m.) of each plant material fraction was determined by weighing.

At the end of the growing season in 2009 (mid-September), i.e. after two years of summer drought simulation, standing below-ground biomass was sampled at Furka Pass (HC and HS sites). At Albula Pass (LC site), the soil had a high content of rocks and was very shallow, with bedrock reaching the top 10 cm of the profile, which made a collection of biomass samples below the ground impossible. To prevent disturbance on the 1 × 1 m sampling plots for above-ground biomass, below-ground biomass was sampled at regularly arranged subsampling positions perpendicular to the slope direction just above the upper edge of each plot. To collect soil cores, we used a split tube sampler (Eijkelkamp Soil & Water, Giesbeek, The Netherlands) with an inside diameter of 53 mm. By inserting the sampler perpendicular to the slope surface, we took four soil cores per plot with a length of 10 cm. The total subsampling area corresponded to an area of 88 cm² and accordingly 0.88% of the entire area of the 1 × 1 m plot. Each soil core was separated into two layers according to a soil depth of 0–5 and 5–10 cm. The four subsamples of each layer were pooled per plot for further preparation and stored in polyethylene bags at 4 °C for a maximum of one week. The above-ground plant material was removed from the soil cores with a knife, and below-ground biomass in the cores was manually separated from soil and rock fragments using a 2-mm and 1-mm sieve and tweezers. Afterwards, biomass was washed with tap water and separated from remaining soil using a 2-mm and 0.4-mm sieve, tea strainer and tweezers. Subsequently, sand adhering to the biomass was removed with tweezers. Finally, biomass was put into small water-filled polyethylene bags and was treated in an ultrasonic cleaner with water for 2 min before being rinsed with water. Biomass was separated into roots and storage organs. All biomass samples were dried at 70 °C for at least 48 h to constant weight and thereafter dry matter (d.m.) of each biomass component was determined by weighing. The volume of rock fragments (diameter > 1mm) in each core was measured by water displacement in a volumetric flask. Since the total below-ground biomass in the core volume was independent of the rock volume (data not shown), biomass was related to the total core volume and rock fragments were not taken into account. Since necromass, cryptogam mass and litter were negligible below the ground, these plant material fractions were not collected.

Below-ground biomass productivity was measured at Furka Pass (HC and HS sites), using the ingrowth core method. Shortly after sampling standing below-ground biomass (mid-September 2009), four ingrowth cores per plot were inserted into the existing 10 cm deep drilled sampling holes. An
ingrowth core consisted of an aluminium cylinder with an interior diameter of 4.6 cm and a length of 10 cm. Three lateral rectangular openings allowed for the growth of roots into the cylinder. Soil, collected at each corresponding site and sieved to 2 mm and thus free of gravel and plant material, served as substrate to fill the cores. We removed the ingrowth cores with the split tube sampler at the end of the growing season in 2010 (mid-September), i.e. after three years of summer drought simulation, to measure the increment of the below-ground biomass during the growth period in 2010. The ingrowth cores were stored in polyethylene bags at 4 °C for a maximum of one week. After removing each soil core from the aluminium cylinder, it was separated into two layers according to a soil depth of 0–5 and 5–10 cm. For further preparation, the four subsamples of each layer were pooled per plot. The ingrown biomass in the cores was washed and separated from soil as well as ultrasonically cleaned with the same procedure as for standing biomass. Thereafter, biomass was separated into roots and storage organs. All biomass samples were dried at 70 °C for at least 48 h to constant weight before being weighed to determine dry matter of each biomass component.

6.3.4 Data analysis

All dry matter data were spatially upscaled to 1 m². The data of the standing above- and below-ground biomass, measured at the end of the growing season in 2009 (mid-September), were used to calculate the total standing biomass (sum of standing above- and below-ground biomass) and the root-shoot ratio (ratio of standing below- to above-ground biomass) per plot. All data were summarised by the mean and standard error of the mean (s.e.m.) based on four replicated measurements for each factor level combination (balanced design, no missing data). Statistical analyses were performed using IBM SPSS Statistics 20. Data were analysed with either a factorial mixed analysis of variance (ANOVA) or a two-way ANOVA. The factorial mixed ANOVA included multiple between- and within-subjects factors and, thus, corresponded to an extension of the repeated measures ANOVA, whereas the two-way ANOVA included only two between-subjects factors. A plot served as experimental unit (subject) and, hence, the data from measurements on different plots were independent. The between-subjects factors were site (LC, HC, HS), block (1–4 at each site) and treatment (CT, MD, ED). Block was nested within site and was omitted from the specific model when its main effect was not statistically significant (p > 0.05). Since measurements were taken also on the same plot, repeated in time and space, moreover, our experiment yielded correlated data. To account for this, year (2009, 2010), harvest date (H1, H2) and soil depth (0–5, 5–10 cm) were used as within-subjects factors.
Prior to the analyses we inspected a boxplot to ensure that there were no significant outliers and ran a Shapiro-Wilk test of normality to guarantee that data were normally distributed. We checked these assumptions on data split by site since there were only four values in each cell of the design. The factorial mixed ANOVA was carried out using the “General linear model (GLM)/Repeated measures” procedure and the two-way ANOVA using the “GLM/Univariate” procedure. These procedures also include a Levene’s test of equality of error variances to check if data met homogeneity of variances. All within-subject factors had two levels and therefore, the assumption of sphericity (equal variances of the differences between groups) was consequently met for all correlated data. Finally, we performed a residual analysis for each specific model by visually testing the residuals for homoscedasticity. All data could be included in the analyses without transformation.

To statistically evaluate standing above-ground biomass data (and data of other above-ground components), we applied a model with site, treatment, year and harvest date as factors. A model considering site (only with HC and HS levels), treatment and soil depth was employed for standing below-ground biomass data. We used the same model to analyse below-ground biomass productivity data, but in this case, we kept block as a factor. We finally evaluated the total standing biomass and the root-shoot ratio data with a model including site (only with HC and HS levels) and treatment. In each specific model we tested for the main effects and all interactions of the factors, except for the interactions with block. Model calculations were based on type III sum of squares. To analyse the specific effects of the treatment at each site separately, we tested the simple main effects of treatment on the dependent variables at each level of site across all other factor levels using the overall error terms. To follow up a statistically significant simple main effect of treatment, we performed all pairwise comparisons of the group means of the dependent variables. Because multiple comparisons within each simple main effect were considered a family of comparisons, a Bonferroni adjustment was applied to the significance values. In all analyses, $P$-values $\leq 0.05$ were considered statistically significant.
Table 6.1 Terminology used to describe plant material fractions of alpine grassland. The weight of each plant material fraction was specified in gram dry matter (d.m.) and related to 1 square metre.

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
<th>Measurement unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomass</td>
<td>Attached living phanerogam material</td>
<td>g d.m. m⁻²</td>
</tr>
<tr>
<td>Necromass</td>
<td>Attached dead phanerogam material</td>
<td>g d.m. m⁻²</td>
</tr>
<tr>
<td>Cryptogam mass</td>
<td>Attached cryptogam material (mosses and lichens), no distinction between living and dead</td>
<td>g d.m. m⁻²</td>
</tr>
<tr>
<td>Litter</td>
<td>Detached senescent phanerogam and cryptogam material</td>
<td>g d.m. m⁻²</td>
</tr>
<tr>
<td>Phytomass</td>
<td>All attached plant material (aggregation of biomass, necromass and cryptogam mass)</td>
<td>g d.m. m⁻²</td>
</tr>
<tr>
<td>Dead plant mass</td>
<td>All dead plant material (aggregation of necromass and litter)</td>
<td>g d.m. m⁻²</td>
</tr>
<tr>
<td>Total plant mass</td>
<td>All plant material (aggregation of biomass, necromass, cryptogam mass and litter)</td>
<td>g d.m. m⁻²</td>
</tr>
</tbody>
</table>
Figure 6.1 Volumetric soil moisture content (VSMC) of the treatment plots of the drought experiment in alpine grassland. Measurements were taken just before the start of the drought simulation (pre trmt, late June), at the end of the moderate drought simulation (early August) and at the end of the extreme drought simulation (mid-September) in both years 2009 and 2010. LC: low precipitation, calcareous bedrock; HC: high precipitation, calcareous bedrock; HS: high precipitation, siliceous bedrock. CT: control, ambient rainfall; MD: moderate drought, six weeks rainfall exclusion; ED: extreme drought, twelve weeks rainfall exclusion. Displayed are means ± 1 standard error, n = 4 per site and treatment.
6.4 Results

6.4.1 Above-ground biomass responses

Standing above-ground biomass differed between the sites (Fig. 6.2, Table 6.2, p\text{site} < 0.001), with the LC site having the highest amount of standing biomass (533 g m\(^{-2}\), measured at the time of peak standing biomass H1 in 2009 under CT conditions), followed by the HC (263 g m\(^{-2}\)) and HS site (232 g m\(^{-2}\)). Standing above-ground biomass differed between the years (p\text{year} < 0.001). It was lower in the year 2010 compared to 2009 at the LC (-18%, H1, CT) and HS site (-21%), whereas there were minor differences at HC site (+2%, p\text{year*site} = 0.003). And finally, standing above-ground biomass differed between the harvest dates (p\text{hdate} < 0.001), with a lower biomass at the end of the growing season (harvest date H2). In 2009, the die-back of the vegetation towards the end of the growing season amounted to 25% at HC site (CT conditions), 27% at LC site and 45% at HS site. This reduction was less pronounced in 2010 (p\text{year*hdate} = 0.002) and ranged from 19% at LC site to 29% at both HC and HS sites. This indicated a delayed senescence in 2010.

The drought treatments led to a reduction of the standing above-ground biomass (Fig. 6.2, Table 6.2, p\text{trmt} < 0.001) at each site (p\text{site*trmt} = n.s.) as well as at each harvest date (p\text{hdate*trmt} = n.s.) in both years (p\text{year*trmt} = n.s.). The reduction of the biomass pools over the three sites and both years differed in the extent and ranged at the time of peak standing biomass (harvest date H1) from 12 to 37% under the MD treatment and from 5 to 47% under the ED treatment, while it ranged at the end of the growing season (harvest date H2) from 4 to 40% when treated with MD and from 12 to 53% when treated with ED. At the first harvest date (H1), standing above-ground biomass of the plots treated with both MD (p < 0.001) and ED treatments (p = 0.001) significantly differed from the plots with CT conditions, when statistically analysed over the two years and the three sites. As expected, the two drought treatments (MD, ED) did not differ at the H1 harvest date (p = n.s.). At the second harvest date (H2), both the MD (p = 0.019) and ED treatments (p = 0.004) again differed significantly from the CT treatment. Surprisingly, the ED treatment did not have a stronger effect on standing above-ground biomass than the MD treatment at the end of the growing season, since the two drought treatments did not differ significantly at the H2 harvest date (p = n.s.).

The above-ground dead plant mass differed between the sites (Table 6.3, p\text{site} < 0.001). It ranged from 189 g m\(^{-2}\) at HS site (H1, 2009, CT conditions) over 489 g m\(^{-2}\) at HC site to 561 g m\(^{-2}\) at LC site. But it was not influenced by the drought treatments (p\text{trmt} = n.s.). Similarly, the sites differed in their standing above-ground cryptogam mass (p\text{site} < 0.001), which ranged from 10 g m\(^{-2}\) at LC site (H1, 2009, CT conditions) over 52 g m\(^{-2}\) at HS site to 63 g m\(^{-2}\) at HC site, whereas the drought treatments did not affect the cryptogam mass (p\text{trmt} = n.s.).
6.4.2 Below-ground biomass responses

The two HC and HS sites differed in their standing below-ground biomass (Fig. 6.3, Table 6.4, $p_{site} < 0.001$), whereas the HS site with 822 g m$^{-2}$ contained almost twice as large pools as the HC site with 505 g m$^{-2}$ under CT conditions. Standing below-ground biomass differed between the layers of 0–5 and 5–10 cm soil depth ($p_{depth} < 0.001$). In both alpine swards, the main fraction of the below-ground biomass was found in the uppermost layer (77% at HC and 79% at HS site). Under CT conditions, the storage organs were missing (HC site) or their amount was not of great importance as observed at the HS site.

Drought led to a significant increase of standing below-ground biomass ($p_{trmt} < 0.001$) at both sites ($p_{site\timestrmt} = \text{n.s.}$), with a clear effect on both components, the roots ($p_{trmt} = 0.004$) and the storage organs ($p_{trmt} = 0.005$). Total below-ground biomass at HC site increased from 505 g m$^{-2}$ under CT conditions to 713 g m$^{-2}$ (+41%) under MD conditions to 909 g m$^{-2}$ (+80%) under ED conditions. At HS site, the biomass pools increased from 822 g m$^{-2}$ under the CT treatment to 1209 g m$^{-2}$ (+47%) when treated with MD to 1231 g m$^{-2}$ (+50%) when treated with ED. The drought treatments had not the same effect in each soil layer ($p_{depth\timestrmt} = 0.001$), while the lower soil layer remained largely unaffected by drought.

On the other hand, the below-ground biomass productivity measured by ingrowth cores during the growing season did not significantly differ between the two HC and HS sites and was about 250 g m$^{-2}$ a$^{-1}$ under CT conditions (Fig. 6.4, Table 6.5, $p_{site} = \text{n.s.}$). Storage organs did hardly grow into the ingrowth cores, only some small organs were found in the ED treatment cores. Surprisingly, by using the ingrowth cores, the roots also grew in the lower layer. There were differences in the biomass productivity in the two soil layers ($p_{depth} = 0.013$), but different patterns at the two sites ($p_{depth\timessite} = 0.005$). At HC site, the amount of produced roots was balanced between the two layers, whereas at HS site the production was lower in the bottom layer.

The drought treatments led to an increase of the biomass productivity ($p_{trmt} < 0.001$) at both HC and HS sites ($p_{site\timestrmt} = \text{n.s.}$) and in both 0–5 and 5–10 cm soil layers ($p_{depth\timestrmt} = \text{n.s.}$). Total below-ground biomass productivity at HC site increased from 248 g m$^{-2}$ a$^{-1}$ under CT conditions to 285 g m$^{-2}$ a$^{-1}$ (+15%) under MD conditions to 348 g m$^{-2}$ a$^{-1}$ (+40%) under ED conditions. At HS site the productivity was enhanced from 251 g m$^{-2}$ a$^{-1}$ under the CT treatment to 258 g m$^{-2}$ a$^{-1}$ (+3%) when treated with MD to 312 g m$^{-2}$ a$^{-1}$ (+24%) when treated with ED. The drought treatments did not stimulate the formation of below-ground storage organs in the ingrowth cores, which may be due to the aluminium cylinders impeding the penetration by storage organs.
6.4.3 Overall system biomass responses

The two sites differed in total standing biomass (sum of standing above- and below-ground biomass, Fig. 6.5, Table 6.6, $p_{\text{site}} = 0.001$), with the HC site containing 701 g m$^{-2}$ biomass under CT conditions and the HS site 950 g m$^{-2}$. The BGB-AGB ratios (below-ground biomass to above-ground biomass ratio) differed significantly between the two sites (Fig. 6.6, Table 6.6, $p_{\text{site}} = 0.012$), the one at HC site was 2.7 (CT conditions), whereas the one at HS site was clearly higher and amounted to 6.5.

With increasing drought severity, we observed a significant decrease of the above-ground biomass pools, whereas the below-ground pools significantly increased. The enlargement of the below-ground biomass pools clearly overcompensated the decrease of the above-ground pools resulting in an increase of the total standing biomass at both sites (Fig. 6.5, Table 6.6, $p_{\text{trmt}} = 0.005$, $p_{\text{site} \times \text{trmt}} = \text{n.s.}$) under drier conditions. Total standing biomass increased from 701 g m$^{-2}$ under CT conditions to 900 g m$^{-2}$ under MD conditions to 1001 g m$^{-2}$ under ED conditions at HC site and from 950 g m$^{-2}$ under the CT treatment to 1297 g m$^{-2}$ under the MD treatment to 1344 g m$^{-2}$ under the ED treatment at HS site. At HC site, the shift in standing biomass from above to below the ground was gradual from CT to MD to ED conditions. In contrast, we found an abrupt shift at HS site from CT to MD conditions, with no further change between the two drought treatments differing in severity. Due to the changed pattern in the above- and below-ground biomass pools under drought, the BGB-AGB ratio responded strongly to drier conditions (Fig. 6.6, Table 6.6, $p_{\text{trmt}} = 0.005$) at both sites ($p_{\text{site} \times \text{trmt}} = \text{n.s.}$). The ratio increased from 2.7 to 4.0 to 12.3 from CT to MD to ED conditions at HC site, whereas it increased from 6.5 to 14.4 to 12.2 from CT to MD to ED conditions at HS site.
Table 6.2  Results of the factorial mixed analysis of variance (ANOVA) testing for the main effects of site, treatment, year and harvest date and their interactions on standing above-ground biomass. Significant test results are given in bold face; n = 4 per site and treatment.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of squares</th>
<th>d.f.</th>
<th>Mean square</th>
<th>F</th>
<th>Sig.</th>
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<td><strong>Tests of between-subjects effects</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
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<td>7409170.584</td>
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<td>87550.195</td>
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<td>10552.796</td>
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<tr>
<td>Error</td>
<td>178117.056</td>
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<td>6596.928</td>
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<tr>
<td><strong>Tests of within-subjects effects</strong></td>
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<td></td>
<td></td>
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<td></td>
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<td>2606.918</td>
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<td>0.613</td>
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<td>Year * harvest date * treatment</td>
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<td>50397.774</td>
<td>27</td>
<td>1866.584</td>
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Table 6.3 Standing above-ground cryptogam mass and above-ground dead plant mass (necromass and litter) harvested in 2009 and 2010 at harvest date H1 (early August) and H2 (mid-September) at three alpine grassland sites treated with ambient rainfall (CT), moderate drought (MD) and extreme drought (ED). LC: low precipitation, calcareous bedrock, HC: high precipitation, calcareous bedrock, HS: high precipitation, siliceous bedrock. Displayed are means ± 1 standard error, n = 4 per site and treatment.

<table>
<thead>
<tr>
<th>Site Treatment</th>
<th>2009, H1</th>
<th>2009, H2</th>
<th>2010, H1</th>
<th>2010, H2</th>
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<tr>
<td></td>
<td>Crypto-</td>
<td>Dead</td>
<td>Crypto-</td>
<td>Dead</td>
</tr>
<tr>
<td></td>
<td>gams</td>
<td>plants</td>
<td>gams</td>
<td>plants</td>
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<tr>
<td>LC CT</td>
<td>10±13</td>
<td>561±44</td>
<td>25±15</td>
<td>443±59</td>
</tr>
<tr>
<td>LC MD</td>
<td>9±5</td>
<td>562±56</td>
<td>7±3</td>
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<tr>
<td>LC ED</td>
<td>13±5</td>
<td>643±82</td>
<td>15±5</td>
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<tr>
<td>HC CT</td>
<td>63±4</td>
<td>489±42</td>
<td>88±25</td>
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<tr>
<td>HC MD</td>
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<td>508±93</td>
<td>63±11</td>
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<tr>
<td>HC ED</td>
<td>62±21</td>
<td>518±46</td>
<td>130±27</td>
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<tr>
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<td>62±18</td>
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<td>HS MD</td>
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<td>171±53</td>
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<td>HS ED</td>
<td>34±9</td>
<td>179±36</td>
<td>33±5</td>
<td>283±60</td>
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Table 6.4 Results of the factorial mixed analysis of variance (ANOVA) testing for the main effects of site, treatment and soil depth and their interactions on standing below-ground biomass. Significant test results are given in bold face; n = 4 per site and treatment.

<table>
<thead>
<tr>
<th>Source</th>
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<td>594.170</td>
<td>(&lt; 0.001)</td>
<td>85.692</td>
<td>(&lt; 0.001)</td>
<td>654.430</td>
<td>(&lt; 0.001)</td>
</tr>
<tr>
<td>Site</td>
<td>1</td>
<td>11.750</td>
<td>(0.003)</td>
<td>33.644</td>
<td>(&lt; 0.001)</td>
<td>29.082</td>
<td>(&lt; 0.001)</td>
</tr>
<tr>
<td>Treatment</td>
<td>2</td>
<td>7.443</td>
<td>(0.004)</td>
<td>7.180</td>
<td>(0.005)</td>
<td>11.965</td>
<td>(&lt; 0.001)</td>
</tr>
<tr>
<td>Site * treatment</td>
<td>2</td>
<td>0.313</td>
<td>0.735</td>
<td>1.314</td>
<td>0.293</td>
<td>0.698</td>
<td>0.511</td>
</tr>
<tr>
<td>Error</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tests of within-subjects</td>
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<td></td>
<td></td>
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</tr>
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<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Soil depth</td>
<td>1</td>
<td>278.904</td>
<td>(&lt; 0.001)</td>
<td>103.460</td>
<td>(&lt; 0.001)</td>
<td>342.536</td>
<td>(&lt; 0.001)</td>
</tr>
<tr>
<td>Soil depth * site</td>
<td>1</td>
<td>8.453</td>
<td>(0.009)</td>
<td>36.280</td>
<td>(&lt; 0.001)</td>
<td>23.988</td>
<td>(&lt; 0.001)</td>
</tr>
<tr>
<td>Soil depth * treatment</td>
<td>2</td>
<td>6.379</td>
<td>(0.008)</td>
<td>7.618</td>
<td>(0.004)</td>
<td>9.898</td>
<td>(0.001)</td>
</tr>
<tr>
<td>Soil depth * site * treatment</td>
<td>2</td>
<td>0.558</td>
<td>0.582</td>
<td>1.291</td>
<td>0.299</td>
<td>1.201</td>
<td>0.324</td>
</tr>
<tr>
<td>Error(soil depth)</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 6.5 Results of the factorial mixed analysis of variance (ANOVA) testing for the main effects of site, block within site, treatment and soil depth and their interactions on below-ground biomass production. Significant test results are given in bold face; n = 4 per site and treatment.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>Roots</th>
<th></th>
<th>Storage organs</th>
<th></th>
<th>Total biomass</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>Sig.</td>
<td>F</td>
<td>Sig.</td>
<td>F</td>
<td>Sig.</td>
</tr>
<tr>
<td>Tests of between-subjects effects</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>2439.205</td>
<td>&lt; 0.001</td>
<td>10.994</td>
<td>0.006</td>
<td>2452.135</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Site</td>
<td>1</td>
<td>3.594</td>
<td>0.082</td>
<td>5.321</td>
<td>0.040</td>
<td>3.204</td>
<td>0.099</td>
</tr>
<tr>
<td>Block(site)</td>
<td>6</td>
<td>12.438</td>
<td>&lt; 0.001</td>
<td>1.442</td>
<td>0.277</td>
<td>12.094</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Treatment</td>
<td>2</td>
<td>16.854</td>
<td>&lt; 0.001</td>
<td>3.435</td>
<td>0.066</td>
<td>17.540</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Site * treatment</td>
<td>2</td>
<td>1.130</td>
<td>0.355</td>
<td>0.889</td>
<td>0.437</td>
<td>1.041</td>
<td>0.383</td>
</tr>
<tr>
<td>Error</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tests of within-subjects effects</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil depth</td>
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<td>8.423</td>
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<td>1.932</td>
<td>0.190</td>
<td>8.574</td>
<td>0.013</td>
</tr>
<tr>
<td>Soil depth * site</td>
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<td>11.083</td>
<td>0.006</td>
<td>0.004</td>
<td>0.950</td>
<td>11.870</td>
<td>0.005</td>
</tr>
<tr>
<td>Soil depth * block(site)</td>
<td>6</td>
<td>1.096</td>
<td>0.418</td>
<td>3.729</td>
<td>0.025</td>
<td>1.326</td>
<td>0.318</td>
</tr>
<tr>
<td>Soil depth * treatment</td>
<td>2</td>
<td>3.383</td>
<td>0.068</td>
<td>1.827</td>
<td>0.203</td>
<td>3.607</td>
<td>0.059</td>
</tr>
<tr>
<td>Soil depth * site * treatment</td>
<td>2</td>
<td>0.285</td>
<td>0.757</td>
<td>0.276</td>
<td>0.763</td>
<td>0.301</td>
<td>0.745</td>
</tr>
<tr>
<td>Error(soil depth)</td>
<td>12</td>
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<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>
Table 6.6  Results of the two-way analyses of variance (ANOVA) testing for main effects of site and treatment and their interaction on standing biomass components and the BGB-AGB ratio. Significant test results are given in bold face; n = 4 per site and treatment.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>Above-ground biomass</th>
<th>Roots</th>
<th>Storage organs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>Sig.</td>
<td>F</td>
</tr>
<tr>
<td>Corrected model</td>
<td>5</td>
<td>4.452</td>
<td>0.008</td>
<td>5.453</td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>218.069</td>
<td>&lt; 0.001</td>
<td>594.170</td>
</tr>
<tr>
<td>Site</td>
<td>1</td>
<td>7.204</td>
<td>0.015</td>
<td>11.750</td>
</tr>
<tr>
<td>Treatment</td>
<td>2</td>
<td>3.642</td>
<td>0.047</td>
<td>7.443</td>
</tr>
<tr>
<td>Site * treatment</td>
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<td>3.885</td>
<td>0.040</td>
<td>0.313</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corrected total</td>
<td>23</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>Below-ground biomass</th>
<th>Total biomass</th>
<th>BGB-AGB ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>Sig.</td>
<td>F</td>
</tr>
<tr>
<td>Corrected model</td>
<td>5</td>
<td>10.881</td>
<td>&lt; 0.001</td>
<td>6.545</td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>654.429</td>
<td>&lt; 0.001</td>
<td>692.245</td>
</tr>
<tr>
<td>Site</td>
<td>1</td>
<td>29.082</td>
<td>&lt; 0.001</td>
<td>17.663</td>
</tr>
<tr>
<td>Treatment</td>
<td>2</td>
<td>11.965</td>
<td>&lt; 0.001</td>
<td>7.229</td>
</tr>
<tr>
<td>Site * treatment</td>
<td>2</td>
<td>0.698</td>
<td>0.511</td>
<td>0.303</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corrected total</td>
<td>23</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 6.2 Standing above-ground biomass of alpine grassland treated with summer drought. Biomass was collected at the time of peak standing biomass (early August, harvest date H1) and at the end of the growing season (mid-September, harvest date H2) in both years 2009 and 2010. LC: low precipitation, calcareous bedrock, HC: high precipitation, calcareous bedrock, HS: high precipitation, siliceous bedrock. CT: ambient rainfall, MD: moderate drought, ED: extreme drought. Displayed are means ± 1 standard error, n = 4 per site, treatment and harvest.
Figure 6.3 Standing below-ground biomass (separated into roots and storage organs) of alpine grassland treated with summer drought. Biomass was collected at the end of the growing season (end of September) in 2009 in two soil layers (soil depth 0–5 and 5–10 cm). HC: high precipitation, calcareous bedrock, HS: high precipitation, siliceous bedrock. CT: ambient rainfall, MD: moderate drought, ED: extreme drought. Displayed are means ± 1 standard error, n = 4 per site and treatment.
Figure 6.4 Below-ground biomass production (separated into roots and storage organs) of alpine grassland treated with summer drought. Biomass was collected at the end of the growing season (end of September) in 2010 in two soil layers (soil depth 0–5 and 5–10 cm) and corresponds to the net biomass production during the growing season 2010. HC: high precipitation, calcareous bedrock, HS: high precipitation, siliceous bedrock. CT: ambient rainfall, MD: moderate drought, ED: extreme drought. Displayed are means ± 1 standard error, n = 4 per site and treatment.
Figure 6.5 Standing above- and below-ground biomass components (shoots, roots and storage organs) of alpine grassland treated with summer drought. Biomass was collected at the end of the growing season in 2009. HC: high precipitation, calcareous bedrock, HS: high precipitation, siliceous bedrock. CT: ambient rainfall, MD: moderate drought, ED: extreme drought. Displayed are means ± 1 standard error, n = 4 per site and treatment.
Figure 6.6 Ratio of below-ground to above-ground standing biomass (BGB-AGB ratio) in alpine grassland treated with summer drought. Biomass was collected at the end of the growing season in 2009. HC: high precipitation, calcareous bedrock, HS: high precipitation, siliceous bedrock. CT: ambient rainfall, MD: moderate drought, ED: extreme drought. Displayed are means ± 1 standard error, n = 4 per site and treatment.
6.5 Discussion

6.5.1 Comparison with other studies

The Carex curvula swards are well studied in their biomass pools and biomass productivity. The standing above-ground biomass ranges from 104 g m$^{-2}$ (Grabherr et al. 1978) over 110 g m$^{-2}$ (Rehder & Schäfer 1978) to 175 g m$^{-2}$ (Klug-Pümpel 1982). The below-ground biomass pools are significantly larger and range from 1077 g m$^{-2}$ (Mähr & Grabherr 1983) over 1258 g m$^{-2}$ (Grabherr et al. 1978) to 1750 g m$^{-2}$ (Rehder & Schäfer 1978). Both, Mähr & Grabherr (1983) as well as Rehder & Schäfer (1978) documented that about 80% of the below-ground biomass was found in the uppermost soil layer (0–5 cm). The below-ground biomass productivity amounts to 65 g m$^{-2}$ a$^{-1}$ (Mähr & Grabherr 1983) and 69 g m$^{-2}$ a$^{-1}$ (Grabherr et al. 1978), respectively. However, there is only one study describing the situation in a Sesleria caerulea sward. According to Rehder (1976), this sward is characterised by 320 g m$^{-2}$ standing above-ground biomass and 1400 g m$^{-2}$ standing below-ground biomass. The below-ground biomass productivity was not measured.

During summer drought events, a reduced above-ground biomass production as well as withering and senescing leaves are commonly observed in temperate grassland ecosystems. For example, during the 2003 European heat wave, this phenomenon was extensively observed in various grassland systems below the tree line in Switzerland (personal observations). This phenomenon was also widely confirmed in experimental drought studies, which were conducted in temperate grassland systems in the colline, montane and sub-alpine zone (Kahmen et al. 2005, Gilgen & Buchmann 2009, Hartmann & Niklaus 2012, Vogel et al. 2012, Cantarel et al. 2013, Deléglise et al. 2015, Prechsl et al. 2015, Hofer et al. 2016). With our study, we confirmed that experimental summer drought leads to a reduction of above-ground biomass production also in alpine grassland systems. This finding is in line with the outcome of a short-term study of De Boeck et al. (2016) who found that a drought exposure of 17 days is sufficient to negatively affect biomass production in alpine grassland.

Only few studies have tested the influence of an experimental summer drought on below-ground biomass production in grassland systems. Our study, which was conducted in alpine grassland, revealed that drier conditions resulted in a clear increase of below-ground biomass pools and productivity. Other experiments, performed in temperate grassland systems in the colline, montane and sub-alpine zone, show inconsistent effects of decreased precipitation on below-ground biomass production. Some found an enhanced below-ground productivity (Kahmen et al. 2005), some found only trends of increased root biomass (Prechsl et al. 2015) and some found no significant change in below-ground biomass productivity (Gilgen & Buchmann 2009). This suggests that alpine grassland...
systems are more responsive to drier conditions below the ground compared to grassland systems in lower elevation.

The duration of the simulated droughts in this experiment (6 weeks for moderate drought and 12 weeks for extreme drought) approximately corresponded to the duration of droughts in experiments carried out in temperate grassland systems. For example, Hofer et al. (2016) covered the grassland plots during 9 weeks, whereas Gilgen & Buchmann (2009) excluded rainfall during 12 weeks. Due to the much shorter growing season in alpine grassland systems, the simulated droughts in our study covered the half or full growing season. This is in contrast to the studies in temperate systems with droughts covering about 30% (Hofer et al. 2016) to 40% (Gilgen & Buchmann 2009) of the growing season. This strongly suggests that the droughts might have more strongly affected the alpine system. However, this was not the case. A possible explanation for the mitigated effect of the droughts in alpine grassland systems could be that the shelters excluded rainfall only to c. 50% from the experimental treatment plots, whereas the shelters applied in temperate grassland completely excluded rainfall during the drought treatment periods.

6.5.2 Role of roots and storage organs in the drought response of alpine grassland

This study showed that in alpine grassland, the below-ground biomass compartment, i.e. roots and storage organs, plays a key role during summer drought. This conclusion arises not only from the fact that the below-ground responses are so clear, but also because these responses may be essential for the maintenance of the functioning of the grassland ecosystem during and after drought periods.

In contrast to decreased biomass pools above the ground, the below-ground pools increased substantially under summer drought at the community level in both swards at Furka Pass (no data for the sward at Albula Pass). At both sites, independent of the sward community, most of the standing below-ground biomass was found in the top 5 cm of the soil. The increase of the biomass pools under drought conditions mainly took place in this soil layer, in the 5–10 cm layer almost no rooting activity was detected. The alpine swards responded to drought basically by the formation of fine roots, but also by creating below-ground storage organs. At the site with calcareous bedrock, no below-ground storage organs were present under control conditions, but with increasing drought we observed a gradual increase of storage organ biomass. At this site, summer drought seems to be a trigger for the formation of storage organs. It is impressive how much of storage organs were newly formed under drought in the first two years of the experiment. On siliceous bedrock, a larger amount of storage organ biomass was existing on control plots and under moderate drought condi-
tions there was a strong increase in biomass, but under extreme conditions, no further increase was observed, meaning that there was an abrupt response to increasing drought severity.

The fine roots of a plant are used to absorb water and nutrients. Under drought conditions, the plant extends the root system to get access to additional water supplies. Alternatively, root production may be enhanced to forage for nutrients, which may show a reduced availability due to drought-induced shortage of mineralisation rates. We expected that the drought-induced root formation would have taken place primarily in the subsoil to provide access to water in deeper soil layers. But the response in below-ground biomass was only found in the upper 5 cm of the soil. Possible explanations for this are: (1) After a rainfall, the short-term available water in the topsoil can be rapidly taken up. (2) Since litter de-composition and nutrient mineralisation mainly takes place in the topsoil, nutrient availability is highest there. (3) There is no ground water existing on steep slopes, therefore a water supply from the subsoil could not be guaranteed. (4) Due to a high proportion of soil skeleton, deeper soil layers could be poorly penetrated by roots. The last hypothesis is supported by the ingrowth core data. We found that the ingrowth cores were occupied by roots also in the lower part, i.e. 5–10 cm below the ground. In contrast to the natural soil, the substrate in the ingrowth cores was free of gravel and thus also the lower soil layer could be penetrated by roots without any mechanical obstruction. The fact that in the ingrowth cores rooting took also place in the lower layer shows that alpine grassland plant species in fact would be able to use water in deeper soil layers, but this is prevented due to the physical properties of alpine soils. The anchorage function of roots on steep grassland slopes is of great importance, not only for the plant itself, but also for the soil stability and thus landslide risk. Hence, the significantly increased rooting density led to an increased soil stability, which is a useful side-effect, especially under drier conditions.

A storage organ is a part of a plant specifically modified for storage of energy (generally in the form of carbohydrates), nutrients and water. It acts as a perennating organ, which allows plants to survive periods with adverse conditions and provides resources to resprout when conditions become favourable again. In the investigated alpine swards, most of the species are perennials. They have structures which allow them to endure the adverse conditions in the period between the growing seasons. Many of these species have storage organs (tap roots, rhizomes, tubers and bulbs), this is particularly obvious at the site on siliceous bedrock. Possible hypotheses for the drought-induced increase in storage organ biomass are: (1) Under drought conditions plants allocate more resources to reserve formation. The stored energy and nutrients can be used to better survive the drought period and to regrow early and rapid in the next growing season. (2) Under drought conditions photosynthesis might still produce assimilates (water availability is not limiting). Due to a shortage of nu-
trient availability above-ground growth is limited and resource supply exceeds demand. The surplus assimilates are accumulated as carbohydrates (mainly starch) in storage organs.

Since it was not possible to sample the below-ground biomass at Albula Pass, we do not have any information about the below-ground responses there. But, we suggest that the changes in the below-ground pool of biomass are restricted in the sward at Albula Pass due to the high content of rocks in the soil.

### 6.5.3 Biomass allocation under drought in alpine grassland

The key finding of our study was that alpine grassland plants change the biomass allocation from above- to below-ground in response to recurring experimental summer droughts. An observational study by Patty et al. (2010) describes the biomass allocation in herbaceous plants in the high semi-arid Andes and found that both a drought driven seasonality and strong grazing pressure led to a massive investment in below-ground biomass compartments (roots and storage organs). Li et al. (2011) experimentally studied the interactive effects of water and nitrogen on above- and below-ground biomass partitioning in grassland in Inner Mongolia. They found that the fraction of below-ground to total biomass was higher for a limited supply of resources, which is in accordance with findings from our study in alpine grassland. Peterson & Billings (1982) investigated the growth of alpine plants under controlled drought in phytotron environments. They found that under drought stress, the mean total plant weight decreased in most alpine plant species, while the root-shoot ratio increased in some of the species. The outcome of this study is contrary to the results of our study concerning the total biomass, which did not decrease at community level in our study, but in line concerning the root-shoot ratio, which clearly increased under drier conditions in our experiment.

Sanaullah et al. (2012) and Hasibeder et al. (2015) studied the responses of carbon allocation in grassland communities to drought by combining experimental drought simulation with carbon pulse labelling. Drought significantly affected assimilate allocation in both studies. In general, plants under drought conditions transferred a larger portion of recent photosynthates to below-ground storage compounds, which underpins our observations in alpine grassland. Palta & Gregory (1997) studied the carbon allocation in *Triticum aestivum* and found that the internal C allocation changed under drought conditions. They showed that more C was allocated to the roots under limited water conditions at the expense of shoots. This resulted from a smaller reduction in root growth rates than in shoot growth rates under drought.

Total standing biomass (above- plus below-ground biomass) showed a clear increase with drought, which is rather counterintuitive at a first glance. However, this finding suggests that either water
availability was yet not limiting so that gas exchange was not reduced under experimental drought and production was increased, or the below-ground loss of biomass has decelerated under drought leading to an accumulation of below-ground biomass. An increase of the primary production and thus an accumulation due to an increased allocation of biomass to the below-ground compartment under dry conditions is very unlikely. Thus, the only explanation for the increase of the pools is a reduced below-ground loss of root and storage organ biomass and hence an accumulation of biomass during the drought periods.

In grassland, the rates of C loss from roots are about 1 year\(^{-1}\) (Schneider et al. 2006), meaning that the whole amount of roots are replaced once per year. For the below-ground biomass, we collected data for both pools and net production. A simple calculation provides evidence that the loss of below-ground biomass decreased under drier conditions. The difference between the biomass pools under the CT and ED treatments at HS site in 2009 was about 400 g d.m. m\(^{-2}\) (cf. Fig. 6.3). The net production under ED conditions at HS site in 2010 was about 300 g d.m. m\(^{-2}\) (cf. Fig. 6.4). This clearly shows that the increase in the biomass pool under the ED treatment could not only be due to the production. 100 g d.m. m\(^{-2}\) was accumulated due to a decreased loss of root and storage organ biomass.

Our study suggests that both, an increased allocation of C to below-ground plant organs (confirmed by ingrowth core data), but also an increased accumulation of C due to a decreased loss of below-ground plant organs (see calculation above) led to the increase of the below-ground biomass compartment. A decreased loss of root biomass is a strategy of plants that grow with low nitrogen content such as alpine plants. A decreased root loss may also be an acclimation strategy of the plants to cope with droughts and to recover quickly with the accumulated resources after the droughts.

The ingrowth core method allowed to measure the below-ground biomass productivity, i.e. the amount of new biomass accumulated over the growing season. The biomass measurements obtained by above-ground clipping and below-ground split tube sampling yielded standing biomass, which corresponded to the total biomass (i.e. the pool of biomass) per unit ground area at the harvest date. Our observations revealed that above the ground, only necromass, cryptogam mass and litter still existed after winter at each of the three grassland sites. Since biomass was largely lacking at the beginning of the growing season and biomass removal by herbivores was prevented during the growing season, the pool of above-ground biomass reflected roughly the newly produced biomass in the current growing season (net production). Therefore, standing above-ground biomass represented a good estimate for the above-ground biomass production in the current year. However, all other above-ground plant material fractions allowed only an assessment of the pools. Standing
below-ground biomass obtained by split tube sampling also clearly represented the pool, since in alpine grassland, most of the roots and storage organs persist over winter.

Finally, this study showed that the key ecosystem service of alpine grassland, i.e. slope stability, could be largely maintained. Although above-ground responses in vegetation structure indicated a higher erosion risk (see Study 1 of this thesis), below the ground, the rooting density was increased significantly, leading to a higher soil stability and thus lower landslide risk. This below-ground effect counteracts the above-ground responses and suggests that the slope stability may not be jeopardised after prolonged summer droughts in the future.

### 6.5.4 Functional equilibrium theory

Plant individuals seem to preferentially allocate biomass to those organs, which acquire the most limiting resource and are able to shift this allocation under changing environmental conditions (Poorter & Nagel 2000, Poorter et al. 2012). This mechanism of optimal partitioning is known as the “functional equilibrium theory” (Brouwer 1962, Wilson 1988) or “balanced growth hypothesis” (Shipley & Meziane 2002). This theory states that plants will allocate relatively more biomass to roots in response to a limitation in a below-ground growth factor (such as nutrients or water), whereas they will allocate relatively more biomass to shoots, if the limiting factor for growth is above the ground (such as light or CO$_2$). The altered carbon allocation to roots under summer drought as observed in this study corresponds to this “functional equilibrium theory”.

However, alpine plants not only accumulated biomass in the root system under drier conditions, but also allocated significantly more biomass to the storage organs. Since the storage organs are not responsible for resource acquisition but only for resource storage, the “functional equilibrium theory” does not explain the increase allocation of biomass to the storage organs in our study. Bloom et al. (1985) state that resources may be stored by plants to promote regrowth following fire, herbivory, drought, unusually cold temperatures, etc. Storage serves as insurance against catastrophes and guarantees a long-term persistence in a variable environment. They state that also an annual unfavourable period such as a summer drought may be seen as a catastrophe for which most perennial plants accumulate stores to utilise in subsequent regrowth. The increased amount of storage organs under summer drought as observed in this study corresponds to this theory.
6.6 Conclusions

Our climate change study provided strong experimental evidence that recurring summer droughts affect the resource allocation in alpine grassland systems by inducing a significant shift from above- to below-ground biomass production. The fact that the overall production was not restricted during the drought periods points to the resistance of these ecosystems under changing environmental conditions. The intensified allocation of resources to roots and storage organs turns out to be a successful acclimation strategy of alpine plants when exposed to recurring summer droughts. This strategy allows them to escape the damaging consequences of a summer drought by surviving the adverse conditions below the ground. The increased amount of storage organs of hemicryptophytes and geophytes under drought conditions in alpine grassland facilitates to quickly recover after a drought period when conditions become favourable again. A fast regeneration is an essential attribute of plants in the alpine zone, which have to cope with a short growing season that is further reduced by a summer drought. Thus, our findings clearly emphasise the key role of below-ground biomass in alpine grassland to resist and recover from recurring summer droughts and hence to maintain ecosystem stability when subjected to extreme climatic events. In addition, our data demonstrate that it is essential to consider the entire system, including the above- and below-ground biomass compartments, when evaluating the resistance and resilience of alpine ecosystems under climate change.

6.7 References


ETH Zurich, ETH Rat, Bundesamt für Statistik & swisstopo (2004): Atlas der Schweiz 2.0


7 Elevational species shifts in a warmer climate are overestimated when based on weather station data (Study 3)

Daniel Scherrer, Samuel Schmid & Christian Körner (2011)

7.1 Abstract

Strong topographic variation interacting with low stature alpine vegetation creates a multitude of microhabitats poorly represented by common 2 m above the ground meteorological measurements (weather station data). However, the extent to which the actual habitat temperatures in alpine landscapes deviate from meteorological data at different spatial scales has rarely been quantified. In this study, we assessed thermal surface and soil conditions across topographically rich alpine landscapes by thermal imagery and miniature data loggers from regional (2-km²) to plot (1-m²) scale. The data were used to quantify the effects of spatial sampling resolution on current micro-habitat distributions and habitat loss due to climate warming scenarios. Soil temperatures showed substantial variation among slopes (2–3 K) dependent on slope exposure, within slopes (3–4 K) due to microtopography and within 1-m² plots (1 K) as a result of plant cover effects. A reduction of spatial sampling resolution from 1 × 1 m to 100 × 100 m leads to an underestimation of current habitat diversity by 25% and predicts a six-times higher habitat loss in a 2-K warming scenario. Our results demonstrate that weather station data are unable to reflect the complex thermal patterns of aerodynamically decoupled alpine vegetation at the investigated scales. Thus, the use of interpolated weather station data to describe alpine life conditions without considering the micro-topographically induced thermal mosaic might lead to misinterpretation and inaccurate prediction.

Keywords
Alpine, soil temperature, spatial scale, suitable climate space, surface temperature, thermometry
7.2 Introduction

The alpine life zone is dominated by strong topographic variation and extreme climatic conditions forcing plants and animals to a high degree of specialisation and adaptation (Billings and Mooney 1968; Körner and Larcher 1988; Körner 2003). The steep environmental gradients and the reduction in land area with increasing elevation supposedly cause alpine environments to be particularly sensitive to global warming (Beniston et al. 1996; Diaz et al. 2003; Beniston 2006). In addition, most climate warming scenarios predict higher than average warming in most alpine areas (Meehl et al. 2007; Nogués-Bravo et al. 2007). The Alps warmed by +1.5 K compared with the global average of +0.7 K during the last century and therefore are often considered as particularly threatened (Beniston et al. 1997; Theurillat and Guisan 2001; Schröter et al. 2005; Nogués-Bravo et al. 2007). It is widely believed that the recent and future climate warming is driving species ranges polewards and towards higher elevations (Beniston et al. 1996; Theurillat and Guisan 2001; Walther 2004; Colwell et al. 2008) and may cause regional species extinctions. In fact, there is evidence of upslope migration of plant species in the Alps (Grabherr et al. 1994; Walther et al. 2002, 2005; Pauli et al. 2007; Lenoir et al. 2008) as well as evidence for substantial resistance to climatic forcing in plants inhabiting the same location over thousands of years (Steinger et al. 1996; Bahn and Körner 2003).

Species distribution models (SDMs; Guisan and Zimmermann 2000; Guisan and Thuiller 2005) have been employed to project the impact of future climate change on species distributions (Bakkenes et al. 2002; Thomas et al. 2004; Thuiller et al. 2005; Randin et al. 2009). SDMs statistically fit the environmental niche (Hutchinson 1957; Kearney and Porter 2004) by relating abiotic habitat conditions with occurrences of a species (Guisan and Thuiller 2005; Araújo and Guisan 2006). Strong impacts on biodiversity and species abundance have been predicted (Bakkenes et al. 2002; Thuiller et al. 2005), especially in mountain ranges.

Yet the predicted habitat loss in mountainous regions strongly depends on model selection (Araújo et al. 2005b; Algar et al. 2009) and the spatial resolution of the SDMs (Trivedi et al. 2008; Randin et al. 2009). Scherrer and Körner (2010a) showed that in alpine landscapes there is substantial variation in actual plant surface and soil temperature within 1-km² test areas, not reflected in the commonly referred to 2-m-aboveground air temperature. The thermal mosaic created by micro-topography, in fact, offers suitable habitats for many species with different thermal preferences requiring hardly any migration for a 2-K warming scenario (Scherrer and Körner 2010b). This results from both geo-diversity (topography) as well as aerodynamic decoupling of low stature alpine vegetation from atmospheric conditions at a centimetre scale (Körner 2003). Most models work on interpolated weather station data at much larger scales, with the noteworthy exception of an attempt for a small-
scale resolution by Randin et al. (2009). Although not based on actual plant temperatures, this study revealed the significance of scale. Given the key role of spatial sampling resolution of climatic conditions to describe patterns of current micro-habitats, fact-based life conditions need to be assessed, the aim of the work presented here.

Modern thermal imagery techniques and miniature data loggers allow us to record surface and soil temperature data at high spatial resolution across rough alpine terrain. In this study we recorded surface (plant canopy) and soil temperature (root zone) data at different spatial resolutions ranging from centimetre to kilometre scale. This data were used (1) to partition the surface and soil temperature variation into among-slopes, within-slope and centimetre scale variation, (2) to identify the most influential factors for surface and soil temperature at different spatial scales, (3) to quantify the observed variation in surface temperature dependent on spatial sampling resolution, and (4) to estimate the projected habitat loss under climate warming scenarios and the dependence of predictions on spatial resolution. This information will improve predictions of future habitat conditions and thus reduce uncertainties in projected habitat distribution.

7.3 Materials and methods

7.3.1 Study sites

The study area is situated in the temperate-alpine zone near the Furka Pass in the Swiss Central Alps (46°34′35″N, 08°25′17″E), well above the climatic tree line (which is at c. 2,150 m in this region). Within an area of about 2-km² (study area), we chose three steep mountain slopes with NNW (centre at 2,500 m), W (2,480 m) and SSE (2,430 m) exposure. All slopes showed strong variation in microtopography but no change in macro-exposure and covered elevation ranges of 400–600 m on the NNW and W slope and 200 m on the SSE slope. Within each slope, we defined four 1-m² plots (near the centre) which were used for detailed small-scale measurements. For logistical reasons (power supply, road access) and a field station for night measurements, we designated the NNW slope as our core site.

7.3.2 Field data

The surface temperatures of the study slopes and plots were measured with a thermal camera (VarioCAM®; Infra Tec, Dresden, Germany) which records the long-wave infra-red at a resolution of 76,800 image points and transforms the radiation directly into temperature. The accuracy of the ab-
Solute temperature is ±1 K and the relative differences between measurement fields (pixels) have a resolution of ±0.1 K. To create mean thermal images (integrated over time) of whole slopes, the thermal camera was placed on the opposite slope (to have optimal angle of vision), and for each target slope, we recorded at least one (if possible more) diurnal series of thermal images under clear sky conditions. The series of images had a temporal resolution of 15 min (time between two images), started at midnight and ended 2 h after sunset. The detailed surface temperature of the twelve 1-m² plots (four per slope) was recorded three times during the growing season (16 July 2009, 18 August 2009 and 08 September 2009) by placing the camera directly over the centre of each plot (90° angle and fixed distance). The ground resolution for the slope measurements was about 0.75-m² per pixel and 0.2-cm² for the plot measurements.

Longer-term soil temperature within slopes and plots was recorded with 281 small waterproof temperature loggers (iButtons; Maxim Integrated Products, Sunnyvale, CA, USA) which have a resolution of 0.5 K and record for 80 days with one temperature reading per hour. To capture the spatial and temporal variation of the soil temperature within each of the three mountain slopes, we defined at least one horizontal and one vertical transect (three horizontal and three vertical ones at our core site, the NNW exposed slope) of a minimum length of 150 m (varying from 150 to 350 m depending on topography). The loggers were buried in the top soil rooting zone at a depth of 3 cm along the horizontal (one logger every 10 m) and vertical transects (one logger every 15 m). In total, we placed 86 temperature loggers on the NNW, 33 on the SSE and 54 on the W exposed slope along transects which recorded the soil temperature for 75 days (22 June–8 September 2008). Additionally, to get an impression of the small-scale variation of top soil temperature, we placed 36 loggers within one 1-m² plot per slope (20 × 20 cm grid) which recorded the soil temperature for 75 days in 2009 (29 June–13 September 2009). These 75-day periods represented the main growing season at the Furka Pass in the study years 2008 and 2009. Standard meteorological data 2 m above the ground (air temperature, air humidity, solar radiation) were recorded with a 10-min temporal resolution by a weather station (Vantage Pro2 Plus™ with solar radiation sensor; Davis Instruments, Hayward, CA, USA) within the study area at 2,445 m.

To identify the most influential abiotic factors on soil temperature at the centimetre scale, we measured (at the position of each logger within the 1-m² plots) the inclination, exposure and surface structure (concave, convex or flat). By a grid-point intercept method applied to the 25-cm² above each logger (1 × 1 cm grid, 36 points; modified from Herrick et al. 2005), we measured the specific cover of each vascular plant species, mosses, lichens, litter and rocks, the percentages of bare ground and the mean and maximum vegetation height. Additionally, functional classifications of
plant species (classifications for functional group, growth form, life form, stem growth type, leaf distribution) were performed following Cornelissen et al. (2003).

7.3.3 Data analysis

The many thermal images of one time series were aggregated to a mean image representing the 6 h with highest insolation and daytime warming (‘day time’, 1200–1800 hours). By aggregating over time, we averaged out short-term fluctuations and obtained more reliable information about the micro-climatic conditions within a given slope (Scherrer and Körner 2010a). Because the time series were not recorded on the same day, we standardised the surface temperature of a slope by subtracting the air temperature 2 m above the ground for the corresponding period. This makes the data of different days more easily comparable. From the detailed thermal images of the 1-m² plots, we extracted leaf temperature of eight individuals for 14 different plant species. All the species are common in the study area and prominent in at least one of the study slopes (the 14 species are listed in Table 7.1).

For each soil temperature logger, we calculated three different mean values: first, the mean temperature for the complete measuring period (‘seasonal mean’), second, the mean for night hours (0000–0600 hours), and third, the mean for day hours (1200–1800 hours).

We analysed the surface and soil temperature variation on three different scales: first, the regional variation (variation among whole slopes), second, the within-slope variation, and third, the within-plot variation. For each slope, we calculated a mean surface temperature during ‘day time’ and the mean soil temperatures for seasonal mean, night-hours and day-hours. These mean slope temperatures were then compared to obtain the among-slopes variation. The within-slope and within-plot variation was calculated by taking 90% of the data points (loggers, IR-pixels) within one slope and plot, respectively. We excluded the 5% of the lowest and highest values to exclude bias due to extreme values of single data points such as, for example, stones heating up to 80°C under strong insolation. This was done separately for surface temperature during ‘day time’ and soil temperature during seasonal mean, night-hours and day-hours. To identify the most important physical and biological factors influencing the small-scale pattern of soil temperature within our 1-m² plot we conducted a correlation analysis of the recorded parameters (see above) and the seasonal mean, night-time and day-time soil temperatures.

While the soil temperature data (loggers) represent point measurements, the IR images deliver integrated data over an area (slope, plot). This allowed us to artificially manipulate (decrease) the spatial resolution of our IR images. For example, we can observe the same slope with a 1-m², 10-m² or 100-
m² resolution just by aggregating pixel information. By doing this, we not only lose information but also decrease the surface temperature variation observed within a slope and thus underestimate the real micro-climatic variation. We therefore analysed the variation within each slope and plot at different spatial resolutions by randomly sampling 10,000 points per resolution, slope and plot respectively. This results in a correlation of the spatial resolution of sampling and the observed variation in surface temperature.

To quantify the losses of micro-habitats within a single mountain slope dependent on the sampling resolution, we simulated mean temperature increases of 2, 3 and 4 K. This was done by taking the current distribution of surface temperature at 1 × 1, 5 × 5, 10 × 10, 25 × 25 and 100 × 100 m resolution and shifting the temperatures by the desired temperature increase. This way, only the mean temperature was increased, while the spatial variation of temperatures stayed the same. By comparing (overlapping) the two temperature distributions (current and future), we can estimate the micro-habitat temperatures of the current distribution that are lost in a warmer climate assuming a similar air-surface temperature correlation and similar solar forcing. We excluded the coldest and warmest 5% of the recorded micro-habitats to avoid conditions that are extremely rare and therefore biologically not significant on the applied scale of this study. This was done for the different spatial resolutions (1 × 1, 5 × 5, 10 × 10, 25 × 25 and 100 × 100 m) and the three warming scenarios (2, 3 and 4 K).

### 7.4 Results

On clear sky days during day time, we observed increasing variation in surface temperature with increasing resolution. The difference in surface temperature among slopes was only 2.4 K while the range containing 90% of the data points within a given slope (c. 0.5-km²) was 4.8±1.06 K (mean ± SE) and 14.1±1.13 K within a 1-m² plot (Fig. 7.1). The range containing 90% of the data points was similar for all 1-m² plots, irrespective of their macro-exposure (NNW, W, SSE).

The soil temperature data showed a different pattern. The largest variation in soil temperature was always found within a slope, with a range containing 90% of the data points of 3.2±0.14 K (mean ± SE) for seasonal mean, 3.2±0.58 K during night-hours and 4.1±0.20 K during day-hours (Fig. 7.2). The within-plot soil temperature range containing 90% of the data points was larger during day-hours with 3.2±0.77 K than for the seasonal mean, with 1.4±0.05 K, and night-hours with 1.65±0.29 K (Fig. 7.2). The differences among slopes were 2.3 K for seasonal mean, 3.1 K during night-hours and 1.9 K during day-hours (Fig. 7.2). The macro-exposure had no significant influence on the within-slope or within-plot variation of soil temperature, but significantly influenced the mean soil temperatures of
slopes with a seasonal mean of 8.7±0.13°C (mean ± SE) on the NNW, 10.1±0.12°C on the W and 11.0±0.11°C on the SSE exposed slope.

The 1-m² plots showed large differences in their seasonal mean soil temperature with 8.0±0.28°C (mean ± SE) on the NNW, 10.4±0.34°C on the W and 11.7±0.30°C on the SSE slope. Therefore, we used macro-exposure as a random factor for the analysis of the influence of surface and vegetation structure on the within-plot soil temperature variation. Otherwise, the strong signal of macro-exposure would have covered all effects of small-scale temperature variation. The most influential factors for within-plot seasonal mean soil temperature were inclination (ANOVA, p < 0.001), followed by plant canopy cover, and mean vegetation height (p < 0.05). During day-hours with bright sky insolation the influence of inclination, canopy cover and mean vegetation height was strongest while there was no effect on night-time soil temperature. Plant species identity as well as the functional group, life form, stem growth type and leaf distribution of the plants had no consistent influence on small-scale soil temperature. Only the growth form (namely cushion versus tussock) had a tendency to influence day-hours soil temperature but this was likely the result of a strong correlation of percent cushion and tussock plants respectively and mean vegetation height. The leaf temperatures of all 14 plant species were higher than concurrent air temperature 2 m above the ground (c. 16°C) and showed significant differences among species (Table 7.1). These differences basically could be explained by the different plant architecture: plants with leaves concentrated close to the soil surface (mainly rosette plants) had the highest leaf temperature (28.2±5.3°C; mean ± SD), plants with leaves concentrated in middle parts of the stem had a medium leaf temperature (24.8±3.3°C), and tussocks (graminoids), exposing their long erect leaves to the wind, had the lowest leaf temperature (21.9±1.6°C; Table 7.1).

The artificial manipulation of spatial resolution on both slope and plot level led to an exponential decrease of surface temperature variation with decreasing resolution (Fig. 7.3). As expected, the spatial sampling resolution had absolutely no influence on the estimated mean surface temperature of both the plot and slope. The reduction of the spatial resolution from 1 × 1 m to 100 × 100 m strongly narrowed the distribution of the observed surface temperatures (Fig. 7.4). This led to an underestimation of the true habitat variability within the study area. With decreasing spatial resolution, a substantial part of currently existing micro-habitat conditions were cooler or warmer than the detected range of temperatures (Table 7.2). A decreasing sampling resolution led to an increase in the proportion of current micro-habitats (suitable climate space) that would disappear in the event of a warmer climate (Table 7.3), especially if the spatial resolution was lower than 10 × 10 m. As expected, the fraction of current micro-habitats that disappeared within a given slope under climate warming scenarios increased with increasing temperature difference (Table 7.3).
Table 7.1  Plant species-specific leaf temperatures of 14 selected plant species with different growth forms (mean ± SD).

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Growth form&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Life form&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Leaf temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sesleria caerulea</em></td>
<td>Tus</td>
<td>Hem</td>
<td>21.4±1.7</td>
</tr>
<tr>
<td><em>Elyna myosuroides</em></td>
<td>Tus</td>
<td>Hem</td>
<td>21.9±1.5</td>
</tr>
<tr>
<td><em>Carex curvula</em></td>
<td>Tus</td>
<td>Hem</td>
<td>22.5±1.4</td>
</tr>
<tr>
<td><em>Helictotrichon versicolor</em></td>
<td>Mid</td>
<td>Hem</td>
<td>22.5±1.1</td>
</tr>
<tr>
<td><em>Gentiana punctata</em></td>
<td>Mid</td>
<td>Hem</td>
<td>23.3±4.1</td>
</tr>
<tr>
<td><em>Trifolium alpinum</em></td>
<td>Bas</td>
<td>Hem</td>
<td>23.3±1.9</td>
</tr>
<tr>
<td><em>Leontodon helveticus</em></td>
<td>Bas</td>
<td>Hem</td>
<td>23.9±2.7</td>
</tr>
<tr>
<td><em>Anthyllis vulneraria</em></td>
<td>Mid</td>
<td>Hem</td>
<td>24.0±2.2</td>
</tr>
<tr>
<td><em>Polygonum viviparum</em></td>
<td>Mid</td>
<td>Geo</td>
<td>25.4±3.5</td>
</tr>
<tr>
<td><em>Aster alpinus</em></td>
<td>Mid</td>
<td>Hem</td>
<td>26.8±3.4</td>
</tr>
<tr>
<td><em>Geum montanum</em></td>
<td>Mid</td>
<td>Hem</td>
<td>26.9±2.5</td>
</tr>
<tr>
<td><em>Homogyne alpina</em></td>
<td>Bas</td>
<td>Hem</td>
<td>27.3±2.0</td>
</tr>
<tr>
<td><em>Dryas octopetala</em></td>
<td>Bas</td>
<td>Cha</td>
<td>32.3±3.6</td>
</tr>
<tr>
<td><em>Saxifraga paniculata</em></td>
<td>Bas</td>
<td>Cha</td>
<td>34.0±4.7</td>
</tr>
</tbody>
</table>

<sup>a</sup>Bas leaves concentrated in basal parts of plant, Mid leaves concentrated in middle parts of plant, Tus leaves concentrated in tussocks

<sup>b</sup>Geo geophyte, Hem hemicryptophyte, Cha chamaephyte
Table 7.2 Fraction of undetected thermal micro-habitat conditions dependent on spatial sampling resolution based on IR surface temperatures of three alpine slopes (mean ± SD).

<table>
<thead>
<tr>
<th>Spatial resolution (m)</th>
<th>Undetected conditions (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 x 1</td>
<td>-</td>
</tr>
<tr>
<td>5 x 5</td>
<td>0</td>
</tr>
<tr>
<td>10 x 10</td>
<td>1.8±0.4</td>
</tr>
<tr>
<td>25 x 25</td>
<td>9±2.8</td>
</tr>
<tr>
<td>100 x 100</td>
<td>22.5±6.3</td>
</tr>
</tbody>
</table>

Table 7.3 Fraction of the coldest thermal micro-habitat conditions that are assumed to disappear under different climate warming scenarios depending on spatial sampling resolution based on IR surface temperature data of three alpine slopes (mean ± SD).

<table>
<thead>
<tr>
<th>Spatial resolution (m)</th>
<th>2 K scenario habitat loss (%)</th>
<th>3 K scenario habitat loss (%)</th>
<th>4 K scenario habitat loss (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 x 1</td>
<td>7.5±0.9</td>
<td>20.3±8.0</td>
<td>40.4±19.0</td>
</tr>
<tr>
<td>5 x 5</td>
<td>16.8±9.9</td>
<td>40.0±22.2</td>
<td>57.5±30.0</td>
</tr>
<tr>
<td>10 x 10</td>
<td>17.4±7.6</td>
<td>42.8±20.1</td>
<td>67.1±24.3</td>
</tr>
<tr>
<td>25 x 25</td>
<td>44.1±24.3</td>
<td>68.1±25.6</td>
<td>86.2±11.3</td>
</tr>
<tr>
<td>100 x 100</td>
<td>64.7±28.9</td>
<td>95.5±3.7</td>
<td>100±0.0</td>
</tr>
</tbody>
</table>
Figure 7.1 Surface temperature range at three different scales and sampling resolutions (mean, SE). The data were collected on clear sky days during June 2008 and June 2009 from 1200 to 1800 hours.
Figure 7.2  a Density distribution of seasonal mean soil temperatures for individual plots (1-m$^2$; dotted lines), whole slopes (0.5-km$^2$; dashed lines) and total region (2-km$^2$; solid line). The inset shows the soil temperature range for three spatial scales (among slopes, within slopes, within plots). b The same information, but for daytime mean temperatures, and c for night-time mean temperatures. The data for the 1-m$^2$ plot level were collected from 29 June to 13 September 2009 and for the slope level from 22 June to 8 September 2008.
Figure 7.3 Observed surface temperature range as a function of spatial resolution of sampling (means, SD). The left panel shows data at slope scale (0.5-km$^2$) and the right panel at plot scale (1-m$^2$). The insets represent sample thermal images of a slope and a plot.
Figure 7.4 The observed micro-habitat temperatures based on surface temperature measurements at different spatial scales (1 × 1 m, 10 × 10 m, 100 × 100 m).
7.5 Discussion

7.5.1 Within-plot variation

Our results show substantial variation in both surface and soil temperature on all three scales (among slopes, within slopes and within plots). The variation in surface temperature was highest on the finest scale (within plots) and independent of macro-exposure. This can partly be explained by a technical issue. For logistical reasons (only one thermal camera), it was impossible to monitor the 1-m² plots for longer time intervals (6 h) and we only have repeated snapshots. Therefore, some of the observed variation in surface temperature would likely average out in longer term means. But the strong variation in surface temperature at the centimetre scale illustrates the important effect of radiative heating in aerodynamically decoupled systems such as alpine vegetation (Körner 2003). Many studies have shown that leaf temperatures in alpine landscapes largely deviate from 2 m above the ground air temperature (e.g., Takasu 1953; Salisbury and Spomer 1964; Cernusca 1976; Larcher and Wagner 1976; Körner and Cochrane 1983; Larcher et al. 2010; Scherrer and Körner 2010a). Our results show that plant species were warmer than the air temperature (Table 7.1), and that growth form directly influences the leaf temperature as had been shown in the studies cited above. Upright plant structures such as tussock leaves are far better coupled to the atmosphere and therefore are closer to 2 m above the ground air temperature than rosette leaves attached to the ground (e.g. Körner and Demoraes 1979; Körner et al. 1983; Körner and Cochrane 1983). With thermal imagery, these differences are directly accessible within one image. Leaf temperature provides information about physiological processes such as rate of photosynthesis, respiration or tissue formation. Additionally, leaf temperature can be used as an indicator for evaporative forcing (Smith and Geller 1979). By comparing species-specific leaf temperatures under dry and moist conditions, one can identify the species most affected by water shortage (Schmid, unpublished data).

Within single plots, we observed consistent seasonal (75-day) mean soil temperature differences of several K depending on topography and plant structure. The variation in soil temperature within a 1-m² plot was three times higher during day-time than night-time. Night-time soil heat flux averages out most of the variation within a 1-m² area, while under strong insolation, there are up to 4 K soil temperature differences at the centimetre scale. The dominant factor on the smallest scale was slope inclination, defining the solar incidence angle and therefore the energy balance of the inclined surface. Also, the vegetation height and vegetation cover had a significant influence on soil temperature at the centimetre scale. Both factors increase the shading of the soil and therefore reduce the amount of direct radiation reaching the ground. These shading effects on soil temperature are well documented in forests and are one of the factors which explain sharp tree lines (Körner 1998;
Körner and Paulsen 2004). Root zone temperatures are known to be important for root growth, root development and nutrient uptake (Kaspar and Bland 1992; Körner 2003).

7.5.2 Within-slope variation

Within slopes, we observed substantial soil and surface temperature variation independent of macro-exposure. As was shown by Scherrer and Körner (2010a), these microclimates are mainly the effect of micro-topography and only marginally influenced by plant structure (within the small stature alpine vegetation). Even though the soil and surface temperatures show the same micro-climatic patterns, the quality of their signals differs. The within-slope surface temperatures represent larger scale integrated measurements. All the leaf surface temperatures within one pixel (around 1-m²) are averaged on this scale. Therefore, the thermal image of a slope directly delivers micro-climate temperatures at metre scale, only marginally influenced by the dominating life form (Scherrer and Körner 2010a). For technical and logistical reasons, the thermal imaging data were only available for selected days and not continuously, but we assume the quality of the observed micro-climatic pattern within slopes is retained and only the absolute range varies with irradiance.

Soil temperature measurements in the upper rooting zone, on the other hand, were continuously measured over a 75-day period and therefore show consistent seasonal differences of micro-habitats. But the loggers only integrate over an area of c. 100-cm² and therefore represent point measurements not necessarily representative of the surroundings at metre scale (distance between loggers > 10 m). About 30–50% of the soil temperature variation observed within a slope, achieved by spreading the loggers all over the slope, would also be recorded within a single plot (1-m²; Fig. 7.2). The within-slope variation of soil temperature therefore reflects a combined signal of centimetre scale influences (inclination, vegetation cover, vegetation height) and metre-scale factors such as topography.

7.5.3 Among-slope variation

The among-slope variation was quite similar for surface and soil temperature with south-exposed slopes about 2–3 K warmer than north-exposed slopes. These differences reflect the effects of macro-exposure on the incoming radiation dose due to incidence angle, the duration of direct insolation, and self-shading, respectively. Here, the information from the surface and soil temperature measurements are similar, both delivering mean slope temperatures by aggregating information (pixel, logger) within a slope.
All three spatial scales influence both mean surface and soil temperatures, as well as their variation. As shown by Scherrer and Körner (2010b), the distribution of microhabitat temperatures correlate with the assemblages of plant species to vegetation units. Sampling or describing alpine landscapes, dominated by the high variation in microtopography, with a crude spatial resolution might therefore be dangerous as highlighted by our climate warming modelling experiment.

### 7.5.4 Manipulation of spatial sampling resolution

In this study, we re-sampled the mountain slopes at different spatial resolutions and made simple predictions for warmer climates. The results show that the spatial resolution of sampling strongly biases the outcome of any prediction of climate warming. This bias is mostly the result of a narrowing of the range of micro-habitats, leading to an underestimation of the range of current habitat conditions and an overestimation of the percentage of micro-habitats lost in the event of climate warming. By decreasing the spatial resolution from $1 \times 1$ m to $100 \times 100$ m, we lose almost 25% of the current thermal micro-habitats found within a single slope at highest resolution (Table 7.2). A 2-K climate warming scenario revealed that, based on the high resolution data ($1 \times 1$ m), less than 10% of the current micro-habitat conditions (climate space) disappear from a slope, while, at a lower resolution ($100 \times 100$ m), more than 60% would be predicted to disappear (Table 7.3). In fact, the 10% of current micro-habitat conditions that might disappear under moderate climate warming (2 K) at the $1 \times 1$ m resolution were not detected with a $100 \times 100$ m resolution under current conditions. Therefore, we conclude that none of the micro-habitats identified with a $100 \times 100$ m sampling grid will disappear under a moderate 2-K climate warming within a single slope. The climate warming scenarios of 3 and 4 K yielded similar results with up to 100% predicted micro-habitat loss within our study slopes at low resolutions but only c. 40% at high $1 \times 1$ m resolution. Apart from habitats disappearing within an area due to climate warming, there will also be a large proportion of habitats decreasing and increasing in their abundance (Scherrer and Körner 2010b). The proportion of these habitats is also strongly dependent on the sampling resolution. Changes in micro-habitat abundance will change the competitive situation for many species and may exert biodiversity effects different in nature from those implied by large-scale shifts of isotherms and associated large-scale migration needs. While, due to climate warming, the coldest habitats within a given area will disappear, new warmer habitats will emerge as the area stays constant and new species might replace those which are lost, resulting in no changes in species richness at all.

In this study, we artificially manipulated the spatial resolution of our data (plant canopy and soil temperature) by aggregating information, in contrast to most models which base their predictions...
on interpolated and downscaled meteorological data. Although the modern algorithms employed might be very sophisticated and high resolution digital elevation models are used to incorporate local and regional climate (Zimmermann and Kienast 1999; Guisan and Thuiller 2005; Randin et al. 2006, 2009), we have two major concerns: first, most of the climate models used predict meteorological conditions 2 m above the ground and it is therefore questionable whether such data reflect the actual alpine life conditions, with the majority of organisms living in micro-habitats strongly decoupled from atmospheric conditions and strongly interacting with microtopography at the centimetre to metre scale. Second, the field data used for interpolation might not be representative for a wider region. As shown, there is strong variation in surface and soil temperature but also soil moisture (Hills and Reynolds 1969; Reynolds 1974; Charpentier and Groffman 1992), nutrient availability (Jackson and Caldwell 1993; Reynolds et al. 1997) and precipitation (Cosma et al. 2002) are known to vary at small spatial scales. The environmental envelope achieved by interpolation might therefore strongly differ from real environmental conditions.

The popularity of species distribution models to predict climate warming impacts on biodiversity and species distribution have led to an ongoing debate about model selection (Elith et al. 2006; Pearson et al. 2006; Araújo and New 2007), validation (Araújo et al. 2005a; Araújo and Guisan 2006; Pearson et al. 2007), uncertainty (Thuiller et al. 2004; Araújo et al. 2005b; Pearson et al. 2006), transferability (Randin et al. 2006) and spatial scale (Trivedi et al. 2008; Randin et al. 2009). Apart from SDMs predicting the potential distribution of each species individually, based on their climatic envelope, other models directly predict species richness based on macroecology theory (Fischer 1960; Currie 1991; Hawkins et al. 2003). These models directly correlate various environmental conditions (mainly climatic variables) with regional species richness. While these models often predict lower extinction rates than SDMs (Algar et al. 2009; Sommer et al. 2010), they also seem to be prone to scale issues (Field et al. 2009), with insufficient correlation at small scales. The current debate about modelling future biodiversity and species distribution in mountains leads to numerous new approaches and improved methods, but the modelling community tends to keep their focus mostly on model technical issues and often ignores the source of the data used for modelling. It is important to keep in mind that almost all models discussed here use weather station data for their projections. As shown here and in previous works, this is highly inappropriate for aerodynamically decoupled vegetation such as low stature alpine heath. The correlation of weather station data and real climate conditions for a plant species might strongly vary among life forms, depending on their aerodynamic coupling to the atmosphere. The more strongly an ecosystem is decoupled from atmospheric conditions by topography and vegetation structure, the more thermal micro-habitat variation is observed (Scherer and Körner 2010a). The number of these micro-habitats that are detected depends on the meth-
ods and spatial scale used to collect the climate data. The quality (spatial resolution) of this data might drastically influence or even bias the result of projections, independent of the modelling approach. These scale effects might be less important when the centre of species distributions is modelled, but they distort the results when modelling extinctions near niche boundaries. Based on this study, we advocate not only consideration of the uncertainty and variability in biodiversity projections caused by model technical issues but also the need to account for the effects of the quality and spatial scale of the climate data used. The data presented here re-confirm that alpine habitats are in fact more suitable for organisms to cope with climatic change than had commonly been assumed.

7.6 Acknowledgements

This work was carried out as part of the EC FP6 EcoChange (Challenges in Assessing and Forecasting Biodiversity and Ecosystem Changes in Europe, no. 066866 GOCE) project. Thanks to N. Zimmermann and A. Guisan for the data loggers, E. Hiltbrunner for logistical support and two anonymous reviewers for comments on the manuscript.

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Study 3


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Study 3


8 General discussion

8.1 Impacts of summer droughts on alpine grassland ecosystems

As a consequence of human-induced climate change, the future summer climate in the Swiss Alps is predicted to be drier and warmer, with an increased probability of extreme events such as prolonged periods of drought. Due to a lack of observational and experimental drought studies in the alpine zone, it is widely unclear how recurring summer droughts will affect alpine grassland ecosystems. To our knowledge, this is the first climate change experiment with a multi-site multi-year design investigating the impacts of a drier summer climate on vegetation above the climatic treeline by simulating summer droughts with rainout shelters. The first two studies of this thesis dealt with the above- and below-ground responses of the grassland systems to droughts focussing on changes in vegetation structure and biomass production. They aimed at testing whether the grassland systems are sufficiently stable to endure recurring summer droughts or whether they are susceptible and suffer sustained damage.

Study 1 revealed that, overall, three years of simulated summer droughts strongly influenced vegetation structure of alpine grassland by decreasing foliar and basal cover by up to 37% and 54%, respectively, and by increasing the area of bare ground by a factor of up to 8. We found that summer drought had a gradual effect, meaning that already substantial responses under moderate drought were further intensified under extreme drought. But summer drought had not the same effect at each site since vegetation structure remained unaffected at one of the three sites.

The findings of Study 1 impressively show that a prolonged and recurring summer drought can significantly affect above-ground vegetation integrity of alpine grassland. More precisely, summer drought can have a pronounced thinning effect on above-ground vegetation, detectable by a decreased plant cover in the canopy layer and on the soil surface, a reduced canopy compactness, as well as a decreased amount of standing above-ground vegetation material. The drought-induced structural changes, namely the increased area of bare ground, could restrict the important function of alpine grassland to protect soil against erosion and, thus, to maintain slope stability. But surprisingly, our study also demonstrates that the resistance of alpine grassland to summer drought, assessed on the basis of structural stability, is clearly site-dependent. This means that some sites can strongly counterbalance the effect of drought and maintain vegetation integrity while others cannot. Because changes in vegetation structure of alpine grassland in response to three years of simulated summer drought were highly site-dependent, we conclude that there will be no general re-
General discussion

response to future drier conditions in alpine grassland. Moreover, we predict that the presently exist-
ing high structural variability in alpine grassland ecosystems will be further accentuated under a fu-
ture drier climate.

As shown in Study 2, recurring simulated summer droughts strongly influenced the swards by de-
creasing standing above-ground biomass by up to 53%, while increasing standing below-ground bi-
omass by up to 80%, thereby leading to significantly increased root-shoot ratios. We found that the
gradual responses to increasing drought severity were already visible in the second year of drought
simulation and were further intensified in the third year of the experiment, indicating carry-over ef-
fects. Furthermore, we found that the changes in the biomass pools could be primarily explained by
a drought-induced modification of the biomass productivity in the respective compartments. How-
ever, three years of recurring summer droughts did not affect the overall biomass production in the
alpine swards.

Study 2 provides strong experimental evidence that recurring summer droughts affect the resource
allocation in alpine grassland systems by inducing a significant shift from above- to below-ground
biomass production. The fact that the overall production was not restricted during the drought peri-
ods points to the resistance of these ecosystems under changing environmental conditions. The in-
tensified allocation of resources to roots and storage organs turns out to be a successful acclimation
strategy of alpine plants when exposed to recurring summer droughts. This strategy allows them to
escape the damaging consequences of a summer drought by surviving the adverse conditions below
the ground. The increased amount of storage organs of hemicryptophytes and geophytes under
drought conditions in alpine grassland facilitates to quickly recover after a drought period when
conditions become favourable again. A fast regeneration is an essential attribute of plants in the al-
pine zone, which have to cope with a short growing season that is further reduced by a summer
drought. Thus, our findings clearly emphasise the key role of below-ground biomass (roots and stor-
age organs) in alpine grassland to resist and recover from recurring summer droughts and hence to
maintain ecosystem stability when subjected to extreme climatic events. The fact that below-ground
biomass could buffer and compensate the effects of summer drought on above-ground biomass
suggests a high stability of these ecosystems in a future drier climate. In addition, our data demon-
strate that it is essential to consider the entire system, including the above- and below-ground bio-
mass compartments, when evaluating the resistance and resilience of alpine ecosystems under cli-
mate change.

Bringing together the results of the two studies reporting on the summer drought impacts in the al-
pine zone, we conclude that alpine grassland systems are strongly responsive to drier conditions in
the short term, leading to changes in the vegetation structure and biomass production. In addition,
our findings indicate that these responses are part of acclimation mechanisms to endure the droughts and to recover subsequently, and thus, contribute to the resistance and regeneration capacity of alpine grassland. Both resistance and resilience of grassland vegetation are basic requirements to maintain the stability of these ecosystems when subjected to climatic perturbations such as summer droughts. Another important outcome of the two studies is that the key ecosystem service of alpine grassland, i.e. slope stability, could be largely maintained. Although above-ground responses in vegetation structure indicated a higher erosion risk, below the ground, the rooting density was increased significantly, leading to a higher soil stability and thus lower landslide risk. This below-ground effect counteracts the above-ground responses and suggests that the slope stability may not be jeopardised after prolonged summer droughts in the future.

8.2 Impacts of warming on species distribution in alpine grassland communities

Due to the strong topographic change in the alpine zone, low stature grassland vegetation is characterised by a multitude of micro-habitats. Common 2 m above the ground meteorological measurements captured by a weather station poorly represent such conditions.

Study 3 of this thesis aimed to measure the current surface and soil temperature patterns on grassland slopes to assess the real thermal micro-habitat situation plants have to cope with. Our observations reveal considerable variation in surface as well as soil temperature on all considered scales (among slopes, within slopes and within plots). The strongly varying surface temperature within a plot emphasises the importance of radiative heating in an aerodynamically decoupled system such as an alpine grassland. The substantial soil and surface temperature variation observed within slopes was independent of macro-exposure. The diverse micro-climates that occur on a slope within the small stature alpine grassland vegetation are mainly the effect of micro-topography and only marginally influenced by vegetation structure. The variation of soil temperature within the slope thus reflects a signal integrating centimetre scale influences (inclination, vegetation cover, vegetation height) as well as metre-scale factors such as topography. By characterising the current thermal micro-habitats, this study provides an accurate description of the real life conditions on alpine grassland slopes.

The main goal of this study was to quantify how spatial sampling resolution influences the current micro-habitat distribution and potential habitat loss under climate warming scenarios. An artificial manipulation of the temperature data allowed for a re-sampling of the mountain slopes at different
spatial resolutions. On the basis of several warming scenarios we made simple predictions of the habitat conditions under warmer climates. Our findings reveal that the outcome of any climate warming prediction was strongly biased by the spatial sampling resolution. For example, a 2-K warming scenario resulted in a disappearance of only less than 10% of the current micro-habitat conditions (climate space) when based on the high resolution data (1 × 1 m), whereas more than 60% of the climate space is predicted to disappear from a slope when based on the low-resolution data (100 × 100 m). Thus, a reduction of the spatial sampling resolution clearly leads to an underestimation of the current habitat diversity and predicts a much higher habitat loss in each warming scenario. It is important to keep in mind that most of the models used to project future biodiversity and species distribution in mountainous terrain use weather station data, captured 2 m above the ground. As shown in this study, this is highly inappropriate for alpine vegetation such as low stature alpine grassland, which is aerodynamically decoupled and strongly interacting with micro-topography at the centimetre to metre scale. Our results demonstrate that interpolated and downscaled meteorological data from weather stations are unable to reflect the complex thermal patterns of such vegetation. Thus, using interpolated weather station data to characterise alpine life conditions without considering the small-scale thermal mosaic induced by micro-topography may result in misinterpretation and inaccurate prediction. Therefore, we conclude that elevational species shifts in a warmer climate are clearly overestimated when based on weather station data.

The data presented in this study confirm that habitats in the alpine zone are in fact more suitable for organisms to cope with climatic change than had commonly been assumed. On the basis of this study, we predict that future warming will only lead to moderate elevational migration needs for cold-adapted plant species in the alpine zone. We show that under a warmer climate, species have the opportunity to utilise the diverse micro-habitats occurring within the grassland slope. They may move horizontally to occupy colder niches instead of migrating upwards to higher elevations. This is in contrast to the observations and predictions of elevational species shifts in the sub-nival and nival zone (see studies mentioned in the General introduction). Hence, Study 3 of this thesis suggests that warming-induced impacts on cold-adapted plant species will be less pronounced in the alpine zone compared to the sub-nival and nival zones.

8.3 Alpine grassland ecosystem stability in the face of climate change

There is evidence for substantial resistance to climatic forcing in plants living in high elevation and inhabiting the same location over thousands of years (Steinger et al. 1996, De Witte & Stöcklin 2011, De Witte et al. 2012). The pronounced longevity of alpine plant species such as Carex curvula con-
tributes to the stability of alpine grassland ecosystems under a changing climate. Theurillat & Guisan (2001) state in their review article on potential impacts of climate change on vegetation in the European Alps that these ecosystems appear to evince a natural inertia and thus tolerate a climate change of the order of 1–2 K as far as plant species and ecosystems are concerned. However, for a change of the order of 3 K or more, profound changes may be expected.

Monitoring permanent plots or revisiting places with historical species records provide valuable information about long-term influences of climate change on vegetation. Such long-term observational studies carried out in the Northern Prealps and Central Alps reveal that the effect of climate change on plant community composition depends on the elevational zone. Vittoz et al. (2009) report on low impacts of climate change on grassland in the sub-alpine elevational zone in the last 50–60 years. Sub-alpine grassland communities showed negligible long-term compositional changes and thus were assessed as stable. Changes were generally limited to increasing or decreasing frequency and cover of certain taxa and only a few species appeared or disappeared on the permanent plots. A long-term study in alpine grassland (Carex curvula sward) revealed almost no changes in community composition and only very small changes in species cover since 1980 (Windmaißer & Reisch 2013).

The persistence of grassland in the alpine zone was attributed to the extreme longevity of many alpine grassland species. Matteodo et al. (2016) confirm that sub-alpine and alpine grassland communities were only weakly affected by climate change in the last 25–50 years. Independent of the bedrock type, grassland vegetation was quite stable in terms of species composition and some newly arrived species belonged to the typical species pool of the colonised community. In contrast, a monitoring study on Piz Linard summit (3410 m a.s.l.) uncovered an accelerated increase in plant species richness since 1992 in the lower nival zone (Wipf et al. 2013). The summit of Piz Linard is the oldest site in the Alps whose flora has been recorded since the Little Ice Age (1835). Most of the already present species responded with an increased abundance and a colonisation of new areas of the summit, while new arrivals from lower elevations mainly established at sites with already high species richness. These significant floristic changes point to the high impacts of climate change (especially warming) on vegetation in the sub-nival and nival zone. These observational studies show that sub-alpine and alpine grassland is characterised by a pronounced stability, and until now, does not seem to be affected by a changed climate, whereas vegetation in the sub-nival and nival zone is very susceptible to climate change.

Climate change experiments carried out in the alpine zone of the Alps do not support the hypothesis that climate change may have serious consequences on alpine ecosystems in the long term. Two experimental studies using the free-air CO$_2$ enrichment (FACE) method, both performed in the Furka Pass region, revealed that several years of elevated CO$_2$ did not stimulate growth of alpine grassland.
plants (Körner et al. 1997) and alpine glacier forefield plants (Inauen et al. 2012). These results indicate that plants in the alpine zone are not carbon limited at current atmospheric CO$_2$ concentration and may not respond to a further increase of the atmospheric concentrations of CO$_2$ due to climate change. On the other hand, experimental studies applying open top chambers (OTCs) or transplanting soil monoliths to lower elevations to passively enhance temperature revealed contradictory results about the responses of alpine grassland to warming. Egli et al. (2004) showed in a short-term translocation experiment that warming negatively affected above- and below-ground biomass production in alpine grassland. In another translocation experiment, which was conducted in parts at Furka Pass, De Boeck et al. (2016) confirmed short-term negative responses in above-ground phytomass production, but only when warming was combined with drought. In contrast to these short-term translocation experiments, longer-term OTC experiments detected neutral or weak positive (Gugerli & Bauert 2001), but also significantly positive (Kudernatsch et al. 2008) responses in growth and reproduction of alpine grassland species when exposed to higher temperatures. This suggests that warming leads to a stimulation of growth in the long term.

The first two studies presented in this thesis (drought studies) found that alpine grassland ecosystems are unexpectedly responsive to summer droughts in the short term. If only the above-ground responses to summer drought are taken into account, as this is done in the first drought study, the strong responses of two of the grassland systems lead to the assumption that these systems are adversely affected and not very stable. But, under the consideration of the below-ground responses, as this is done in the second study, a completely different assessment results. The shift from above- to below-ground biomass production in alpine grassland triggered by drought is an acclimation response and leads to an increased resilience of the systems. The strong responses to drought observed in both studies, which are all based on changes in the resource allocation, suggest a high stability of alpine grassland systems under drier conditions. In addition, the third study of the thesis found that cold-adapted grassland species may occupy new places within the grassland slopes, when temperatures continue to rise in the future, and are not forced to migrate upwards into the subnival elevational zone. This suggests that alpine grassland communities will not be subjected to profound changes in their species compositions, if warming will be in the range of 3–4 K.

Based on the findings of this thesis and on the above-mentioned outcomes of other observational and experimental studies, I conclude that alpine grassland ecosystems are characterised by a high stability, when exposed to climate change in the next 80 years. This statement applies to changes not exceeding the extent of the simulated changes in precipitation in the drought experiment (MD treatment) and temperatures in the manipulation of spatial sampling resolution in the observational study about habitat temperatures, i.e. a reduction of summer precipitation by 25% during 3 years
and a warming of up to 3–4 K. I further conclude that the predicted high stability of alpine grassland systems under a changing climate and thus a longer-term integrity of these ecosystems will be a decisive property to ensure the maintenance of the ecosystem services, especially slope stability.

This thesis investigated potential impacts of a warmer and drier future summer climate on alpine grassland ecosystems. Consequently, it contributes to a better understanding of the climate change impacts on the dominating vegetation in the alpine zone. It improves the scientific knowledge on the behaviour of alpine ecosystems under changing environmental conditions. Moreover, it emphasises that both experimental and observational studies are needed to assess the consequences of environmental change on alpine ecosystem structure and function.

### 8.4 References


Acknowledgements

9 Acknowledgements

First of all, I would like to express my special thanks and my very great appreciation to my supervisor Nina Buchmann for her great support during my doctorate at ETH Zurich. She gave me the opportunity to carry out my doctoral research project and to write my doctoral thesis as a member of the Grassland Sciences Group. I am particularly grateful to her for the opportunity to work at very nice field sites at Albula and Furka Pass in the Swiss Central Alps during several summers, to participate in several national and international conferences and to gain experience in teaching.

I wish to acknowledge the very valuable support provided by my two co-supervisors Andreas Lüscher and Michael Scherer-Lorenzen. Their help in planning the experiment, analysing data, interpreting results and writing the thesis was greatly appreciated. Without their guidance and persistent help the work presented in this doctoral thesis would not have been possible.

In addition, I am very grateful for the help provided by Erika Hiltbrunner, Eva Spehn and Werner Eugster, who have contributed significantly with their great expertise to the success of my doctoral research project and my doctoral thesis.

I would like to express my gratitude to Daniel Scherrer and Christian Körner. I greatly appreciated the research collaboration with them at Furka Pass.

Let me cordially thank the two master students Gwendolin Bitter and Simone Schmies for their valuable cooperation in my research project.

Furthermore, I would like to express my sincere thanks to the members of the Grassland Sciences Group. The scientific, technical, analytical and administrative staff of the research group supported me during my doctorate in a number of ways. Special thanks go to my office mates.

I would like to warmly thank Johanna Hänger for her field and lab assistance, which was essential for the successful realisation of my research project.

In addition, I wish to thank all the student helpers, who were involved in field and lab work.

My special thanks also go to Patrick Flütsch, who designed and produced the rainout shelters used in my experiment.

Many thanks go to the staff of the ETH research station Alp Weissenstein at Albula Pass and the staff of the research station ALPFOR at Furka Pass for the great hospitality and the help in field work.
Finally, I owe my deepest gratitude to my family and friends for their great support during my doctorate.

Studies 1 and 2 of this doctoral thesis were carried out as part of the IMEXCLIME project (Impacts of extreme climatic events on ecosystem functioning in alpine grasslands), which was funded by a PSC-Syngenta Graduate Research Fellowship of the Zurich-Basel Plant Science Center.

Study 3 of this thesis was realised in collaboration with the Institute of Botany, University of Basel, as part of the EU-funded EC FP6 Eco-Change project (Challenges in assessing and forecasting biodiversity and ecosystem changes in Europe, no. 066866 GOCE).
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