DISSERTATION

Titel der Dissertation

Effekte des Klimawandels auf alpine Vegetation: Artenvielfalt, Alter der einzelnen Individuen, Methoden zur Datenerhebung und ein Transplantationsexperiment

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Effects of climate change on alpine vegetation: species richness, age of individual plants, transplantation experiment and observation methods

Effekte des Klimawandels auf alpine Vegetation: Artenvielfalt, Alter der einzelnen Individuen, ein Transplantationsexperiment und Methoden der Datenerhebung

Dissertation

To attain the degree of *Doctor rerum naturalium* at the faculty of Life Sciences at the University of Vienna

Zur Erlangung des akademischen Grades Doktor der Naturwissenschaften an der Fakultät für Lebenswissenschaften der Universität Wien

von Barbara Friedmann geb. Holzinger

bei o.Univ.-Prof. Mag. Dr. Georg Grabherr

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We do not inherit the Earth from our Ancestors,
we borrow it from our Children.

Native American Proverb

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Abstract (English)

Different aspects of climate change effects on alpine vegetation are explored in four detailed studies. First, species richness on ten out of twelve mountains in SE-Switzerland has increased in the past century. Calculated migration rates of species on these mountains suggest that most species have migrated upwards at an average rate of 14m per decade. Second, three of those species that are considered as potential migrant species were carefully studied by determining the age of individuals using herbchronology in populations in high altitudes and comparing them to low altitude ones. No difference between high and low altitude populations were found in terms of age, root growth rate and root diameter. It was tested if herbchronology could be avoided in future studies as it is a very destructive technique, by comparing age and root diameter. The fits were satisfactory, so it was concluded that age could be predicted by measuring root diameter. In the third study, a transplantation experiment was conducted, where blocks containing high alpine species were grown in the gardens of the University of Vienna and observed over the course of four years. Most individuals increased in size which led to an increased competitive pressure. Changes in the size of individuals could not be attributed to certain species. This points out the limitations of trying to predict the reaction of a particular species in increasing temperatures. The fourth study focused on methods that are useful for long-term observation of high altitude vegetation, especially for vegetation cover determination. It was found that visual estimation is most suitable, effective and in that superior to the point-quadrat method, but study question and aim always need to be kept in mind.

Abstract (Deutsch)

Der Effekt des Klimawandels auf die alpine Vegetation wird in vier detaillierten Studien erörtert. Zunächst wurde auf zehn von zwölf Bergen der Südost-Schweiz eine erhöhte Artenanzahl im Vergleich mit dem letzten Jahrhundert gefunden. Eine Analyse von Migrationsraten zeigte für den Großteil der dort erhobenen Arten ein Höhersteigen mit einer Durchschnittsgeschwindigkeit von 14m pro Jahrzehnt. In der zweiten Studie wurde mit Hilfe der Herbchronologie, die das Alter bei Kräutern anhand von Jahresringen in der Wurzel feststellen kann, der Frage nachgegangen, ob potentielle Migrantenarten in höheren Lagen bereits zu einer Verjüngung der Populationen beitragen im Vergleich zu niedrigeren Lagen. Es wurden keine Unterschiede gefunden, weder im Alter noch im Wurzelwachstum oder des Wurzeldurchmessers. Die Messung des Wurzelumfangs konnte als sinnvolle und zielführende Alternative zur Herbchronologie für die Altersfeststellung von Kräutern bestätigt werden. In der dritten Studie wurden einige Ziegel mit alpinen Arten nach Wien transplantiert, um sie vier Jahre lang zu beobachten. Es wurden bei den meisten Arten gesteigertes Wachstum beobachtet, was zu unterschiedlichen Konkurrenzsituationen führte. Konkurrenzbedingte Zu- oder Abnahmen von Ididuengrößen konnte nicht bestimmten Arten zugeordnet werden. Das Experiment zeigte, dass sich die Strukturen der bestehenden Vegetation unter wärmeren Bedingungen oftmals überraschend ändern können, und dass Vorraussagungen auf Basis des aktuellen Verhaltens womöglich irreführend sind. In der vierten Studie wurden Methoden zur Vegetationserfassung, im speziellen der Deckung, auf ihre Tauglichkeit für die Langzeitbeobachtung von Hochgebirgsvegetation verglichen. Die visuelle Deckungsschätzung wurde für besser befunden als die Punkt-Quadrat Methode, da sie bei hohen und besonders bei niedrigen Deckungen einsetzbar ist, wobei Ziel und Aufgabe der jeweiligen Studie berücksichtigt werden müssen.

Summary (English)

This work comprises four scientific papers, some of which have been published and others submitted or in preparation to be submitted to the international community. Three of them address different aspects of the phenomenon of climate change and its impacts in alpine environments, and one addresses the methodological issue of vegetation sampling in those habitats.

The first paper deals with a few available long-term studies comprising lists of plant species and their elevations, dating back to 1885, in the Grisons of Switzerland. Summits were revisited and complete lists of vascular plant species were collected on each of the 12 summits. On most mountains, species richness increased at an average rate of 11 % per decade of historical species number. Two thirds of all species migrated uphill at rates up to 14 altitudinal meters per decade. Several detailed analyses showed that some families and dispersal methods were more prone to migration than others. Summits with carbonate bedrock had more migration than those free of carbonates. Contrary to the hypothesis, it was not found that the alpine-nival ecotone has more species number increase than other elevational zones.

Following up on this study, we tested three alpine species on their migration behaviour in the last years. After testing herbchronology, a dating method for herbivorous species, on 24 alpine species, three species were found to be suitable, as they are very common and potential migrators. The hypothesis we tested was that due to migratory behaviour, individuals making up high altitude populations should be younger than those of low altitude populations. The results, however, showed that the populations of *Anthyllis vulneraria* subsp. *vulneraria, Minuartia gerardii* and *Trifolium pallescens* investigated in both high and low altitudes did not differ in terms of age. Similarly, root growth rates and root diameter were the same in high and low altitudes. Herbchronology is very destructive; it involves rooting out the whole plant in order to cut the root. Therefore, the usefulness of diameter (circumference) measurements for age determination purposes was investigated and found to be suitable.

As a second follow-up of the first study in Switzerland, some ten blocks of alpine plants including their soil were brought to the Vienna lowlands and observed for the changes that take place after such a drastic change of environment and especially temperature. All species increased in size and growth rate, some were found to even germinate outside the blocks on soil, while others did not adapt as fast and decreased in cover or even disappeared. The study showed very clearly that the reaction of species differ depending on

the competitors. It should be followed up by more detailed studies of the species under question or of interest.

The forth paper compared three vegetation sampling methods for their suitability in high alpine environments. Special attention was paid to their usefulness and effectiveness for long-term monitoring projects with the special requirements of being cheap, quick and able to produce quality data. It was found that visual estimation, although often criticised, is the method that produces the required data better than the point-framing method, often regarded as more objective and therefore better for long-term projects with changes of observers over the years being inevitable.

Zusammenfassung (Deutsch)

Die vorliegende Dissertation besteht aus vier wissenschaftlichen Arbeiten, die entweder bereits publiziert sind, bei internationalen Journalen zur Begutachtung und Publikation eingereicht wurden oder dafür vorbereitet werden. Drei davon beschäftigten sich mit der Auswirkung des Klimawandels auf alpine Vegetation im weitesten Sinne, während der letzte Artikel auf Methoden zur Erfassung der Vegetation in alpinen Höhenlagen eingeht und ihre Tauglichkeit für Langzeitstudien prüft.

In der ersten Arbeit wurden 12 Gipfel im schweizerischen Engadin auf Veränderungen in den letzten 100 Jahren bezüglich Artenvielfalt untersucht. Artenzahlen stiegen um 11% pro Dekade, und die Mehrheit der Arten wanderte bergauf mit einer Geschwindigkeit von bis zu 1,4 m pro Jahr. Arten mit Windverbreitung sowie früh- und spätblühende zeigten mehr Wanderlust als andere. Man konnte auch Unterschiede im Substrat feststellen, das heißt es gab mehr Wanderer auf Kalkgestein als auf Silikat. Die Hypothese, dass der alpin-nivale Ökoton mehr Artenzahlveränderungen aufweist als die umliegenden Höhenzonen, konnte nicht bestätigt werden.

Die Erkenntnisse dieser Arbeit waren ausschlaggebend für zwei weitere Arbeiten, die im Folgenden beschrieben werden.

Die Herbchronologie-arbeit stellte sich im Wesentlichen zwei Fragen: Angenommen die meisten Arten wandern nach oben, dann sollten die höheren Populationen jünger sein als die weiter unten: kann das bestätigt werden? Die Herbchonologie ist eine relativ neue, aber auch sehr destruktive Methode der Altersbestimmung, da es mit dem Ausreißen der gesamten Pflanze einhergeht: gibt es Alternativen für die Altersbestimmung von krautigen Hochgebirgspflanzen? Die Ergebnisse der Studie zeigten, dass es keinen Unterschied im Alter zwischen höheren und niedrigeren Populationen gab, somit wurde die Ausgangshypothese nicht bestätigt. Ebenso sind die Wachstumsgeschwindigkeit und der Wurzeldurchmesser gleich in hohen und tiefen Lagen. Die Bestimmung des Alters aufgrund von Stammumfangmessungen erwies sich als relativ genau, wodurch weitere Studien von Populationsstrukturen im alpinen Gelände vor allem in Bezug auf das Alter der Individuen ermöglicht werden.

Die zweite Arbeit, die im direkten Zusammenhang mit der einleitenden Arbeit in der Schweiz stand, war ein Transplantationsversuch, indem alpine Pflanzen über 4 Jahre im Wiener Becken beobachtet wurden. Es wurden folgende Erkenntnisse gewonnen: Die Mehrzahl der Arten zeigten gesteigertes Wachstum bis zum Doppelten ihrer Größe, ebenso waren Konkurrenzeffekte offensichtlich. Zwei Arten siedelten sich außerhalb der Versuchsziegel an. Bryophyten konnten vor allem in den Wintermonaten über die andere

Arten hinauswachsen. Dieses Experiment zeigte deutlich, dass sich die Strukturen der bestehenden Vegetation unter wärmeren Bedingungen oftmals überraschend ändern können, und dass Vorraussagungen auf Basis des aktuellen Verhaltens womöglich irreführend sind.

Die vierte Arbeit beschäftigte sich mit der unterschiedlichen Tauglichkeit von drei verschiedenen Methoden zur Datenaufnahme im alpinen und subnivalen Gelände für Langzeitstudien. Punkt-Quadrat Methode, Visuelle Schätzung und Frequenzaufnahmen wurden verglichen. Es wurde befunden, dass die Punkt-Quadrat Methode zwar objektiv und bei höheren Deckungen auch relativ genau und vergleichbar ist, jedoch bei seltenen Arten versagt. Im Vergleich dazu ist die visuelle Deckungsschätzung zwar oft kritisiert, jedoch im Falle der wenig deckenden Vegetation im subalpinen Gelände, geeigneter. Frequenzaufnahmen brauchen die meiste Zeit, jedoch sind sie am präzisesten für die Aufnahme aller Arten. Eine Kombination aus visueller Schätzung und Frequenzaufnahmen resultiert also in der besten Datenqualität.

Introduction

Climate change

The increase of temperature as a consequence of human-induced, or at least -enhanced, global warming and its implications have been subject to an enormous number of studies in the past years (Grabherr et al., 1994; Walther et al., 2002; Parmesan and Yohe, 2003; Alcamo et al., 2007). Temperature has been found to have increased by 0.6C in the past 100 years (Walther et al., 2002). Ecosystems of all major life zones from the Arctic to the Tropics, and many different life forms, from butterflies (Roy and Sparks, 2000) to alpine plants (Grabherr et al., 1994), have been under investigation in the attempt to predict and/or observe possible impacts caused by a changing climate. To date, there are different and to some extent controversial hypotheses on possible responses of aquatic and terrestrial ecosystems and their animal and plant composition to changing temperature regimes. The majority of observational studies, however, suggest an already ongoing impact caused by climate warming in different biomes: Parmesan (2003) summarises a large number of studies on different organisms and finds overwhelming evidence that the majority (80%) of the studied organisms respond to climate change in the direction predicted, which means earlier spring events, shift of range distribution upwards and northwards, new colonisation events and decreasing range size of some arctic species. Earlier spring events at an average rate of 2.3 days per decade were observed in over 173 species. This includes, for example, the earlier arrival of migrant birds (Forchhammer et al., 1998) and earlier flowering of plants (Post and Stenseth, 1999). Maximum range shifts from 200 km for butterflies (Parmesan et al., 1999) to 1,000 km for marine copepods (Sagarin et al., 1999) over the past 40 years have been observed. New colonisation events have been observed for example in tree-line shifts (Payette et al., 1989; Moiseev and Shiyatov, 2003) and bird distribution changes (Thomas and Lennon, 1999). Invasions of introduced plants spreading from gardens to the countryside are another common example (Dukes and Mooney, 1999; Walther, 2000). Arctic fox species have declined in their range size (Hersteinsson and MacDonald, 1992). The combination of these abundance shifts with increases and decreases in range result in rapid community reorganisations, because species composition and the dynamics of ecosystems are also changing (Walther et al., 2002).

Public perception and opinion

The general public has been confronted with possible worst-case scenarios (including newspaper articles or Hollywood movies such as "The Day After Tomorrow") as well as proposals for actions that can be taken by individuals to reduce the increase of

temperatures (see ecological footprint inspired by Wackernagel and Rees, 1996, or offset emissions for flight travels, etc.). Some parts of the world have already been struck by various extreme weather events: hurricanes (Mexico Sept 2009), typhoons (Philippines/Vietnam Sept 2009) and flooding (southern USA Sept 2009), all of which are predicted to increase in their intensity and frequency. It is well known that the inhabitants of the developing world are and will be suffering more in the short term due to the effects of global warming, although it is the developed world which is mostly responsible (e.g. CARE Österreich, 2009).

The Kyoto protocol of the UNFCCC (The United Nations Framework Convention on Climate Change) of 1997 aimed at reducing and combating the human contributions to the progress of global warming. It contained the binding commitment to decrease greenhouse gas emissions as well as the possibility of emission trading and other measures aimed at reducing human-induced climate change to a "level that would prevent dangerous anthropogenic interference with the climate system" (UNFCCC, 1997). As the targets have not been met by all countries (including Austria, which is far from reaching the target of decreasing emissions by 13%, having instead increased them by 15%) and greenhouse gases are continuing to rise, the Kyoto protocol will be replaced and succeeded by a hopefully more powerful document and a synthesis of efforts by all major players in the worldwide economy in Copenhagen in December 2009. With the change of attitude on the part of the USA (which as the only industrialised country had not ratified the Kyoto protocol) that came about through the new President and Nobel Peace Price Winner Barak Obama - "I don't think I have to emphasise that climate change is one of the defining challenges of our time. The science is clear and conclusive and the impacts can no longer be ignored." (BBC, 2009) – there is hope that even the USA will join the efforts to reduce the damage.

How interested, however, is the general public in this matter? Surveys have shown that climate change is indeed seen as a problem by a majority of Europeans (ECRA, 2009). Scientific surveys found that the public both in the United States and in other regions, "perceives substantial threat from global warming, but the threat levels tend to be significantly less than those from other environmental and social problems" (Bord et al., 1998; Poortinga and Pidgeon, 2003; quoted in Lowe et al., 2006). Also, the obligation to actually take action is often seen as the politicians' responsibility (Lorenzoni, 2003), although effective measures can only and must be taken by the individual. However, politicians need to set incentives and make appropriate action plans otherwise the individual tends to blame others rather than take responsibility himself. The following

quote puts it succinctly: "The South blames the North, cyclists blame drivers, activists blame oil companies and almost everyone blames George Bush" (Marshall and Lynas, 2003). Lowe et al. (2006) report public reactions to the movie "The Day After Tomorrow" and conclude that the lay audience is confused about the actual scientific basis, the causes, and the action that can be taken by each individual; this is worrying. Other survey findings are also disconcerting: public concern about global warming correlates negatively with factors that should suggest high, not low, concern: wealth, responsibility (CO_2 emissions), and direct future threats (see Sandvik, 2008). Also, individual willingness to "pay" and sacrifice is very low (Bord et al., 1998), although the only way to change or reduce the risks is to incorporate the entire worldwide community.

Scientific community

It is the responsibility and moral obligation (Sandvik, 2008) of the scientific community to be aware of the confusion and respond accordingly with more "down-to-earth" talks and communication to the general public on the topic of climate change (see also Lowe et al., 2006; Sandvik, 2008). Science has been aware of the phenomenon and has warned of many possible consequences since long before the public has realised and been confronted with some of the findings. In fact, the first mentions of global warming can already be found in the 1970's, including notions about sea-level rise and temperature increase (Benton, 1970; Kopec, 1971). The overwhelming evidence and observations of global temperature increase and its consequences have not stopped sceptics and critics presenting their view; in fact, even popular science sometimes denies or at least questions the phenomenon (e.g. Michael Crichton's novel *State of fear*). Lowe 2006 explains that the media has tried to provide a balanced view of both supporters and critics, although in reality supporters are a far larger group, thus simulating to the general public a balanced debate that does not exist. A recent poll in the US showed that the public views the disagreement among scientists as larger than it actually is: 35% of people thought scientists do not agree the earth is getting warmer due to human activity, while in fact 84% of scientists do believe that this is the case (Pew Research Center, 2009).

This majority that agree with the theory of human influence on the world's climate have shown their agreement by contributing to the IPCC (International Panel of Climate Change) and by approaching political leaders and sending out warnings (e.g. "world scientists call for action" 1997, Union of Concerned Scientist).

Europe and the Alps

In Europe, the IPCC (International Panel of Climate Change) predicts a decrease in annual precipitation and more summer heat for the south, loss of coastal area due to sea-level rise, an increase of climate-related hazards like flooding, an increase in precipitation and forests in the North and difficulties for organisms to adapt in all areas (Alcamo et al., 2007). The organisms studied range from marine organisms and butterflies (Thomas and Lennon, 1999; Thomas et al., 2001) to alpine animal (Hughes, 2000) and alpine plant species (Grabherr et al., 1994). In plant populations, the IPCC reports the overall trend to be towards "increased growing season, earlier phenology and shifts of species distributions towards higher elevations (Grabherr et al., 1994; Kullman, 2002; Körner, 2003; Egli et al., 2004; Sandvik, 2008)."

This thesis presents another piece of the puzzle, looking at impacts of climate change in high-mountain environments of the Alps. Particular attention was paid to plant responses. Why the alpine environment? The reason why alpine and polar regions are popular when it comes to studying the effects of climatic change is that these ecosystems are adapted to existence at low temperature conditions and short growing seasons (summers) and that they are controlled mostly by temperatures and precipitation, i.e. the abiotic environment (Sakai and Larcher, 1987; Kammer and Mohl, 2002; Körner, 2003). Therefore, changes in these factors should bring about a sensitive and above all recordable reaction in those environments. A high percentage of endemic and unique species can be found in alpine regions, e.g. in Europe, where 20% of the continent's species richness in native vascular plants is found in areas above the timberline, which cover only 3% of Europe (Väre et al., 2003). Also, most people's fresh water supply originates in alpine areas, making them critical for human survival. In fact, more than half of the world's population depends on water stored in mountain regions (University of Innsbruck, 2009). Mountain ecosystems all over the world have experienced and are likely to experience more enhanced and rapid warming than lowland areas in comparable latitudes (Theurillat and Guisan, 2001; Halloy and Mark, 2003; Pickering and Armstrong, 2003). Another very important feature of alpine environments is that most of the earth's mountain regions are not permanently inhabited by humans and only restrictively used. Therefore, they are relatively undisturbed, which in turn means that the observed changes are very likely to be due to changes in physical factors rather than changes in human land use activities.

Focus of this thesis

Vegetation studies in alpine environments

Several studies have focused on the change of species ranges in alpine environments at different elevation belts (Grabherr et al., 1994; Gottfried et al., 1999; Kullman, 2002 etc.; for an overview see Grabherr et al., submitted). The transition zone between the closed upper alpine grassland belt and the scarce and scattered vegetation of the nival belt (i.e. the alpine-nival ecotone) is considered to be particularly sensitive to effects climate warming. One of the attached studies (**Paper 1, Changes in species number**) attempted to answer the questions of (1) whether the number of species has increased or decreased in this alpine-nival ecotone and (2) the vertical magnitude of species migration per decade. The species composition on twelve summits in the Alps was surveyed and compared to historical findings, some of them over 100 years old. In the course of mapping the vegetation on the summits, species were found to be different in their migration abilities. Following up on the evidence of increasing species numbers on the resurveyed summits, a further focus was taken on the age structure of selected migratory species. Age and longevity of migratory alpine species may be of particular relevance for the interpretation of warming-induced population dynamics. Non-woody plants, representing the majority of alpine species, were used to test herbchronology techniques and root diameter measurements for the suitability for age measurements. (**Paper 2, Herbchronology**). As herbchronology is destructive and thus does not allow a continued observation of the same individuals, we questioned if non-destructive simple root diameter measurements would yield consistent results with herbchronology.

Plant species have also in other studies been divided into "winners" and "losers" according to the observed changes that have taken place or are predicted to take place (see e.g. Erschbamer, 2007; Schoeb et al., 2009). Migrating species (often also termed invader species) that move upwards over the course of only a few decades and/or those that adapt quickly in certain environments are the "winners." Those species found to stick to their habitats without expanding their ranges, instead being invaded and decreasing in their range, are the "losers". This simple catagorisation suggests that either group of species reacts consistently and predictably. In order to examine whether this idea holds true, one experiment subjected related plant assemblages to an extreme change of temperatures and the reactions of the species were recorded. The outcome did not conform to previous ideas of certain reactions being attributable to certain species (**Paper 3, Transplantation experiment**).

Methodological aspects

Alpine environments are harsh not only for plants, but also for researchers. As mentioned, there are a few strong arguments that support the advantages of research in remote and uninhabited high mountain areas, such as the influence of the abiotic environment in shaping the communities or the aforementioned relatively small anthropogenic importance. However, there are of course a few drawbacks, such as the harsh and often unpredictable working conditions and, sometimes, a difficult access to the monitoring sites. A careful methodological planning and time management are crucial, and additionally, an effective quality control of recording methods, particularly for long-term monitoring studies. The most suitable method, of course, will depend on the particular type of study aim and study question. Planning of long-term field studies should question the available methods in terms of data quality, time effort and equipment costs. How do the methods compare? Vegetation observation often incorporates counts of species number in a particular area. Species count alone does not yield results over short periods of time; therefore more quantitative measurements such as species cover or abundance should also be considered. Vegetation and species cover is recorded by means of various more or less criticised methods. **Paper 4** (**Methods**) of this thesis focuses on the usefulness of three different methods for vegetation recording in scattered high alpine to nival vegetation.

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Paper 1

Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates

Barbara Holzinger, Karl Hülber, Martin Camenisch, Georg Grabherr

Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates

Barbara Holzinger · Karl Hülber ·
Martin Camenisch · Georg Grabherr

Abstract Areas of 2,800–3,000 m a.s.l. represent the alpine-nival ecotone in the Alps. This transition zone connecting the closed swards of the alpine belt and the scattered vegetation of the nival belt may show particularly strong climate warming driven fluctuations in plant species richness compared to the nival belt. To test this hypothesis, 12 summits within this range were investigated in the canton of Grisons, Switzerland in 2004. Complete lists of vascular plant species consisting of 5–70 species were collected on each summit and the elevation of the uppermost occurrence of each species was recorded. These data were compared to historical records over 120 years in age. Within this time, vascular plant species richness increased by 11% per decade on summits in the alpine-nival ecotone. Despite this considerable change, a comparison with nival summits did not support the hypothesis that species richness increase at the alpine-nival ecotone is higher than in the nival belt. A general trend of upward migration in the range of several metres per decade could be observed. Anemochorous species were more often found to be migrating than zoochorous or autochorous species and migration was higher on calcareous than on siliceous bedrock. A comparison between the summits with the adjacent slopes in our study revealed that changes in species number could be used as an indicator for climate-induced changes—if at all—only for the narrow summit areas.

Keywords Alpine-nival ecotone · Climate change · Functional species groups · Migration rates · Species richness change · Switzerland

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Introduction

Climate-induced vegetation change has been documented in various mountain regions (Walther et al. 2001) and for high-alpine assemblages in particular (Keller et al. 2000; Theurillat and Guisan 2001; Körner 2003). Temperature increase is considered to be linked to the increased species richness found in high altitudes (Hofer 1985; Grabherr et al. 2001; Walther et al. 2005).

Alpine areas offer good opportunities for studying the influence of climatic change on plant migration, as plant life at high elevation is mostly

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governed by abiotic factors like temperature and snow fall, which are directly influenced by global warming (Sakai and Larcher 1987; Kammer and Mohl 2002; Körner 2003). These habitats are therefore considered very sensitive to climatic change (Theurillat and Guisan 2001). Furthermore, anthropogenic impact that potentially masks climate change related effects is low compared to lowland regions.

In the Alps, the lower boundary of the alpine-nival ecotone lies at approximately 2,800 m a.s.l (Gottfried et al. 1998). This is the transition zone between the alpine belt, dominated by closed dwarf shrub heath and grassland swards, and the nival belt, characterised by scarce and scattered vegetation on rocks and scree. Some studies suggest that this transition zone might be characterised by larger increases in species richness than adjacent belts (Grabherr et al. 1994; Camenisch 2002; Walther et al. 2004). However, no direct comparisons of changes in species richness between the alpine-nival ecotone and the nival belt have been made.

Reliable historical records of species richness on mountain summits and uppermost occurrence of species in the European Alps reach over 120 years in age (Heer1885; Schibler 1898; Rübel 1912; Braun-Blanquet 1913; Braun-Blanquet 1958). Comparisons with recent findings enable us to investigate both species richness changes and altitudinal shifts of species i.e. migration rates. To identify traits that facilitate migration, species can be grouped according to functional or taxonomic criteria. The specific reaction of a group to past changes could potentially indicate future behaviour of that same group. Diaspore morphology, dispersal mode and dispersal time affect the direction and distance of migration (van der Pijl 1972; Müller-Schneider 1986), whilst bedrock has an a priori impact on vegetation patterns (Ellenberg et al. 1991; Grabherr 1997) and species richness of habitats (Virtanen et al. 2003) and might therefore affect subsequent migration processes.

In our study, we addressed the following questions: Are there changes in species richness on high mountain summits during the last century? Do these changes depend on altitude, and are they linked to the bedrock type? At what rate are species migrating? Which taxonomic or functional groups show Particularly strong migration abilities?

Material and methods

Study area and historical records

A total of 12 mountains between 2,844 and 3,006 m were chosen in Grisons, Switzerland (see Table 1). The selection of summits was based on the availability of reliable historical data of acknowledged botanists. Such records were available from Heer (1885), Schibler (1898), Rübel (1912) and Braun-Blanquet (1913, 1958). Heer, Schibler and Rübel worked exclusively on the summit areas, from here on defined as the uppermost 15 m. Braun-Blanquet additionally included records about the accessible areas from the summit down to 2,800 m along the ascension path. Calcareous, siliceous and mixed bedrock was covered by the selected summits.

Data collection

To enable comparisons, we re-visited the study areas of historical investigations. On summit areas (SA), a complete inventory of vascular plant species was made. Additionally, moving down from the SA to 2,800 m, we compiled complete lists of vascular plant species and recorded the altitude of the uppermost individual of each species with an accuracy of 10 m. We followed the ascension path of historical investigators as accurately as possible.

Data analysis

Summit area

Recent and historical species numbers were compared by calculating the change in species richness per decade (SC_{SA}) for the summit area of each mountain:

$$SC_{SA} = (n_{rSA} - n_{hSA})/d_h$$

where n_{rSA} is the recent number of species on SA, n_{hSA} is the historical number of species on SA, and d_h represents the number of decades since historical investigation.

Additionally, the relative change in species richness was calculated as percentage change in species richness per decade of historical species number (pSC_{SA}):

Table 1 Descriptions of investigated mountains

Mountain	Altitude	Substrate	Summit description	Year (hist)	Investigator (hist)	Coordinates N	Coordinates E
Weissfluh	2844	calcareous	stony, scree	1893	Schibler	46°51'	9°48'
Piz Padella	2856	calcareous	steep, stony, N face inaccessible; S and NW steep, but accessible; frequented peak	1835	Heer	46°32'	9°50'
Sass Corviglia	2862	calcareous	Flat, meadow	1835	Heer	46°31'	9°48'
Piz Tschüffer	2916	mixed	calcareous and siliceous parts very obvious on peak	1912	Rübel	46°29'	10°00'
Piz Alv	2975	calcareous	stony, many different microhabitats	1889	Rübel	46°27'	10°00'
Las Sours	2978	calcareous	scree, stony	1906	Rübel	46°30'	9°56'
Piz Chatscheders	2986	siliceous	elongated peak, S face with strips of closed vegetation	1907	Rübel	46°29'	10°01'
Alplihorn	3006	calcareous	steep, stony, scree	1893	Schibler	46°43'	9°50'
Aroser Älplihorn	2842	siliceous	half-open vegetation cover, E species rich, W monotonous	1910	Braun-Blanquet	46°45'	9°37'
Parpaner Rothorn	2899	siliceous	E and N face inaccessible (too steep).Very frequented peak, S face with strips of closed vegetation	1910	Braun-Blanquet	46°45'	9°36'
Piz Daint	2968	calcareous	N and W faces inaccessible, varied microhabitats on E and S faces. Frequented peak	1920	Braun-Blanquet	46°38'	10°18'
Aroser Rothorn	2980	mixed	half-open vegetation cover, not very stony, calcareous and siliceous parts	1902	Braun-Blanquet	46°45'	9°37'

Mountain	summit area				2800 m asl upward		
	species number hist	species number 2004	SC_{SA}	pSC_{SA}	species number hist	species number 2004	pSC_{2800}
Weissfluh	12	37	2.3	18.8			
Piz Padella	28	40	0.7	2.5			
Sass Corviglia	23	70	2.8	12.1			
Piz Tschüffer	8	28	2.2	27.2			
Piz Alv	14	50	3.1	22.4			
Las Sours	30	43	1.3	4.4			
Piz Chatscheders	31	56	2.6	8.3			

$$pSC_{SA} = (SC_{SA}/n_{hSA}) * 100$$

Data of this study was combined with the data set collected by Grabherr et al. (2001). That study compared complete recent vascular plant species lists for 30 summits in the nival belt in adjacent areas of eastern Switzerland and western Austria to historical data to examine changes in species richness. Thus, not only a geographical but an altitudinal extension could be achieved. The calculations mentioned above were applied to the combined data set (42 summits). The dependence SC_{SA} and pSC_{SA} on altitude was examined using linear regressions. Differences of pSC_{SA} between calcareous and siliceous bedrock were calculated using a two-sided t-test.

Species groups

For the following calculations, only data from the 12 summits investigated for the present study were used. All species found above 2,800 m a.s.l. (including the SA) in the recent investigation of a mountain, but absent from the SA of the respective summit in historical data were considered as the pool of potentially migrating species (species pool). Species already present on the summit area in historical investigations were excluded, as their migration potential could not be estimated, because further upward migration is impossible. Species present in the summit area today but not in historical data were classed as migrators on that mountain.

To identify traits facilitating migration, species were merged into species groups considering functional traits potentially relevant to migration or the taxonomic status. The following groups with the respective categories were used: taxonomy (plant family), dispersal mode (anemochores, zoochores, autochores), dispersal timing (month in which dispersal begins) and diaspore length (larger than or equal to and smaller than the median (1.6 mm) over all species used). The data were compiled from Müller-Schneider (1986), Fischer et al.(1994) and Rothmaler (2002).

If a trait used to distinguish the categories of a species group has no impact on the migration abilities of species, the species composition of migrators should be a random selection out of the species pool: e.g. if the dispersal mode does not influence migration, the proportion of anemochorous migrators will not statistically differ from the proportion of anem-

Table 1 continued

Mountain	summit area				2800 m asl upward		
	species number hist	species number 2004	SC_{SA}	pSC_{SA}	species number hist	species number 2004	pSC_{2800}
Alplihorn	10	5	−0.5	−4.5			
Aroser Älplihorn	33	60	2.9	8.7	78	73	−0.7
Parpaner Rothorn	28	28	0.0	0.0	89	70	−1.7
Piz Daint	0	20	2.4	[a]	15	44	23.0
Aroser Rothorn	11	34	2.3	20.5	71	72	0.1
Average (mean ± standard error)	19 ± 3.1	39.2 ± 5.2	1.8 ± 0.3	10.9 ± 3.0	63.2 ± 16.5	64.7 ± 6.9	5.1 ± 5.9

Summit area was defined as the uppermost 15 altitudinal metres; SC_{SA} represents the change in species number per decade on summit area, pSC_{SA} is the percentage change in species number per decade on summit area and $pSC_{2,800}$ is the percentage change in species number per decade on area above 2,800 m. hist means historical investigation. [a] could not be calculated, because no species were found in the historical investigation

ochorous species in the species pool. Hence, for each category we compared the proportion of species in the species pool with that of migrators belonging to the respective category using a two-sided paired Wilcoxon Rank test.

Investigation area above 2,800 m—migration rates

The following calculations were done for the four mountains of the recent investigation, where historical records down to 2,800 m were available (see Table 1). Percentage change in species number for the area above 2,800 m ($pSC_{2,800}$) was calculated using an equation analogous to that given for pSC_{SA}. Additionally, migration rates of species were calculated as altitudinal shift per decade ($AS_{2,800}$) for each species on each mountain:

$$AS_{2,800} = (O_r - O_h)/d_h$$

where O_r is the recent uppermost elevation for the species and O_h is the historical uppermost elevation. For species absent in one of the investigations, the shortest possible migration distance was assumed in order not to overestimate migration rates. This means that we treated species with no occurrence in historical records, but found today, as migrated from 2,800 m (i.e. the border of the investigation area) to their recent occurrence. Species found in historical records, but not today, were treated as having lost all occurrences in the observed area (above 2,800 m). As there is no information available if the respective species has disappeared from that mountain or has simply lost the uppermost occurrences, we treated

them as having migrated downward to 2,800 m. $AS_{2,800}$ was averaged over mountains where the respective species occurs.

All analyses were done using S-plus (MathSoft 1999). Nomenclature follows Lauber and Wagner (1996).

Results

Summit area

We observed an increase in species number on 10 out of the 12 mountains investigated (Table 1). Species number remained unchanged on Parpaner Rothorn, and decreased on Alplihorn. Change in species richness, SC_{SA}, averaged at 1.8 ± 0.3 (mean ± SE) species per decade ($n = 12$). Percentage change in species richness, pSC_{SA}, varied highly with a mean of $10.9 \pm 3.0\%$ ($n = 11$).

For the combined data set of Grabherr et al. (2001) and this study ($n = 42$), we found that in contrast to SC_{SA}, which decreased with increasing altitude, there was no dependence on altitude of pSC_{SA} (Fig. 1).

pSC_{SA} differences on bedrock were significant (Fig. 2, $t = -2.39$, $P = 0.02$, $n = 39$). In contrast, SC_{SA} did not differ with bedrock type ($t = -0.66$, $P = 0.51$, $n = 40$). Mean percentage changes of species richness were higher on calcareous ($12.4 \pm 2.9\%$, $n = 11$) than on siliceous mountains ($6.0 \pm 1.1\%$, $n = 28$). The highest pSC_{SA} values were found on mixed bedrock ($23.8 \pm 1.3\%$); however, the two mountains concerned were not included in tests, because the sample size was too small.

Fig. 1 Linear regression of the altitude of 42 mountains with the percentage change in species richness per decade, pSC_{SA} ($F = 0.46$, $p = 0.50$, df = 39), and change in species richness per decade, SC_{SA} ($F = 9.65$, $p = 0.003$, df = 40, $R^2 = 0.19$)
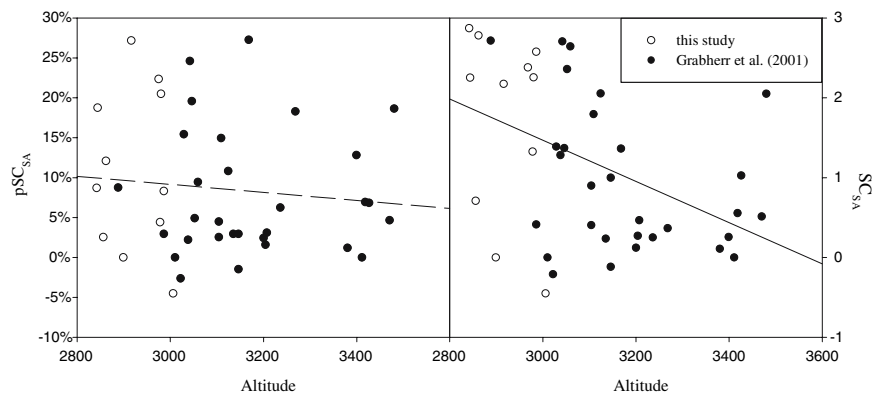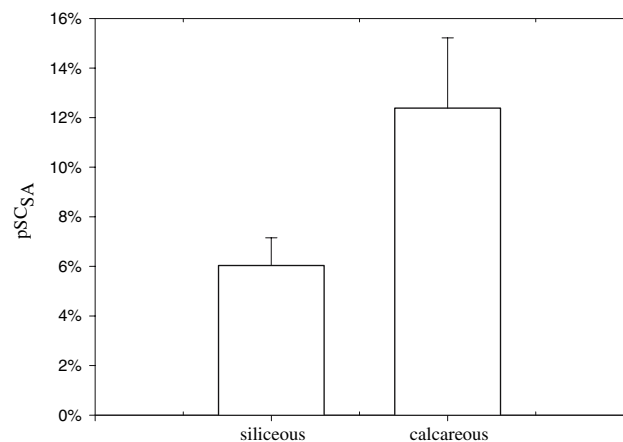
Species groups

Dispersal mode was the only functional trait with
significantly different proportions between migrators
and the species pool. Migrators were more likely to
be anemochorous but less likely to be zoochorous or
autochorous (Fig. 3).

Investigation area above 2,800 m—$pSC_{2,800}$ and migration rates

Percentage change in species richness ($pSC_{2,800}$) was
close to zero on two mountains, negative on the third
mountain, but very high on the forth mountain, where
the number of species tripled (Table 1).

We observed an $AS_{2,800}$ upward migration with a
maximum of 19 m and a mean of 2.2 ± 0.3 per decade
on the four mountains. Of the 140 investigated
species, 97 (69%) migrated upwards (see Appendix
A). Highest $AS_{2,800}$ were achieved by Asteraceae and
Brassicacae species (4.9 ± 2.4m and 4.3 ± 2.1m,
respectively).

Discussion

Summit areas and adjacent slopes

Our findings provide evidence for an increase in
species number of up to three species per decade
within the last 120 years on high alpine summits
(Table 1). This agrees well with other investigations
from the Alps, where similar changes have been
detected (Grabherr et al. 1994; Pauli et al. 2001;

Camenisch 2002; Walther 2003; Walther et al. 2005).
Taking into account further observations from the
past century (between the first and recent study) on
summits studied in this work (Braun-Blanquet 1958;
Hofer 1985), we can assume a continued increase in
species richness. In the same period, mean summer
temperature increased by at least 0.6 K (Bader and
Bantle 2004). A relation between these phenomena is
manifest, possibly making temperature the driving
force of the upward shift of vegetation (Grabherr
et al. 1994; Pauli et al. 1996; Theurillat and Guisan
2001; Klanderud and Birks 2003). In contrast to the
clear species richness increase on summits, however,
no general pattern in species richness change on the
adjacent areas down to 2,800 m (see Table 1) was
found. Possibly, the migration of species originating
from alpine swards may be balanced by the loss of
nival centred species due to competitive pressure
caused by the migrators in these areas. Tolerance
against the harsh abiotic conditions may be replaced
by competitive interactions as limiting factor for
further increases in species richness (Theodose and
Bowman 1997; Choler et al. 2001). We therefore
suggest that an increase in species richness can be
regarded as a potential indicator for climate change
only directly on the summits, but not on adjacent
slopes.

In the context of climate warming several studies
predict the extinction of a considerable number of
high-alpine species (Grabherr et al. 1994; Thuiller
et al. 2005). In our case, 13% of the historical species
occurrences on summits could not be re-confirmed
(see Appendix A), but no species showed a partic-
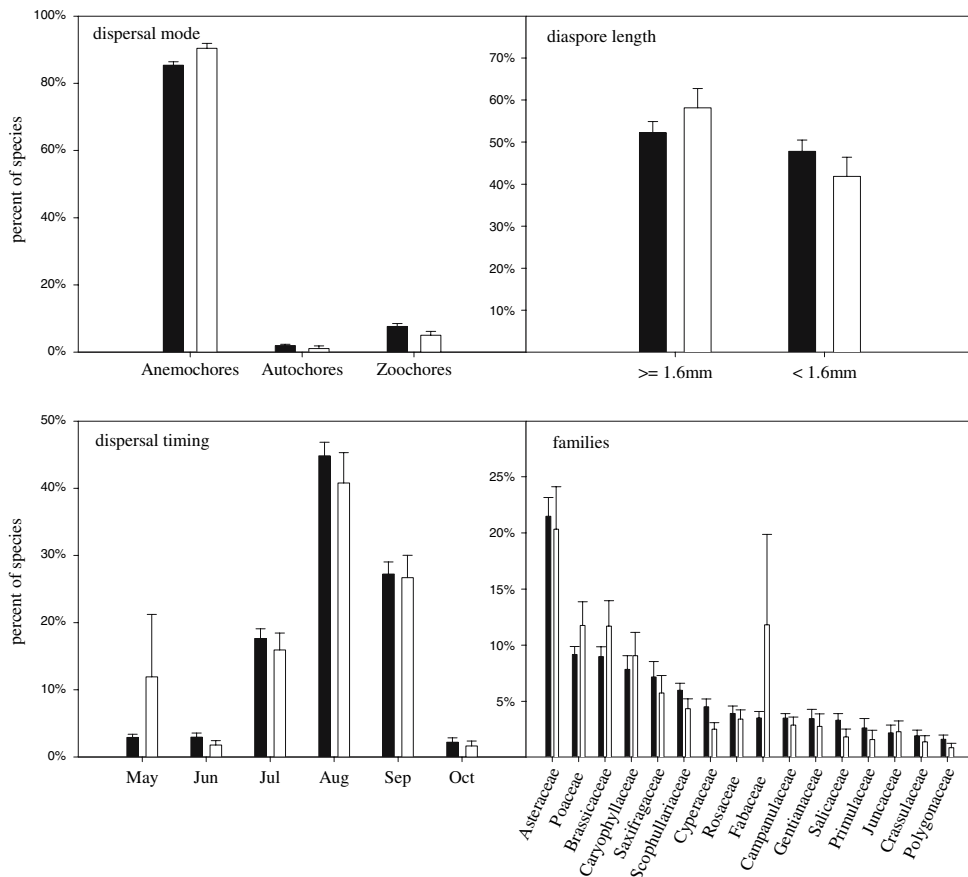ularly high rate of loss. Hence, an outstanding threat

Fig. 3 Mean and standard error of percentages of species within the species pool (black bars) and amongst migrators (white bars). The median of 1.6 mm was used as threshold for the classification of diaspore length. Only dispersal modes showed significant differences (anemochores: $P = 0.002$, $n = 12$; autochores: $P = 0.049$, $Z = 1.97$; zoochores: $P = 0.016$, $n = 12$)

for species to become out-competed "beyond the summits" can neither be confirmed nor rejected with our data.

Low and high altitude summits

Several studies predict the temperature driven increase in species richness to be more pronounced at the alpine-nival ecotone than in the nival belt (Grabherr et al. 2001; Camenisch 2002; Walther et al. 2004). Due to the sensitivity of transition zones to climate change, they are considered highly appropriate to study its impacts (di Castri et al. 1988; Gottfried et al. 1998; Peteet 2000). Our findings confirm that summits at altitudes between 2,800 and 3,000 m experience a much more pronounced increase in species number than summits above this

range (see Fig. 1). Not surprisingly, a larger species pool is available at lower altitudes providing species potentially migrating upwards once conditions permit (Grabherr et al. 1995; Keller et al. 2000; Camenisch 2002; Walther et al. 2004) than at higher altitudes. However, percentage species richness change was independent of altitude within the investigated altitudinal range. Hence, there was no indication for the alpine-nival ecotone to be more dynamic in terms of species richness changes than the nival belt.

Bedrock

We found mountains with calcareous bedrock to have a higher percentage species richness increase than those with siliceous bedrock (see Fig. 2 and Walther et al. 2004). Calcareous bedrock is generally

characterised by a higher number of microhabitats (Gigon and Rorison 1972; Pauli et al. 1999; Körner 2003). Precipitation causes calcareous substrates to locally dissolve, so that neutral or slightly acidic microhabitats develop (Gigon and Rorison 1972). A mosaic of different calcareous and additionally slightly acidic microhabitats may increase the possibility of plant species to migrate to the summits. The notably high increase in species richness on the two mountains with mixed bedrock supports this explanation (see Table 1). The differences may become even more pronounced under changing temperature and precipitation regimes (Begert et al. 2005; IPCC 2007).

Migration rates

The upward migration rates found in this study were within the range of several metres per decade, which is in line with those reported by Grabherr et al.(1994) for summits in the same region. Although highly variable and based on data from only four mountains, we regard these as valuable findings because only little quantitative information is available about plant species migration at high altitudes. Studies of tree-line dynamics (Dubey et al. 2003; Dubey and Yadav 2006; Kullman 2006) also revealed highly variable migration rates, but cannot be directly compared to our findings.

Species groups

Except for dispersal mode, migration behaviour was independent of the investigated functional traits and taxonomic groups (Fig. 3), suggesting that pioneer species of high altitudes are typically wind-dispersed (Theurillat and Guisan 2001). Anemochory seems to be a more effective dispersal mechanism in high altitudes compared to zoo- and autochory. Apart from strong air movements facilitating dispersal, the transportation of snow, soil and seeds to the same microsites potentially improves germination conditions for seeds (Kullman 2002).

To conclude, we could confirm a general upward migration of vascular plants, and hence a species richness increase on high altitude summits, which seems to be connected to the temperature increase of the past century. However, there is no evidence that the alpine-nival ecotone is more dynamic in terms of species richness than the nival belt.

Appendix A Species occurrence on 12 mountains in Grisons, Switzerland

Species	Piz Alv 2975	Las Sours 2978	Sass Corviglia 2862	Piz Tschüffer 2916	Alplihorn 3006	Weissfluh 2844	Aroser Rothorn 2980	Aroser Älplihorn 2842	Parpaner Rothorn 2899	Piz Cha-tscheders 2986	Piz Daint 2968	Piz Padella 2856	migration rate (m)
Achillea atrata	x 2974		x 2850	x 2916		2810	2870					2840	6.8
Achillea erba-rotta ssp. moschata			x							x x 2980			
Achillea nana	2850	2960	x x 2850	2840				x 2830	2860	x 2980			−0.5 ± 1.6
Adenostyles glabra						x 2830							
Adenostyles leucophylla									x				−5.3 ± 4.25
Agrostis alpina		2890						x 2842		2970			0.6 ± 3.8
Agrostis rupestris		x 2978								x 2986			
Alchemilla fissa agg.			x 2850										
Alchemilla glaucescens												x	
Androsace alpina		2960		2900			x x 2980	x 2842	x x 2899	x 2986			1.3 ± 1.5
Androsace chamaejasme							2860	x x 2830					−3.1 ± 3.1
Androsace helvetica			x 2862		x	2810		x 2842				x x 2856	−2.1 ± 3.9
Androsace obtusifolia							2930						−0.4 ± 1.6
Antennaria carpatica			x 2862	2860					2850	x 2986			3.1 ± 4.2
Antennaria dioica										x 2980			
Anthoxanthum alpinum										2950			
Anthyllis vulneraria ssp. alpestris			x 2862	2830								2830	
Arabis alpina ssp.alpina	x x 2974	2950	x 2862	x 2916	2960	x x 2844	x x 2980	x x 2842	x 2899	2830	2870	x x 2856	4.2 ± 1.8
Arabis bellidifolia	x 2974		x 2916			x x 2844	2900				x 2968	2840	8.9 ± 0.8
Arabis caerulea	x 2974		x 2850	x 2916	2920	x 2830	x 2970			2830	x 2968	x 2850	9.9 ± 1.8
Arctostaphylos uva-ursi			x 2862										
Arenaria biflora									2840	x 2980			0.1 ± 4.0
Arenaria ciliata							x x 2940	x x 2842	x x 2899		x 2968		3.5 ± 1.6
Arnica montana										2970			
Artemisia genipi	x 2974	x 2978	x 2862	x 2916		x 2830	x x 2950	x x 2842	x x 2899	2950		x 2856	1.7 ± 1.5
Artemisia umbelliformis												x	
Asplenium viride			x 2850				2870						6.8

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Appendix A continued

Species	Piz Alv 2975	Las Sours 2978	Sass Corviglia 2862	Piz Tschüffer 2916	Alplihorn 3006	Weissfluh 2844	Aroser Rothorn 2980	Aroser Älplihorn 2842	Parpaner Rothorn 2899	Piz Cha-tscheders 2986	Piz Daint 2968	Piz Padella 2856	migration rate (m)
Aster alpinus			x 2862							x 2950			−1.0 ± 1.0
Aster bellidiastrum	x 2974					x 2830	2870				2910	2840	5.7 ± 4.5
Astragalus alpinus				2830									
Astragalus frigidus				2830									
Avenella flexuosa									2830				3.2
Bartsia alpina	2830		x 2862	2810						2830		2840	
Botrychium lunaria				2830		2810						2840	
Campanula barbata										2950			
Campanula cenisia				2860	x x 3006		2810					x	−5.3 ± 3.4
Campanula cochleariifolia	x 2974		x 2850	x 2916	2860	x 2840	x 2980				2900	x 2856	14.7 ± 2.8
Campanula scheuchzeri	2950		x x 2862	2860			2910	x 2842	2810	2950		x 2850	4.3 ± 3.4
Cardamine alpina		x 2978								x			
Cardamine resedifolia					2860			x x 2842	2880	x x 2986		2830	1.9 ± 3.6
Carduus defloratus ssp. defloratus	x 2960		2840	2840									
Carex atrata ssp. atrata	2880			2840			2910					2830	−0.9
Carex capillaris													−4.2
Carex curvula ssp. curvula	2830	x x 2978		2840				x x 2842	2860	x x 2986		x 2850	−5.2 ± 3.8
Carex firma							2860				2830	2830	4.7 ± 1.1
Carex nigra						2820						x	
Carex ornithopodioides	2900												
Carex parviflora	2830		x 2862					x x 2842					−2.0 ± 2.2
Carex rupestris	x 2830	x 2978	x x 2862	x 2916				x 2842	2860	2970	2830	x 2856	4.8 ± 0.8
Carex sempervirens										2960			
Carex sp.	x 2974												
Cerastium alpinum ssp. alpinum			x									x	
Cerastium cerastoides							x 2980	x 2830		2830			8.4 ± 5.2
Cerastium fontanum ssp. fontanum										2950			

Appendix A continued

Species	Piz Alv 2975	Las Sours 2978	Sass Corviglia 2862	Piz Tschüffer 2916	Alplihorn 3006	Weissfluh 2844	Aroser Rothorn 2980	Aroser Älplihorn 2842	Parpaner Rothorn 2899	Piz Cha-tscheders 2986	Piz. Daint 2968	Piz Padella 2856	migration rate (m)
Cerastium latifolium	x 2974	x 2978	x x 2862	x 2916	x x 3006	x 2844	2900				x 2968	x x 2856	0.0 ± 2.0
Cerastium pedunculatum		x							2840	2910			4.2
Cerastium uniflorum	2830 x		2840 x x 2862		2950		x x 2980	x 2842	x 2899	x x 2986		x 2850	3.0 ± 1.2
Cirsium spinosissimum	2950			2850	2950	x 2844	x 2970	2820	2810	x 2986		2840	7.6 ± 4.4
Cystopteris montana												2830	
Daphne striata			x										
Doronicum clusii				2810			2910	x 2842	2860	x 2986			1.1 ± 1.5
Doronicum grandiflorum	x 2970	x x 2970	x 2850	2840 x	2950	x 2830	2900	x 2842				x 2850	9.8
Draba aizoides	x 2974		x 2862	x 2916		2970	2970			2830		x	16.7
Draba dubia		x x 2978	x 2862			x 2830		x 2842		x x 2980		x 2856	−1.4 ± 4.8
Draba fladnizensis		x 2960		2810		x x 2830		x	x 2899	x 2980		x 2856	−5.6 ± 4.8
Draba hoppeana	x x 2974	2930	x 2862				x 2980			2960		x	7.8
Draba siliquosa								x 2842	x 2899				4.8 ± 2.5
Draba tomentosa	x 2974		x 2862	x 2916	x	x x 2844	2910				x 2968	2810	10.4 ± 9.5
Dryas octopetala	x 2974										2830	x 2850	3.5
Elyna myosuroides	2830		x 2862	2830	2830	x 2844		x x 2842	2860	2970	2830	x 2856	−1.7 ± 2.8
Epilobium anagallidifolium	x 2974			x 2916		2820							
Erigeron neglectus	x 2974			x 2916									
Erigeron uniflorus	x 2974	x x 2978	x 2862	x 2916	2950	x 2844	x 2980	x x 2842	x x 2899	x 2986	x 2957	x x 2856	5.9 ± 4.3
Eritrichum nanum		x x 2978	x 2862	2820		2810				x x 2986			
Euphrasia sp.	2850	x 2970	x 2862		2820		2920	x 2842	x 2899	x 2986			1.8 ± 1.2
Euphrasia salisburgensis											2840		
Festuca alpina						x					x 2957	2840	4.4 ± 14.2
Festuca halleri	x 2974	x 2978	x 2862	x 2916	2820	x 2844	x 2980	x 2842	x 2899	x 2986		x 2856	1.6 ± 1.4
Festuca intercedens	x			2900									
Festuca quadriflora	x		x	2830 x				x			x 2957	x 2856	3.7 ± 7.4
Festuca sp.											2830		7.8
Festuca violacea								2820					
Galium anisophyllon										2960		2830	2.1
Gentiana acaulis										2970			

Appendix A continued

Species	Piz Alv 2975	Las Sours 2978	Sass Corviglia 2862	Piz Tschüffer 2916	Alplihorn 3006	Weissfluh 2844	Aroser Rothorn 2980	Aroser Älplihorn 2842	Parpaner Rothorn 2899	Piz Cha-tscheders 2986	Piz Daint 2968	Piz Padella 2856	migration rate (m)
Gentiana bavarica		x 2970					x x 2980	x x 2830	x 2880	x 2860			−1.0 ± 0.5
Gentiana brachyphylla		x 2978	x 2862	2860				x 2842	x 2870	x x 2986			−0.3 ± 2.7
Gentiana nivalis			x 2850	2830				2820	2860				4.2 ± 2.1
Gentiana orbicularis			x 2862			2810				2860			5.3
Gentiana punctata									2830	x 2986			
Gentiana tenella				2820				x 2842	2880				2.7 ± 1.7
Gentiana verna			x 2862	2830			2910	x 2842	2880	2860		x 2856	2.1 ± 1.1
Geum montanum		x x 2978						2810	2830	x 2986			3.1 ± 2.1
Geum reptans	x x 2974	x x 2978	2810	2900	x x 3006	x 2830	x 2980	x x 2842	2850	x x 2980		x 2856	−0.3 ± 2.4
Gnaphalium hoppeanum	x 2974					2830	2900						9.8
Gnaphalium supinum		2830		2810		2820	x 2980	x 2842	2870	x 2986		2840	9.3 ± 4.2
Gypsophila repens	x												
Hedysarum hedysaroides	2830		x 2850									2840	
Helianthemum alpestre	2850	x 2978	x x 2862	2830							2830	x	3.5
Helictotrichon versicolor		x x 2978			2820		x 2970	x 2830	2860	x x 2986			−2.8 ± 4.4
Hieracium alpinum	x 2974	x 2978				x 2830		x 2830	2860	2950			19.6
Hieracium piliferum agg.										x 2980			
Hieracium murorum											2830		
Hieracium pilosella										2950			
Hieracium sp.			2840	x 2916							2840		4.8
Hieracium villosum										x 2986			
Homogyne alpina	x 2970		x 2850	2840		x 2830		x 2842	2830	x 2986		x 2850	0.1 ± 2.2
Juncus jacquinii		x 2978		2810				2810	2830	x 2986			1.5 ± 1.5
Juncus trifidus										2970			0.0
Juniperus communis ssp. nana	2810	x 2978		x 2916							2859		7.0
Leontodon helveticus								2820	2860	x 2986			0.5 ± 0.5
Leontodon hispidus ssp. hispidus										x 2986		2830	
Leontodon montanus	x 2974			2850	2860	x 2844		x 2830			2930	2840	11.1 ± 3.9

Appendix A continued

Species	Piz Alv 2975	Las Sours 2978	Sass Corviglia 2862	Piz Tschüffer 2916	Alplihorn 3006	Weissfluh 2844	Aroser Rothorn 2980	Aroser Älplihorn 2842	Parpaner Rothorn 2899	Piz Cha-tscheders 2986	Piz Daint 2968	Piz Padella 2856	migration rate (m)
Leontopodium alpinum	x 2970		x 2862									x	
Leucanthemopsis alpina ssp. alpina	2950	x x 2978		2900			x x 2980	x x 2842	x x 2899	x x 2986			−0.0 ± 0.1
Leucanthemum halleri						2820							
Ligusticum mutellina					2860					2970		2840	
Ligusticum mutellinoides	x 2960	x 2978	x 2862	2900		2820	x 2980	x 2842	x 2880				0.6 ± 1.7
Linaria alpina ssp. alpina		x 2978	x 2862	2900		2810	x 2980	2820	x 2899	x 2986	2957	x 2856	7.9 ± 3.7
Lloydia serotina		x 2978			x 3006		x 2970	x 2842	2899	2960		x 2856	5.2 ± 2.9
Loiseleuria procumbens												x	
Lotus alpinus										2950			
Luzula alpinopilosa								x 2842	2840				−4.2 ± 4.7
Luzula lutea		x 2978		2810				2810	2830	x 2986			−5.5 ± 3.3
Luzula spicata		x x 2978		2900			x 2980	x 2842	x 2899	x 2986			1.0 ± 0.9
Luzula sudetica				2810									
Minuartia biflora	x 2970					2810	2950				2910		13.9 ± 0.8
Minuartia recurva										2820			
Minuartia sedoides	x 2960	x x 2978		2860		x 2840	x 2980	x 2842	x 2899	x 2986			−0.0 ± 0.1
Minuartia verna	x 2960	x 2978	x 2862	x x 2916		x 2844	2920	x 2842	2860	2960	x 2968		3.0 ± 1.7
Moehringia ciliata	x 2974		2850	2840		x 2830	2900	x 2830			x 2968	2840	0.0 ± 1.8
Myosotis alpestris	x 2974		x 2850	2850				2820		2970		x	−0.5 ± 1.5
Oreochloa disticha	x	x x 2978	x	2810			x 2980	x 2842	x 2899	x 2986			1.5 ± 1.2
Oxyria digyna		x					2930						−0.2 ± 4.7
Oxytropis campestris ssp. campestris	x 2970	x x 2978	x x 2862	2860									−2.1
Oxytropis jaquinii			x										
Oxytropis lapponica				2810									
Papaver auranthiacum	2950			x x 2916							2870		−9.5
Parnassia palustris				2830									
Pedicularis kerneri		x x 2978		2820						x 2980			−3.1
Phyteuma globulariifolium ssp. globulariifol.		x 2978								x 2986			

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Appendix A continued

Species	Piz Alv 2975	Las Sours 2978	Sass Corviglia 2862	Piz Tschüffer 2916	Alplihorn 3006	Weissfluh 2844	Aroser Rothorn 2980	Aroser Älplihorn 2842	Parpaner Rothorn 2899	Piz Cha-tscheders 2986	Piz Daint 2968	Piz Padella 2856	migration rate (m)
Phyteuma globulariifolium ssp. pedemontanum		x		2860			x 2980	x x 2842	x 2899	2950			1.3 ± 1.2
Phyteuma hemisphaericum								2810					
Poa alpina	x x 2974	x x 2978	x 2862	2870		x 2844	x 2980	x 2842	x 2899	2950		x 2856	1.6 ± 1.3
Poa laxa		x x 2978	x 2862	2900			x 2980	x 2842	x 2899	2986		x 2856	0.0 ± 0.0
Poa minor	x x 2974		x 2862	x x 2916	2950	2844	2880	2810	2899	2950	2968		0.0 ± 2.0
Polygonum viviparum	2850 x	2930 x	x 2862	2860		x 2844	2910	x 2842	2880	2986	2830	x 2856	1.8 ± 1.3
Polystichum lonchitis							2870					2830	6.8
Potentilla aurea								2810	2830	2860			
Potentilla brauneana	2850		x x 2850	2840		2810						x	3.1 ± 3.1
Potentilla crantzii	2850		x 2862	2830					x 2899	2980		x 2850	−2.1
Potentilla frigida		x 2978		2900				x 2842	2860	2986			0.1 ± 0.1
Primula glutinosa								x 2842					7.0 ± 1.4
Primula hirsuta								x x 2842		2970			0.6 ± 0.6
Primula integrifolia	2830		x						x				−5.8 ± 3.7
Primula latifolia			x							2980			
Primula sp.							2910						
Pritzelago alpina											x 2968		6.7
Pritzelago alpina ssp. alpina						x x 2844						x 2856	8.1
Pritzelago alpina ssp. brevicaulis	x x 2974		x 2862	x 2916			2950						14.7
Pulsatilla vernalis										2970		2840	
Ranunculus alpestris		2890				2820					2810		1.1
Ranunculus glacialis		x x 2978		2900			x x 2980	2810	x 2899	x 2986			−1.1 ± 1.0
Ranunculus montanus ssp. montanus												2830	
Rhinanthus glacialis				2840		2820							
Rumex alpinus													
Rumex nivalis									x				−9.5
Sagina saginoides									2870				−2.0 ± 4.0
Salix herbacea	2880 x	x	x x 2862	2860		2810	2920	x 2830 x	2870 x	2940	2830		2.4 ± 2.2

Appendix A continued

Species	Piz Alv 2975	Las Sours 2978	Sass Corviglia 2862	Piz Tschüffer 2916	Alplihorn 3006	Weissfluh 2844	Aroser Rothorn 2980	Aroser Älplihorn 2842	Parpaner Rothorn 2899	Piz Chatscheders 2986	Piz Daint 2968	Piz Padella 2856	migration rate (m)
Salix reticulata	2850		x 2850									x 2850	1.7 ± 1.7
Salix retusa	2900		x 2862	2860		2820	2870	x 2842			2830	x 2850	1.4 ± 1.5
Salix serpyllifolia	x 2974		x 2862	x 2916		2820			2820	2940	2830	x 2856	−2.1
Saussurea alpina ssp. alpina	x 2970			2860			2870		2820	2950	x 2960		6.8
Saxifraga aizoides	x 2974		x x 2850	2850	2950		2870						1.3 ± 5.5
Saxifraga androsacea	2950	x 2970	x x 2862	2840		2810	2870						2.5 ± 4.5
Saxifraga aphylla	x x 2974			x x 2916		2810	2900				x 2960	x x 2856	
Saxifraga biflora ssp. biflora					2950	x							
Saxifraga bryoides		x x 2978	2900	2900			x x 2980	x 2842	x x 2899	2986	2840		0.0 ± 0.0
Saxifraga caesia	x 2974		x x 2862				2860	x 2842					5.3 ± 0.5
Saxifraga exarata ssp. exarata	x x 2974	x x 2978	x 2862	x 2916			x 2980	x 2842	x x 2899	x 2986	x 2968	x 2856	9.4 ± 5.4
Saxifraga exarata ssp. moschata				2890		x	2860						−5.8
Saxifraga muscoides							2930	x	x x 2899			x x 2856	0.4 ± 0.4
Saxifraga oppositifolia	x x 2974	x x 2978	x 2862	x x 2916	x x 3006	x x 2844	x x 2980	x 2842	x x 2899	x 2986	x 2968	x x 2856	2.2 ± 1.9
Saxifraga paniculata	2850	x 2978	x 2862	2840	2950	x 2844	x 2980	x	2880	2950	2950	x x 2856	−5.7 ± 2.0
Saxifraga seguieri	2960	2960		2840	2950		x 2980	x 2842		x 2986	x 2968		7.6 ± 4.1
Saxifraga stellaris	x	2960								2986			2.1
Sedum alpestre		2960					x 2980	x 2842	2820	2986			1.7 ± 1.1
Sedum atratum	x x 2974	x 2978	x 2862	2860		x 2844	2880		2870	x 2986	2810		−0.6 ± 0.9
Selaginella selaginoides													
Sempervivum montanum										x x 2986			−1.0 ± 1.0
Senecio doronicum	x 2960												
Senecio incanus ssp. carniolicus	x 2960	x x 2978				2860	x 2980	2820	2830	x x 2986	2850	x 2856	4.6 ± 3.3
Sesleria caerulea	x 2974		x 2862	x 2916		x 2830	2860				2850		0.7 ± 2.8
Sibbaldia procumbens	2830		2840	2840		x 2830	2920		2830	x 2986	2860		3.9 ± 4.0
Silene acaulis	x 2974		x 2862	x 2916		x 2844		x 2842			x 2968	x 2856	−1.2 ± 5.7
Silene exscapa		x x 2978	x	x 2916		x 2844	2920	x x 2842	x x 2899	x x 2986		x 2856	−0.2 ± 1.4

Appendix A continued

Species	Piz Alv 2975	Las Sours 2978	Sass Corviglia 2862	Piz Tschüffer 2916	Alplihorn 3006	Weissfluh 2844	Aroser Rothorn 2980	Aroser Älplihorn 2842	Parpaner Rothorn 2899	Piz Cha-tscheders 2986	Piz Daint 2968	Piz Padella 2856	migration rate (m)
Solidago virgaurea ssp. virgaurea	2830												3.1
Taraxacum alpestre agg.			x 2850										
Taraxacum alpinum agg.	x 2974	x 2978	x 2862	x x 2916 x	2950	x 2844	x 2970	x 2842	2880	x 2980	2930	2810	2.7 ± 0.6
Taraxacum officinale agg.						x 2830						2810	
Taraxacum sp.												x 2856	
Thymus sp.												x	
Trisetum distichophyllon													0.0
Trisetum spicatum	x 2974		2810	x 2916		x 2840	x 2980	x 2842	x x 2899	x 2980	x 2968	x x 2856	7.0 ± 4.4
Vaccinium vitis-idaea	x 2974												
Valeriana sp.					2820								
Valeriana supina	2950												
Veronica alpina	x 2974	2960	x 2850	2840	2860	x 2844	x 2970	x 2842	2870	2950		2830	6.1 ± 2.9
Veronica aphylla	x 2960		x 2850	2830			2870	2810			2810	x 2850	−0.5 ± 1.2
Veronica bellidioides		2960	2810	2840					2840	x 2986			1.5 ± 2.6
Veronica fruticans							2870						6.9
Viola calcarata			x 2850									2830	−3.1 ± 1.0

For each mountain, the presence of a species on the summit (defined here as the uppermost 15 m) in the historical and recent observation is indicated by an x. Additionally, the altitude of highest occurrence in recent investigation (2004) is given. Migration rates (mean ± standard error) are listed in the last column for 140 species on four mountains, where historical records down to 2,800 m are available. Nomenclature follows Lauber and Wagner (1996) except for *Taraxacum* spp. where we followed Fischer et al. (1994).

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Paper 2

Comparison of growth parameters in different altitudes and methodological aspects of age measurements of three alpine herbaceous species

Manuscript in preparation

Manuscript in preparation

Comparison of growth parameters in different altitudes and methodological aspects of age measurements of three alpine herbaceous species

Abstract

Increasing temperatures may cause populations of alpine plant species to extend their distributional range towards higher altitudes. Accordingly, upwardly migrating species should have younger populations at their high-elevation habitats than at their low-elevation habitats. Using herbchronology, we investigated if growth parameters such as age, root growth rate and root diameter differed between high alpine and lower alpine populations of *Anthyllis vulneraria* subsp. *vulneraria*, *Minuartia gerardii* and *Trifolium pallescens*, all of them potential migrators. The results showed that none of the three parameters differed between high and low altitude populations in any of the three species of this dataset. We explored the possibility of avoiding the destructive technique of herbchronology by using root diameter measurements for age prediction in alpine environments. The correlation between age and root diameter was good and different for each species investigated, the fit was sufficient to predict age from diameter. This implies the possibility of a continued observation in long-term monitoring studies and allows an increased number of individuals to be studied, as the measurement procedure is more rapid.

Keywords: herbchronology, Alps, *Anthyllis vulneraria* subsp. *vulneraria*, *Minuartia gerardii*, *Trifolium pallescens*

Introduction

Substantial evidence of increasing species numbers on high alpine summits (Hofer, 1985; Gottfried et al., 1994; Grabherr et al., 1994, 2001; Walther et al., 2005; Dubey and Yadav, 2006; Kullman, 2006; Holzinger et al., 2008) suggests that these species have been migrating upwards. Accordingly, high-altitude populations of invading or migrating species should show a population structure biased towards younger individuals compared to low-altitude populations. The age structure of alpine populations has rarely been described because most studies on plant age focus on age states rather than age itself expressed in years (Rabotnov, 1969; Gatsuk et al., 1980). These analyses concentrated on the importance of reproduction dynamics, i.e. flowering versus non-flowering and fruiting versus non-fruiting, where the investigation effort is much reduced, as age itself is not directly measured. For describing the frequency distribution of population age structures or

for monitoring populations over longer periods of time, however, measuring age directly would be more suitable.

Growth increments in herbaceous plants provide essentially the same information as in woody plants, but suitable methods were developed only fairly recently (von Arx and Dietz, 2005, 2006; von Arx et al., 2006). The technique used for both age determination and growth increment analysis is herbchronology, which essentially counts annual rings of the root (Dietz and Ullmann, 1997). The method involves destruction of the individual by dissecting the root. This study is among few that apply this technique in an alpine setting (for others see Kuen and Erschbamer, 2002; Erschbamer and Retter, 2004). As alpine populations, however, are often vulnerable, protected, or part of long-term monitoring studies, this study compares herbchronology to a non-destructive method of age determination by measuring the root diameter.

Material and Methods

Study species

Out of a set of 39 common alpine species that were tested for suitability for herbchronology (Table 2), the following three alpine species were investigated: *Anthyllis vulneraria* subsp. *alpestris* L. (Fabaceae), *Minuartia gerardii* (Willd.) Hayek (Caryophyllaceae) and *Trifolium pallescens* Schreber (Fabaceae). The selection of species was based on two criteria: abundance in the study area and clarity of annual rings in the root. Furthermore, they are considered as potential migrant species.

All three species occur over a broad altitudinal range (subalpine to high alpine) in the Alps and form clear taproots that can be used for herbchronology. *Anthyllis vulneraria* subsp. *alpestris* is found from the montane to the alpine belt (about 1700 to 2900 m a.s.l.) on stony grasslands and calcareous scree, *Minuartia gerardii* from the subalpine to subnival belt (about 2000 to 3150 m a.s.l.) on both calcareous and siliceous grasslands and scree, and *Trifolium pallescens* from the subalpine to subnival belt (about 2000 to 3100 m a.s.l.) on scree, grasslands and moraines on siliceous soil (Fischer et al., 2005).

Study area

Eight of the nine selected mountains were in the central part of the Austrian Alps (Salzburg and Tyrol), and one in Switzerland (Grisons). Table 1 lists study location and population sample sizes. Sampling locations of plant populations were not randomly selected, as all populations found along the hiking trail above 2000 m on each mountain were collected. See the data analysis section for description of how populations were used

for the analyses. If not distinct (scattered distribution across a wider vertical range), some individuals of the lower and upper extreme ends were taken.

Data collection

For each species, we selected sample sites on each mountain that spanned the altitudinal range of the species on that mountain (first/last population that was encountered during ascent). Sample sites were located in treeless, mostly alpine grassland vegetation. Before data collection, population size was roughly estimated by counting. Only populations with more than five individuals were sampled because of the sensitivity of alpine populations and the destructiveness of the method. Not more than 30% of the individuals were selected randomly at each site. Two to 40 individuals of varying size were collected in summer 2005. The study focused on flowering individuals only, as the rings in very small and non-flowering individuals are not clearly visible and therefore unsuitable for analysis of age and growth patterns with herbchronology (compare von Arx et al., 2006). Each plant was rooted out and the plant material was stored in 60% ethanol for further analysis in the laboratory.

Herbchronology

'Herbchronology' emerged from the well-established dendrochronology. It involves analysing growth structures in the roots of herbaceous plants, which in many cases form annual rings just as trees do. Herbchronology has recently been used in studies on age and population structure and has been proven to be a useful method if species form clearly demarcated annual rings (Dietz and Ullmann, 1997). Most studies have investigated weeds or invasive populations (Dietz and Ullmann, 1998; Dietz et al., 1999; Dietz et al., 2004; Perkins et al., 2006), and a database by Křivánek (2003) lists many lowland species, classifying their usefulness in herbchronological studies. This method has recently also been used for alpine species (Kuen and Erschbamer, 2002; Erschbamer and Retter, 2004; von Arx et al., 2006).

In this study, sample slices (~ 10 μm) of the root were cut approximately 3 cm underneath the original soil surface using a microtome (Reichert, Austria). We used the same method as von Arx *et al*. (2006) regarding sample preparation and ring width analysis. Root diameter as well as xylem diameter was measured to the nearest 0.1 mm under a microscope (Leitz Laborlux D).

Data analysis

Root growth rate (RGR) was calculated using the xylem diameter measurements (Dx) according to the following formula:

$$RGR = Dx/age$$

On each mountain where at least two populations of more than four individuals were found, the highest and lowest populations were compared in terms of age, diameter and RGR by applying a Wilcox test for each species (Fig. 1).

To show the relationship between root diameter and age for each species a general linear model (GLM) with Poisson error distribution was used on all individuals found in the study. Confidence intervals (95%) were calculated and shown (Fig. 2). The fit of the models were shown by D^2 values (Guisan and Zimmermann, 2000), an equivalent to the R^2 in linear regression models. They were calculated in the following way:

$$D^2 = (null\ deviance\text{-}residual\ deviance)/null\ deviance$$

The analyses were done using R (version 2.8.1).

Results

Herbchronology worked well on the three selected species. Annual rings were smallest and most difficult to distinguish in *Minuartia gerardii (MG)*, which also had the smallest root diameter. Large differences between xylem diameter and root diameter were found in *Anthyllis vulneraria* subsp. *alpestris (AV)* and *Trifolium pallescens (TP)*, due to a very thick bark.

Age, RGR and diameter versus altitude

There were no significant differences in age between high and low populations (except for AV and TP on one mountain each). Similarly, there was no difference in RGR between high- and low-altitude populations on the mountains except for AV on one mountain. Root diameter differed significantly only for AV and TP on one mountain each. (Fig. 1).

Diameter versus age

Age and root diameter were significantly correlated in all three species, so therefore age can be predicted from diameter (see Table 3 and Fig. 2).

Discussion

Age versus altitude

Differences in age of individuals in high versus low altitude population could be of three kinds: high populations are younger, older or there is no difference. Our hypothesis was that the populations higher up experience rejuvenation due to migration caused by temperature changes. One study that has tackled this question before is von Arx *et al.* (2006). They found higher populations to have a higher proportion of older individuals and argue that the reason is the stress-tolerant and 'conservative' life strategies of plants in high elevations. Low temperatures, very short growing season and high solar radiation make plant life harsh (Mooney and Billings, 1965; Körner, 2003) and call for special adaptations. One argument is that a high level of carbohydrate storage is necessary as a reserve for severe conditions (Stearns, 1976; Chapin III et al., 1990; Roff, 1992). As this happens at the cost of growth and reproduction, longer life spans may be needed to complete the essential cycles.

On most mountains in this dataset, however, the investigated species did not show a significant difference between high and low altitude populations in terms of their age. Reasons for this could be that either both of the two mentioned hypotheses are true, but they counteract, so no effect is visible, or there simply is no difference between the populations in high and low altitudes in terms of age structure. A limitation in all cases is the number of populations and individuals tested in this dataset. A trend might be found if more data could be gathered, however, this would involve destruction of more individuals or the use of an alternative and less destructive method. See below for the discussion and findings regarding herbchronology.

RGR and diameter versus altitude

Better growing conditions at lower altitudes should increase annual growth and possibly root size. Most studies find temperature to be the limiting factor for growth in high altitudes (Körner, 2003), although other factors may play a role. Dendrochronology and studies of alpine tree lines reveal that same-aged individuals have thinner rings (*i.e.* less growth) with increasing altitude. This reflects the limitations of lower temperatures as altitudes increase (Woodward, 1987; Pyrke and Kirkpatrick, 1994; Körner, 1998; Grace et al., 2002; Körner, 2003; Luo et al., 2004). Our data set, however, shows no such trend: the annual growth is the same for all altitudes in all species. The reasons for this pattern are unclear. At lower temperatures, the usage of photosynthetic products rather than photosynthesis itself limits growth (Grace et al., 2002; Körner, 2003). This leads to

increased storage of carbohydrate products (Warren-Wilson, 1966; Sveinbjörnsson et al., 1992; Skre, 1993) rather than growth, and explains the same biomass in same-aged individuals at higher and lower elevations even though plant size and therefore root diameter differs (Bernoulli and Körner, 1999). Although we did not investigate biomass, the constant root growth rate at all altitudes allows the hypothesis that the limits of utilisation of photosynthetic products have not been reached in the studied species. Root growth should therefore be the same in all altitudes, as observed in this study. Similarly, *Ranunculus glacialis* did not grow faster at higher temperatures (Totland and Alatalo, 2002). Alternatively, the limitations of this dataset might be the predominant reason for the absence of significant differences and trends.

Herbchronology – diameter versus age

The results show that herbchronology can be used as a dating method for selected species in an alpine setting (Kuen and Erschbamer, 2002; Erschbamer and Retter, 2004). It is, however, a destructive method, which is not useful for long-term observations of individual plants. An alternative could be simple measurements of the root diameter that were found to be highly related to age for the three species investigated (compare Fig. 3). Moreover, the time effort for age determination per individual would be much reduced and, thus, a large number of samples per unit of time could be studied.

The relationship between diameter and age, however, differed for each species. Therefore, more fundamental research on more species would be required for determining the species-specific ratio of root diameter versus age. This would allow altitudinal gradient studies of larger sets of species. Křivánek's database on lowland species could serve as an example (Křivánek, 2003).

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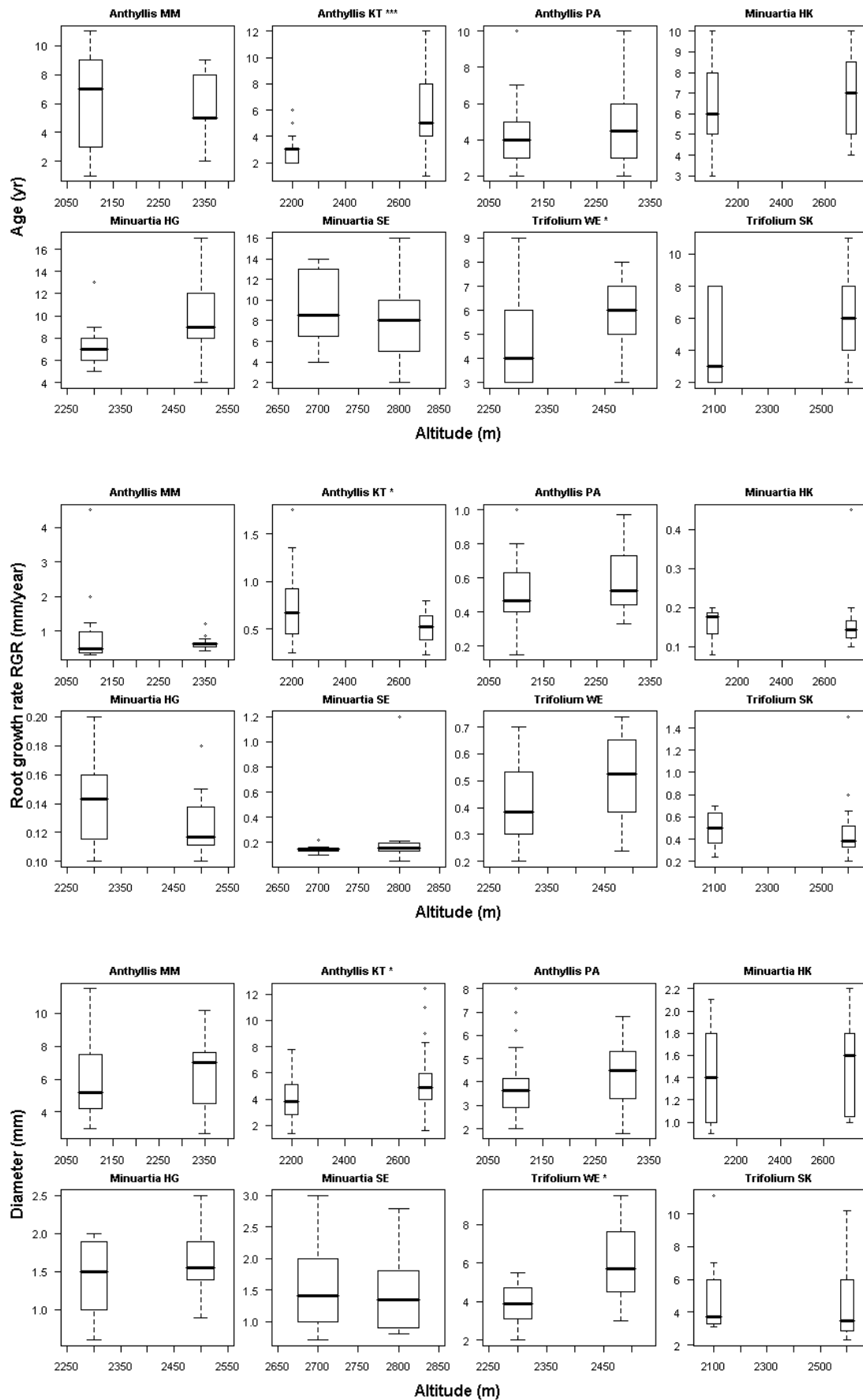
Figure 1

Figure 1: Age, RGR and diameter compared for highest and lowest population of each species on the mountains where two populations of more than four individuals were found. Abbreviations besides genus names indicate mountains (compare Table 1), Anthyllis: *Anthyllis vulneraria* subsp. *vulneraria*; Minuartia: *Minuartia gerardii*; Trifolium: *Trifolium pallescens.* Significance of Wilcox tests is presented as Asterisks (***: p<0.001 ; *: p<0.05).
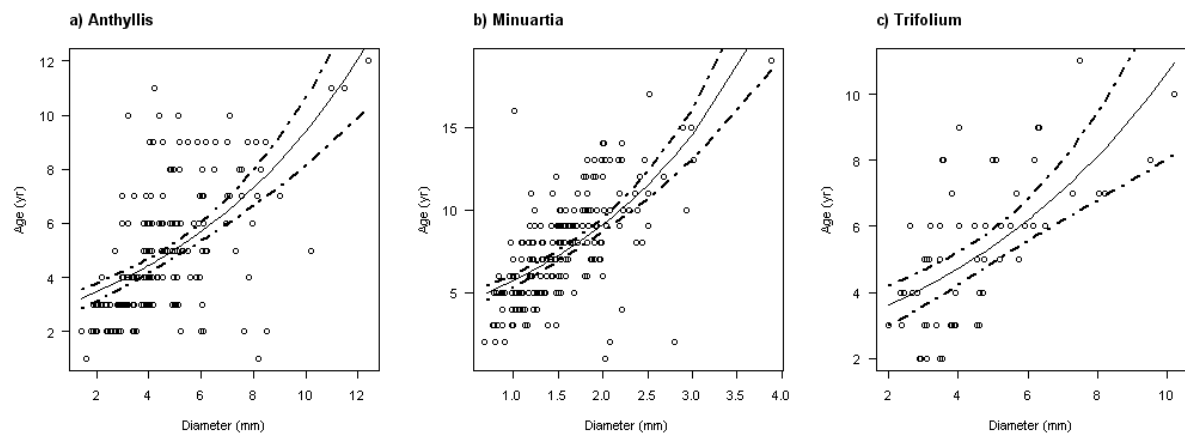
Figure 2

Figure 2: Diameter versus age for three alpine species. Solid line: GLM fit, dashed line: 95% confidence interval of the fit. Points are jittered. Note the different axis scaling in a-c. Anthyllis: *Anthyllis vulneraria* subsp. *vulneraria*; Minuartia: *Minuartia gerardii*; Trifolium: *Trifolium pallescens.*

Table 1

Table 1: Description of sampling sites, position and sample number. Populations are numbered according to their altitude (lowest: 1, highest: 4). AV: *Anthyllis vulneraria* subsp. *vulneraria*; MG: *Minuartia gerardii*; TP: *Trifolium pallescens.*

Mountain	Abbrevi-ation	Max altitude	Longitude	Latitude	species	popu-lation	site altitude	number of samples
Hochkönig	HK	2941	13° 03' 57" E	47° 25' 22" N	MG	1	2080	10
					MG	2	2320	13
					MG	3	2530	11
					MG	4	2720	11
Hoher Göll	HG	2522	13° 04' 01" E	47° 35' 40" N	MG	1	2300	9
					MG	4	2500	13
Kleiner Tenn	KT	3158	12° 45' 24" E	47° 11' 07" N	AV	1	2200	28
					AV	4	2700	39
Mosermandl	MM	2680	13° 23' 44" E	47° 12' 22" N	AV	1	2100	12
					AV	2	2250	16
					AV	4	2350	13
					MG	1	2350	13
Piz Arina	PA	2828	10° 38' 33" E	46° 09' 00" N	AV	1	2100	26
					AV	4	2300	18
					MG	1	2800	33
Schrankogel	SK	3479	11° 05' 57" E	47° 02' 38" N	TP	1	2100	6
					TP	4	2600	22
Silbereck	SE	2804	13° 25' 52" E	47° 05' 14" N	MG	0	2500	3
					MG	1	2700	24
					MG	4	2800	12
					AV	1	2250	13
Weisseck	WE	2711	13° 23' 39" E	47° 09' 45" N	TP	1	2300	18
					MG	1	2300	2
					TP	4	2480	15
					MG	2	2480	25
					MG	4	2700	4
Mainzer Höhenweg	MH	3000	46° 57' 41" N	10° 54' 02" E	MG	1	2900	12
Rettenzink	RZ	2510	47° 13' 26" N	12° 45' 56" E	AV	1	2320	18

Table 2

Table 2: Suitability of a selection of alpine species for herbchronology

Family	Species	annual rings visible?	who tested this
Apiaceae	*Ligusticum muttellina*	no	This study
Apiaceae	*Peucedanum ostrutium*	no	This study
Asteraceae	*Achillea moschata*	yes	This study
Asteraceae	*Artemisia mutellina*	yes	Erschbamer et al. 2004
Asteraceae	*Aster bellidiastrum*	no	This study
Asteraceae	*Cirsium spinosissimum*	yes	Dietz et al. 2004
Asteraceae	*Homogyne alpina*	no	This study
Asteraceae	*Leontodon helveticus*	no	This study
Asteraceae	*Leucanthemopsis alpina*	no	This study
Asteraceae	*Solidago virgaurea*	yes	This study
Boraginaceae	*Myosotis alpestris*	not clear	This study
Brassicaceae	*Draba aizoides*	yes	Dietz et al. 2002
Campanulaceae	*Campanula barbata*	no	This study
Campanulaceae	*Campanula scheuchzeri*	no	This study
Caryophyllaceae	*Minuartia gerardii*	yes	This study
Caryophyllaceae	*Silene acaulis*	yes	Benedict 1989
Cistaceae	*Helianthemum grandiflorum*	yes	Erschbamer 2004
Ericaceae	*Cassiope tetragona*	yes	Havström et al. 1995
Ericaceae	*Rhododendron ferrugineum*	yes	Pornon et al. 1995
Fabaceae	*Anthyllis vulneraria ssp alpestris*	yes	Erschbamer et al. 2004
Fabaceae	*Lotus corniculatus*	yes	A.Münch, R. Schwarz, unpublished (in Erschbamer et al. 2004)
Fabaceae	*Trifolium badium*	not clear	This study
Fabaceae	*Trifolium pallescens*	yes	Kuen et al. 2002
Fabaceae	*Trifolium pratense ssp. nivale*	yes	Erschbamer et al. 2004
Gentianaceae	*Gentiana punctata*	no	This study
Lamiaceae	*Thymus sp.*	yes	This study
Polygonaceae	*Oxyria digyna*	yes	Erschbamer et al. 2004, Humlum 1981
Primulaceae	*Androsace lactea*	no	This study
Primulaceae	*Primula sp.*	no	This study
Ranunculaceae	*Ranunculus sp.*	no	This study
Rosaceae	*Alchemilla alpina*	yes	Dietz et al. 2002
Rosaceae	*Geum montanum*	no	This study
Rosaceae	*Potentilla aurea*	not clear	This study

Paper 2 - Herbchronology

Family	Species	annual rings visible?	who tested this
Rosaceae	*Potentilla crantzii*	yes	This study
Rosaceae	*Sibbaldia procumbens*	yes	This study
Saxifragaceae	*Saxifraga oppositifolia*	yes	Erschbamer et al. 2004
Scrophulariaceae	*Bartsia alpina*	no	This study
Scrophulariaceae	*Pedicularis recutita*	yes	Dietz et al. 2004
Scrophulariaceae	*Pedicularis tuberosa*	yes	This study

Table 3

Table 3: Results of general linear models with Poisson error distribution between age and diameter of individuals for the three species. AV: *Anthyllis vulneraria* subsp. *vulneraria*, MG: *Minuartia gerardii*, TP: *Trifolium pallescens*

Species	z-value	p value	null deviance	residual deviance	residual degrees of freedom	D^2
AV	8.376	<0.001	205.41	141.81	180	0.310
MG	10.67	<0.001	264.5	160.06	193	0.395
TP	4.95	<0.001	56.909	34.29	59	0.397

Paper 3

What happens when alpine plants are exposed to a lowland climate?

Barbara Friedmann, Georg Grabherr

What happens when alpine plants are exposed to a lowland climate?

Barbara Friedmann, Georg Grabherr

Abstract

To explore effects of climate change on alpine plant assemblages, in summer 2004, ten blocks of high alpine vegetation were transplanted to the outdoor part of the greenhouse at the University of Vienna, and observed for four years. Newly appearing weeds were removed. Most plants, but not all, increased up to more than twice their original size and competitive effects were detected in most of the blocks. Seeds of a few species germinated from outside the blocks. Bryophytes appeared in high density during winter. Individualistic growth response was responsible for enhanced competition whereas in most cases the winner and losers were not expected. Climate change will certainly lead to new configurations in alpine plant communities, however, we conclude that predictions of winners and losers derived from current behaviour will be probably misleading.

Zusammenfassung

Um eine Vorstellung zu gewinnen, wie sich in den kommenden Jahrzehnten der Klimaerwärmung auf die Hochgebirgsvegetation auswirken könnte, wurde ein Transplantationsexperiment durchgeführt. Zu diesem Zwecke wurden zehn Ziegel alpiner Pflanzengesellschaften in den Glashausgarten der Universität Wien transplantiert und vier Jahre lang beobachtet. Die Pflanzen zeigten gesteigertes Wachstum bis zum Doppelten ihrer Größe. Ebenso waren Konkurrenzeffekte offensichtlich. Einige Arten konnten sich durch Samen auch außerhalb der Ziegel ansiedeln. Bryophyten füllten in den Wintermonaten die Lücken zwischen den Gefäßpflanzen. Auch wenn das Experiment nur eine grobe Annäherung darstellt, wurde doch klar, dass unter wärmeren Bedingungen Konkurrenz zu neuen Strukturen und Konfigurationen innerhalb der bestehenden Vegetation führt. Aufgrund der vielfach überraschenden winner-loser Effekte sind Voraussagen auf Basis des aktuellen Verhaltens wahrscheinlich falsch.

Keywords

Introduction

Climate change effect on plants and temperature increase in particular, has been subject of many research activities in the last decades as reviewed e.g. by THEURILLAT & GUISAN (2001), PARMESAN & YOHE (2003) and WALTHER et al. (2005). Effects on particular plant

species have been equally focused on as effects on the higher complexity of plant assemblages and regional floras (BAKKENES et al. 2002; DIRNBÖCK et al. 2003; THUILLER et al. 2005; AERTS et al. 2006; ERSCHBAMER 2007; KLANDERUD 2008). In-situ as well as transplantation experiments with increased temperatures and/or increased CO2 concentration have been carried out (WOODWARD 1979; HOLLAND 1980; BENEDICT 1989; LINK et al. 2003; MCKONE et al. 2004; BOWMAN et al. 2008). In-situ experiments, such as those of the ITEX (International Tundra Experiment, http://www.geog.ubc.ca/itex/) network, have found effects on species composition (FONTY et al. 2009; PRIETO et al. 2009), growth (ARFT et al. 1999; KUDERNATSCH et al. 2008), herbivory (HODKINSON & BIRD 1998; WALTHER et al. 2005; O'CONNOR 2009), pollination (STENSTROM et al. 1997), respiration (RYAN 1991), phenology (BORNER et al. 2008), dispersal (KLANDERUD 2008). Evidently, climate change affects all aspects of the species - environment interaction. Transplantation experiments have found for example that warmer and wetter conditions reduce reproductive effort and cover (LINK et al. 2003), while others found that plants only survived in conditions that were similar to those found in their natural habitat (BOWMAN et al. 2008).

So how would alpine plants react if temperatures were to rise to extreme levels? The different aspects of reaction, predicted and observed, are too numerous to be examined at once. Studies are always limited to showing only one or two effects at a time. The present study focused on temperature change, but attempted to observe all possible reactions, both species specific and "community" reactions. Instead of choosing a temperature change of a few degrees as predicted in various models, we selected an extreme temperature increase: high alpine plants were transplanted to the Vienna lowlands, which is a change from about -6°C to +10°C annual mean temperature. These temperatures are without doubt rather fictitious; they will not be reached in the plant's native habitats, not even in the most extreme predictions. However, this gave the opportunity to observe relatively large changes within a short time frame of a few years.

The main questions in this study were: what and how strong are the reactions of the various plants to the sudden warming? Are there "winners" and "losers" and what species were identified as such?

Materials and Method

In the summer of 2004, ten blocks of about 20x20cm size and 10cm depth were dug out on three different mountains in Switzerland and Austria. The sampling sites were all about

between 2400 and 2900 m in elevation. Both siliceous and calcareous bedrock sites were chosen. See Table 1 for details.

*Table 1: Locations of the origin of the blocks used in this transplantation experiment.*
Tabelle 1: Herkunft der Ziegel, die in diesem Transplantationsexperiment verwendet wurden.

block	mountain	altitude	bedrock	location
A1, B1, C1, D1	Dachstein	2400	calcareous	47°28.51'N 13°36.365'E
B2, B3, D2, D3	Leidbachhorn	2610	siliceous	46° 43' 17.1" N 9° 49' 20" E
C2, C3	Piz Chatscheders	2700	siliceous	46° 28' 40.8" N 10° 0' 59.6" E

The blocks were transported to the greenhouse of the University of Vienna (for arrangement see Figure 1).

Figure 1: Overview of the arrangement and numbering of blocks.
Abbildung 1: Anordnung und Nummerierung der Ziegel.
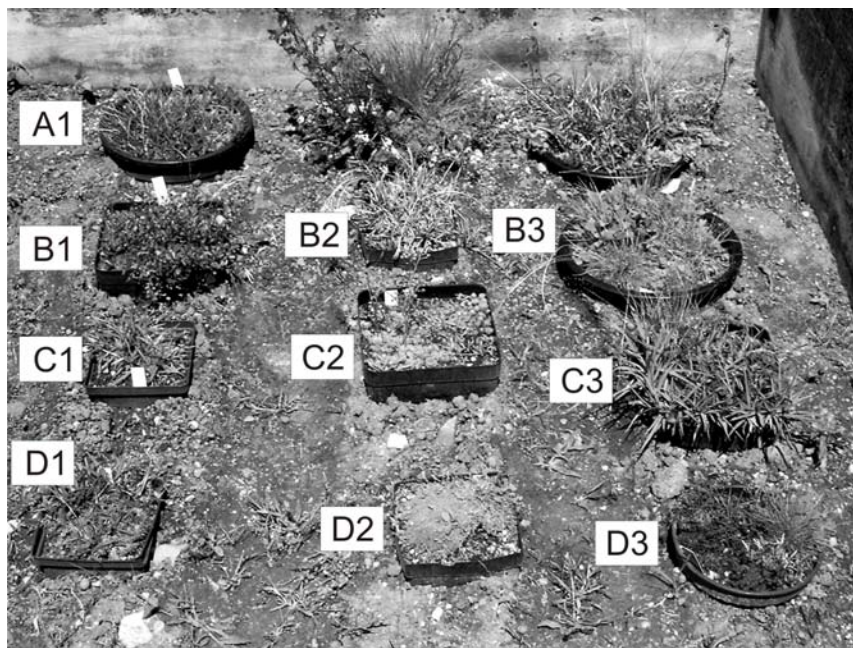
In the outdoor part of the greenhouse, the blocks were planted into buckets about 20cm depth with sand and pebbles to ensure enough humidity was conserved in the soil. The

buckets were dug into soil, to ensure that temperature is kept constant with the surrounding earth (Figure 2).

Figure 2: Schematic depiction of alpine blocks being transplanted in the greenhouse area of the University of Vienna.
Abbildung 2: Schematische Darstellung der Ziegel, die in den Glashausgarten der Universität Wien transplantiert wurden.
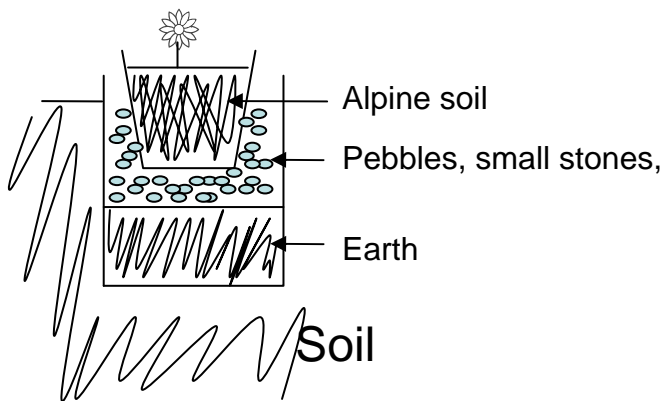
Every day, the blocks were watered twice, once in the morning and once in the evening. A net was put up covering the blocks in about 20 cm distance to protect against birds especially in the spring, but the net-loops were large enough in order to not hinder potential pollinators. Emerging weeds were removed. Besides these precautions, no other measures were taken and the vegetation in the blocks was left to develop by itself.

Every week, photos were taken of each block and of the entire setup. Additionally, the top cover of vegetation was estimated, both total vegetation and individual species. Naturally, adding up the top cover of all species often results in more than the estimated total vegetation cover, but this mostly is due to overlap. In fruiting and blooming season, fruits and flowers were counted.

For compilation and analysis of development of the blocks in their new environment, especially the photographs were used as they give the most apparent indication of change.

Results

Descriptions of the selected blocks

In the following, selected blocks are described in some detail, a synthesis is provided at the end.

Dachstein, Austria

Block A1:

Figure 3: block A1
Abbildung 3: block A1

25.05.2005   29.05.2006   18.05.2007
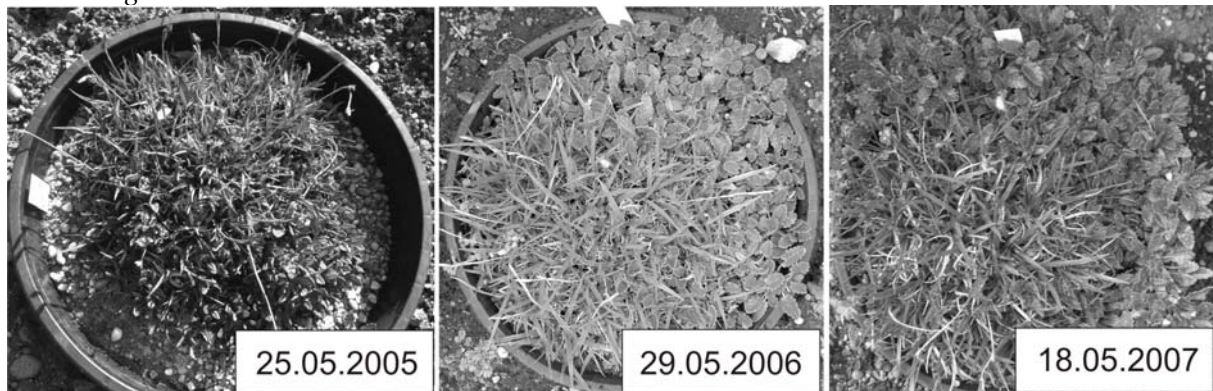
Carex firma Host and *Dryas octopetala* L. dominated this block in the first year. Both *Persicaria vivipara* L. and *Helianthemum nummularium* (L.) Mill. were also present, but only covered a very small proportion of the block. Within the three years, cover of the two dominant species increased, while *P. vivipara* L. disappeared. *H. nummularium* (L.) Mill. only took some space on the edge in year 1 and 2 and then did not appear again. By year 3, both *D. octopetala* L. and *C. firma* Host grew towards the edge of the block, *D. octopetala* L. and its roots outgrew the block. No weed species appeared in this block during the three years, which was possibly due to the high top cover of the dominant species.

Block B1:

Figure 4: block B1
Abbildung 4: block B1

26.05.2005   28.06.2006   25.05.2008
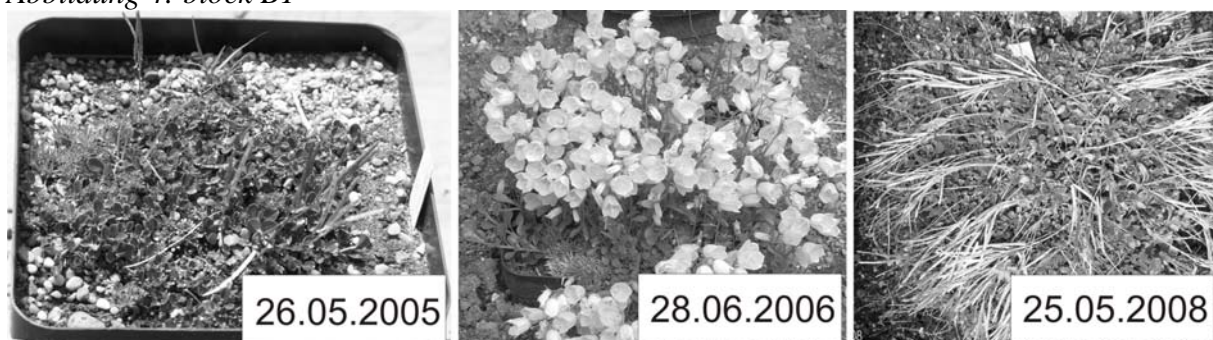
In year 1, the most prominent species were *Salix serpyllifolia* Scop. and *Silene acaulis* (L.) Jacq. mixed in with a few *Arabis pumila* Jacq. and *Campanula cochleariifolia* Lam.

individuals. The first major change was observed in year 2, when *C. cochleariifolia* Lam. bloomed over the entire block, which was repeated every year until the end of the observation. *A. pumila* Jacq. leaves increased in size three times by the first year and showed traces of bite. They were the only leaves not to be shed and remain green during the winter months of year 2 to 3. *A. pumila* Jacq. bloomed in March before *C. cochleariifolia* Lam. and also took up large space. *A. pumila* Jacq. individuals had their first outside block occurrence in year 3, obviously dispersed there. This was the only species to disperse out of the blocks by seed. *Poa alpina* L. from another block dispersed viviparously. *Silene acaulis* (L.) Jacq.*, Moehringia ciliata* (Scop.) Dalla Torre, *Luzula spicata* (L.) DC. and *Cardamine resedifolia* L. disappeared under the dominance of *A. pumila* Jacq. (fruiting plants visible as the brown "grasslike" structures in the right picture, 25.05.2008) and *C. cochleariifolia* Lam. and could not be seen by year 2 and 3. *S. serpyllifolia* Scop. started to extend its aboveground roots towards the edges of the block at the end of year 1 and reached the surrounding soil at the end of year 2. It remained growing outside the block while being rooted in the block until the end of observation.

   Block C1:

Figure 5: block C1
Abbildung 5: block C1
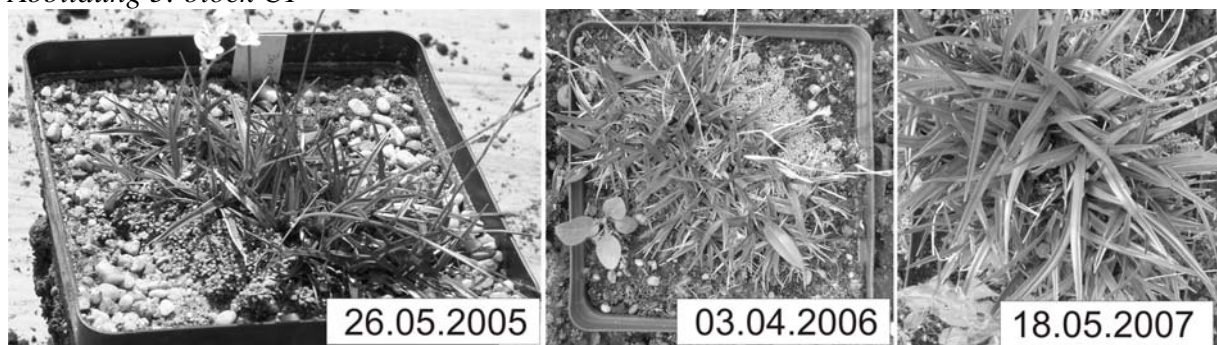
The most prominent species on this block were *Carex firma* Host and *Saxifraga caesia* L., both of which took about equal amount of space. By the end of year 3, *C. firma* Host covered about three quarters of the block, while *S. caesia* L. kept to the top cover of the beginning. Leaf sizes increased in both species. One more species on this block was *Persicaria vivipara* L., which disappeared within the first two years of observation, even though it bloomed in the first year.

Figure 6: block D1
Abbildung 6: block D1
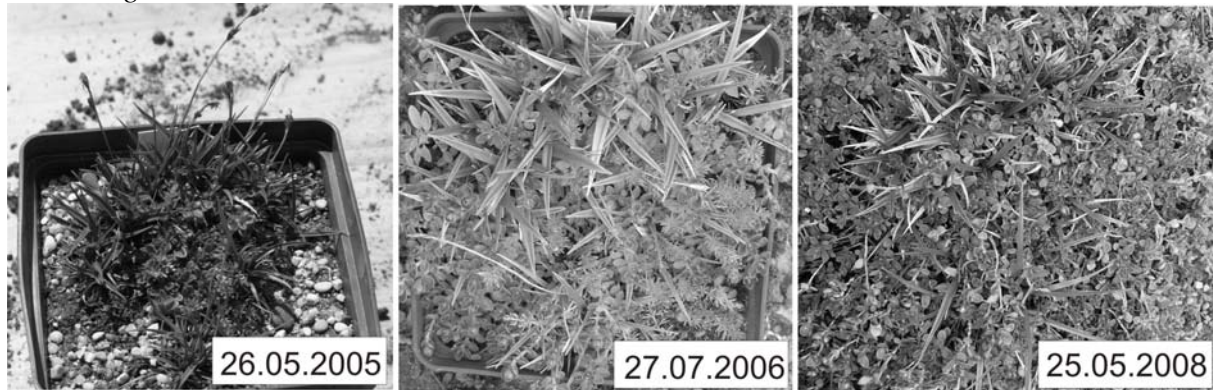
The three dominant species on this block were *Galium noricum* Ehrend.*, Helianthemum nummularium* (L.) Mill.*,* and *Carex firma* Host. In the beginning, *C. firma* Host was blooming and fruiting. In year 1, both G. *noricum* Ehrend. and *H. nummularium* (L.) Mill. grew more quickly than *C. firma* Host and soon the entire block was covered by those two species, but with *C. firma* Host still present. In summer of year 2, *C. firma* Host grew very quickly, but by the end of summer, it was overtaken by especially *H. nummularium* (L.) Mill. and G. *noricum* Ehrend., while after year 2 and especially in year 3, *H. nummularium* (L.) Mill. outgrew both all species and the block itself.

Leidbachhorn, Switzerland

Block B2:

Figure 7: block B2
Abbildung 7: block B2
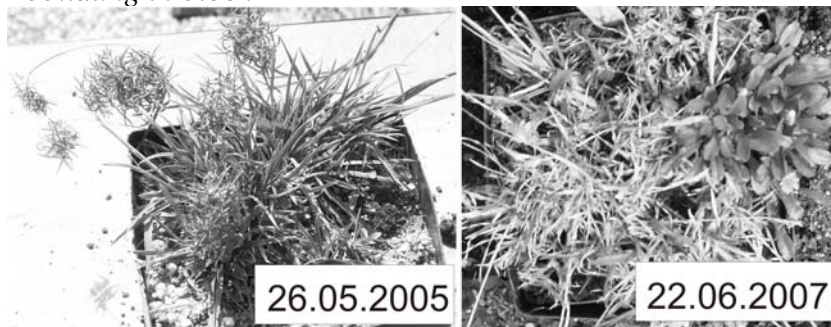
In the beginning, *Poa alpina* L. was dominant, but *Saxifraga bryoides* L. and *Androsace alpina* (L.) Lam. and *Erigeron uniflorus* L. were also found. By year 2, *Poa alpina* L. dominated the entire block, leaving no room for other species, only in the end of summer *E. uniflorus* L. grew on one side. In summer of year 3, *E. uniflorus* L. took almost half the space of the block, while *P. alpina L.* seemed to die off. Outside the block, where *P. alpina*

L. inflorescences (viviparous) had touched the soil, individuals were found. By the beginning of year 4, only *E. uniflorus* L. was left and *P. alpina* L. died off.

     Block B3:

*Figure 8: block B3*
Abbildung 8: Block B3

In this block, the following species were dominant: *Saxifraga bryoides* L., *Sibbaldia procumbens* L., *Leucanthemopsis alpina (*L.) Heywood*,* and *Oreochloa disticha* (Wulfen) Link. A few *Poa alpina* L. and *Gnaphalium supinum* L. individuals were also present. In year 1, *Gentiana bavarica* L. appeared, but disappeared again by the next year. Some *Euphrasia minima* Jacq. ex DC. (annuals) individuals appeared until year 2, but then did not appear again. By year 2, most *S. bryoides* L. was covered by either *O. disticha* (Wulfen) Link or *Agrostis alpina* Scop. or *Festuca sp.*. Also *S. procumbens* L. increased in size and cover. By the end of year 3, the number of grass tussocks had increased from three to seven. Also, the species composition of those grasses changed from *O. disticha* (Wulfen) Link and *P. alpina* L. to *Festuca sp*. and *A. alpina* Scop. *S. procumbens* L. and *S. bryoides* L. were still present, but their cover decreased. *L. alpina (*L.) Heywood and *G. supinum* L. disappeared from the block.

     Block D2:

Figure 9: block D2
Abbildung 9: Block D2
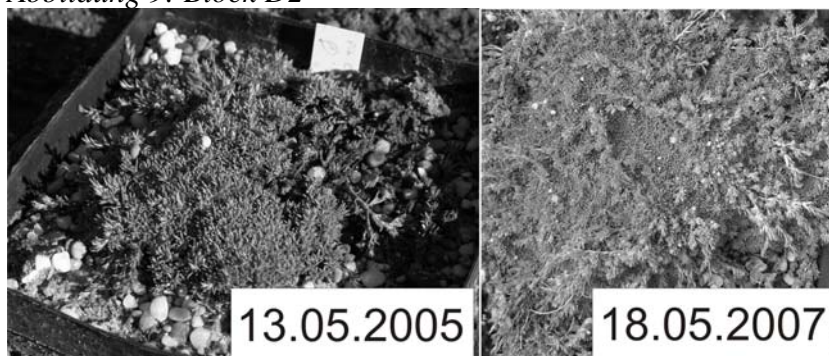
There was one dominant species, which only slowly increased its cover: *Minuartia sedoides* (L.) Hiern. It reached the edges of the block by year 3. However, growth was not omnidirectional, there were some branches that increased more than the rest of the cushion,

similar to *Salix serpyllifolia* Scop. in B1. There was a very short-lived increase of *Veronica alpina* L. at the sides in year 3.

  Block D3:

Figure 10: block D3
*Abbildung 10: Block D3*
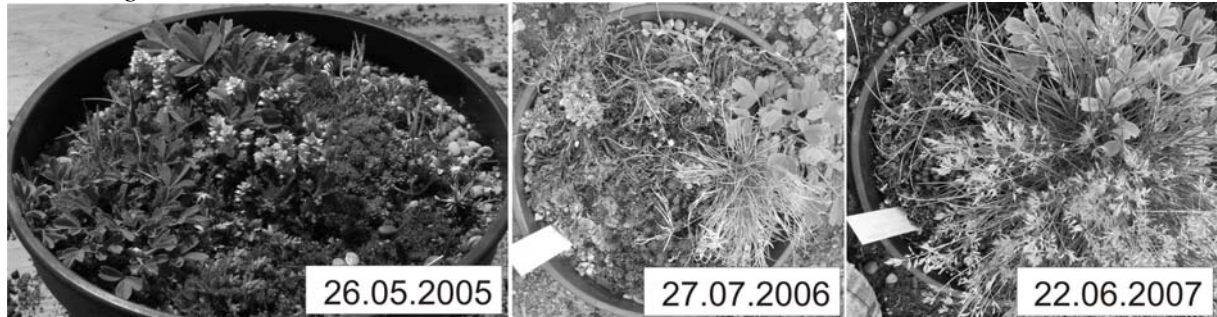
This block was dominated by *Leucanthemopsis alpina (*L.) Heywood and *Sibbaldia procumbens* L., as well as a cushion of *Saxifraga bryoides* L. By year 2, everything died off besides an individual of *S. procumbens* L., as well as *Agrostis* sp. and *Luzula spicata* (L.) DC. The latter both bloomed and fruited after one year. *Cardamine resedifolia* L. appeared in greater numbers (it was also present before). Also, bryophytes had a high cover. By the end of year 2, *Agrostis* sp. dominated, there were a few liverworts and also *C. resedifolia* L. increased slowly in cover. *S. procumbens* L. increased again and *Agrostis sp.* bloomed in the summer of year 3. At the end of the observation, *Agrostis sp* was the most dominating together with *S. procumbens* L. and *C. resedifolia* L. It seemed that after some adaption time, *S. procumbens* L. was able to deal with the temperatures better than the rest of species of this block.

Piz Chatscheders, Switzerland
  Block C2:

Figure 11: block C2
Abbildung 11: Block C2
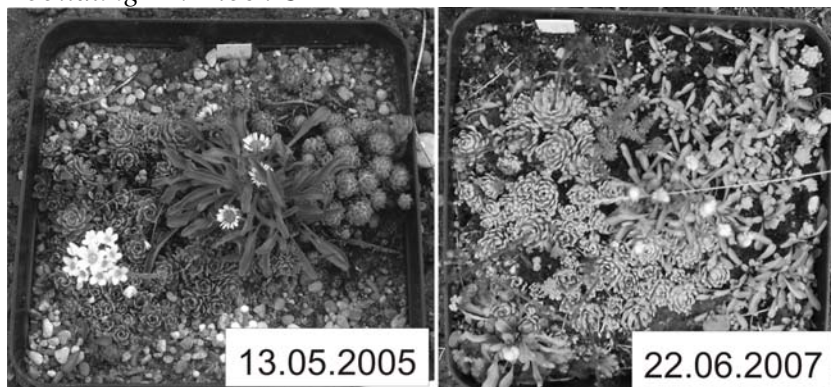
The prominent species on this block were *Saxifraga paniculata* Mill., *Erigeron uniflorus* L. and *Sempervivum montanum* L., in about equal proportions. By May of year 2, *E.*

uniflorus L. had overtaken a large proportion of the block. *S. montanum* L., on the other hand, showed a decrease in cover, which continued to decrease until the end of the experiment. *S. paniculata* Mill. had no essential change in cover. *Galium anisophyllon* Vill. had come into the block by the summer of year 3. The main observation on this plot was the decrease of the high alpine plant *S. montanum* L.

   Block C3:

Figure 12: block C3
Abbildung 12: Block C3

Luzula lutea (All.) DC. dominated the edges of the block. In the middle some individuals of *Homogyne alpina* (L.) Cass., *Ligusticum mutellina* (L.) Crantz, *Carex curvula* All. and *Salix herbaceae* L. were found. By year 1, the first bryophytes were present. All species stayed until the end of year 3, however, in one corner, *Agrostis sp.*, which was there from the beginning strikingly increased in cover, while *L. lutea* (All.) DC. decreased. *Gnaphalium supinum* L. appeared by year 2 and 3, but disappeared again after the summer. Most dominant at the end of the experiment were the bryophytes and *Agrostis sp.*

Bryophyte growth

Bryophytes were observed to be much quicker in response to changing climatic conditions, especially in winter months. By spring, bryophytes dominated many of the blocks, and only in summer, when vascular plant growth resumed, bryophyte top cover decreased again. These bryophytes were not species from the alpine environments but those from the lowlands. It was impossible to limit their growth as was done for other weeds.

Figure 13: Bryophytes in blocks C2 (left) and D3 (right)
Abbildung 13: Bryophyten in den Blöcken C2(links) und D3 (rechts)
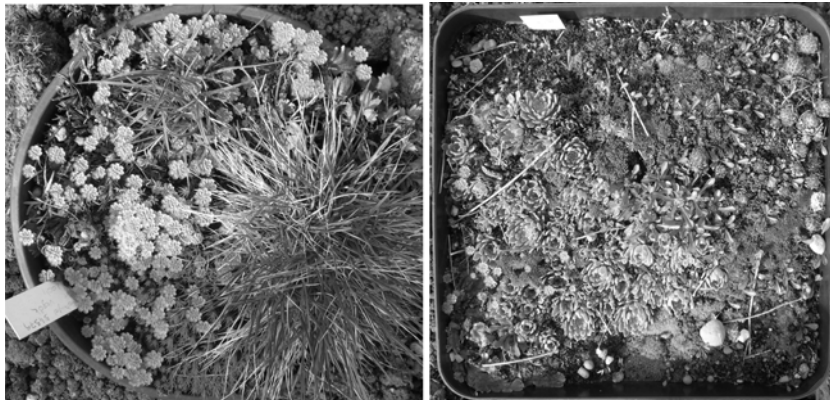
Synthesis:

The observations of the plots revealed the following main results:

1. **All species increased in size** to a certain extent, with only some exceptions such as those that were outcompeted and those bound to the strict leaf forms (e.g. *Saxifraga caesia* L. in C1, *Saxifraga paniculata* Mill. in C2, *Sempervivum montanum* L. in C2).

- Species with "softer" and more **flexible leaves and growth form** seemed to adapt more easily to the new growth situation, while for the species with more or less invariable size (e.g. Crassulaceae species), less change was observed

- **Some cushion plants**, such as *Minuartia sedoides* (L.) Hiern (D2), slowly expanded over the whole block and then extended their roots outside of the block. It seemed like instead of remaining in the cushion form, it grew into a more prostrate form.

- **Graminoids and the like** adapted quickly to the changes (D3, C1, B2), but their mostly tussock-like growth form seemed to hinder their occupation of a larger area within a small time frame (see phalanx and guerilla strategies in LOVETT DOUST & LOVETT DOUST 1982) compared to for example *Helianthemum nummularium* (L.) Mill. (D1) or *Campanula cochleariifolia* Lam. species (B1).

2. Species **reacted contrastingly** in different plots, depending on their competitors: one species dominant in one block was the inferior one in another block (e.g. *Carex firma* Host in A1 and C1).

3. **Bryophyte species** grew quickly and occupied considerable parts of the blocks, especially in the winter and spring months, where temperatures rarely dropped below freezing in Vienna. As bryophytes cease growth in lower temperature than vascular plant species, they utilise the months when the vascular plants halt their growth.

4. Only a few species shed their **seeds outside the blocks** to the soil and grew there. Most extended their roots (see e.g. *Minartia sedoides* (L.) Hiern in D2) towards the outside of the blocks. The two species that were found outside were *Arabis pumila* Jacq. (from B1) and *Poa alpina* L. (B2).

5. Some **species were lost** (*Silene acaulis* (L.) Jacq. in B1, *Gentiana bavarica* L. in B3, *Persicaria vivipara* L. in C1 etc) either because they were outcompeted or they did not tolerate the environmental conditions.

Discussion

Not surprisingly, the exposure of the alpine plants to a much warmer climate led to increased growth and related competitive effects. We found, however, that the various species reacted differently. There were "winners" and "losers", some species increased in size tremendously and some stayed more or less bound to their natural predefined form and size. An individualistic response of plant species was also found at most ITEX sites using open top chamber experiments (e.g. STENSTROM et al. 1997; FUJIMURA et al. 2008; KLANDERUD 2008). Differences in morphological plasticity seem to be important when interactions within whole communities are considered. They determine the competitive power of the particular plants.

A clear advantage of this "shock-experiment" was certainly that the climate change effects were clearly visible, the competitive ones in particular. This is in contrast to in situ experiments simulating realistic scenarios. Most important and surprising were the many discrepancies between what was expected and what then really happened. Probably no alpine ecologists would have expected the "explosion" of *Campanula cochleariifolia* Lam. or the competitive power of *Arabis pumila* Jacq. The main message we could take from our experiment was that predictions about losers and winners in alpine environments derived from current patterns are probably faulty.

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Paper 4

Suitability of three methods for long-term monitoring of alpine vegetation

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Suitability of three methods for long-term monitoring of alpine vegetation

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                       4300 (with captions of tables/figures)
Running title: Methods for monitoring alpine vegetation

Abstract (130 words)

Three methods of vegetation recording – subplot frequency, point-framing and visual cover estimation – were assessed in terms of their usefulness in high alpine environments, with a focus on their suitability for long-term monitoring programmes. Two of the methods for estimating cover (point-framing and visual estimation) were comparable only for covers above 0.7% in 1 m². For detecting the exact species number, point-framing was unsuitable and the other two methods yielded significantly different results. The time taken to complete a quadrat varied for each method, with point-framing being the quickest and most unaffected by species number or vegetation cover. We suggest that, despite its drawbacks, visual estimation is the most suitable method, especially with proper training, cooperation between field workers and possibly a precision control by point-framing in a subset of quadrats.

Keywords: visual estimation, point-framing, subplot frequency, scattered vegetation

Introduction

Vegetation, species cover and composition differ in various environments and over time; cover estimations are an essential tool in detecting these changes. They are used for general biodiversity monitoring, for classifying vegetation samples, and as a basis for gathering supporting evidence for the predicted climate change impacts. The collected data, however, are rarely questioned or quantified for their reliability. It is crucial that applied methodologies best serve the particular requirements and study aims (Brakenhielm and Liu, 1995; Carlsson et al., 2005), rather than be preferentially applied based merely on definition. Legg and Nagy (2006) discuss in detail the importance of adequately planning long-term monitoring projects with regard to methods, study aims and vegetation. A method suitable for densely populated grasslands might not be feasible for scattered low-density vegetation in alpine and subnival environments. Moreover, cost-effectiveness of methods is a fundamental consideration, especially in long-term monitoring.

The most frequently used methods in vegetation sampling are visual cover estimation, point framing, and subplot frequency. Visual cover estimation is the most common of the three. Species cover is visually estimated within a particular plot, either by using some sort of scale, such as Braun Blanquet (1964) or Daumbenmire (1959), or by recording numbers in relation to plot size. The drawbacks of this method have been discussed thoroughly (Kennedy and Addison, 1987; Tonteri, 1990; Klimeš, 2003; Vittoz and Guisan, 2007), the main one being the lack of objectivity, as each observer may estimate differently. Point-

framing (Levy and Madden, 1933) is considered to be objective (Everson et al., 1990), but a major disadvantage is the coarse estimation of species numbers (see Sorrells and Glenn, 1991; Brakenhielm and Liu, 1995; Vanha-Majamaa et al., 2000). Subplot frequency, which does not estimate cover but is rather another method of vegetation recording, has been compared to the others and found to deliver unrelated values (Brakenhielm and Liu, 1995). Numerous comparative studies have been published, predominantly for lowland habitats including sagebrush steppe (Floyd and Anderson, 1987; Seefeldt and Booth, 2006), forests and bogs (Brakenhielm and Liu, 1995), shrubland (Cheal, 2008), grasslands (Klimeš, 2003; Leis et al., 2003; Carlsson et al., 2005) as well as woodlands (Sykes, 1983). Recorded species numbers and cover differed between the methods, as did the time needed to complete fieldwork and therefore the effectiveness of each method. Few studies, however, have focused on alpine environments (Vittoz and Guisan, 2007), and none has compared more than one method for their suitability and efficiency in areas above the treeline. These environments are temperature limited and therefore more sensitive to climatic changes than lowland areas (Sakai and Larcher, 1987; Kammer and Mohl, 2002; Körner, 2003); hence, they are considered a good experimental setting in which to study the impacts of ongoing climate change.

This study was therefore designed to select the most suitable method for long-term monitoring in alpine environments that would deliver reliable data efficiently. The methods were analysed in respect to time required for field work, species capture capacity, and precision in cover estimation both at high and low cover values.

Material and Methods

STUDY AREA

The study area was located at Mt Schrankogel (3497 m; 11°06'E and 47°02'N) in the Stubaier Alpen, Tyrol, Austria. The sampling sites (transects of 1m² plots) were distributed over the south-west, south and south-east sides of the mountain between 2910 and 3155 m, where the closed siliceous grasslands of the alpine zone disintegrate into open and scattered pioneer vegetation, also termed the nival zone (Gottfried et al., 1998; Pauli et al., 1999; Nagy and Grabherr, 2009). The transects were established on Mt Schrankogel in 1994 and resurveyed in 2004 as part of the GLORIA (Global Observation Research Initiative in Alpine Environments; www.gloria.ac.at) monitoring program (Pauli et al., 1999; Pauli et al., 2007). In August 2004, twenty-five permanent quadrats of 1 m x1 m were selected randomly in 14 of the transects.

SAMPLING METHODS

Vascular plant species presence/absence and cover were investigated in the quadrats using three methods: visual cover estimation (VE), point framing (PF), and subplot frequency (FREQ) (Kent and Coker, 1992; Elzinga et al., 1998). The recording procedures for VE and PF followed the protocol described in the GLORIA manual (Pauli et al., 2004). Two observers always worked in pairs when recording each of the 25 1m x 1m quadrats.

For VE, the cover value of each vascular plant species was visually determined (including vegetative individuals) using a percentage scale relative to the total quadrat area of 1m². Transparent plastic templates in various shapes (circle, ellipse, square, etc.) were used to enhance precision (for details see the GLORIA manual Pauli et al., 2004).

A wooden frame of 1m x 1m, with strings dividing the quadrat into 100 subplots of 10cm x 10cm each, was used for PF and FREQ.

In the PF method, each mesh point of the grid was used to position a 2mm-diameter pin that was then lowered into the vegetation perpendicular to the slope. A total of 121 points were surveyed per 1m², as the points at the edges and corners were also used. Every plant species that was touched by the pin was recorded. If no species were present, the surface type was noted (e.g. rock, scree, bare soil). No spatially explicit record (noting the position of each species hit) was produced, but all hits were added up and divided by the total number of points to estimate percentage top cover. For FREQ, each species in a subplot (10cm x 10cm) was recorded as present or absent. This procedure produced a spatially explicit record of the species pattern on the quadrat rather than cover estimations.

The time required for sampling procedures was recorded for each quadrat.

DATA ANALYSIS

We analysed the number of species captured, species cover, and time requirement for the three methods.

Species number: Paired t-tests (two sided) were used to compare the species numbers captured in the quadrats by each method. Linear models showed the correlations of species numbers for all three methods.

Cover: The cover values were log transformed (logarithm base 2) and tested for normal distribution (Shapiro test). A linear model showed the relationship between PF and VE; the correlation was tested using Kendall's Tau. Paired t-tests were used to compare the cover measured by VE and PF across a range of cover values. Additionally, to test for potential differences between growth forms, the PF and VE covers were tested in paired t-tests separately for each species with more than two PF occurrences (23 of 44 species). To

predict the probability of detecting a species using PF on a certain cover level of VE, we adopted a logistic model.

Time requirement: One-sided Wilcox-tests were used to compare the time requirement for the quadrats among the three methods. We used linear regressions to evaluate if time required for a quadrat depended on species number and total vegetation cover (estimated as the sum of species cover assessed by VE). P-values given in the figures are the values for the linear regression models.

R (version 2.8.1, R Development Core Team, 2008) was used for all statistical analyses.

Results

SPECIES NUMBER

The captured species number differed among the three methods: on average, 13.6 (VE), 8.4 (PF) and 14.3 (FREQ) species were found (Fig 1a). The values for each method summed over all quadrats are given in Figure 1b. PF missed 131 species occurrences (39%) compared to VE and 149 species occurrences (42%) compared to FREQ. One species was found by PF and VE but not FREQ and one by PF and FREQ but not VE; these are not depicted. Species numbers captured by PF and VE were correlated (R=0.50, p<0.001), but their means differed significantly (p<0.001, Figure 1c). PF underestimated species richness in all but one case, and differences in total species number in the quadrats varied from 0 to 11 species. Species number captured by VE and FREQ was also correlated (R=0.93, p<0.001) but significantly different (p=0.005, Figure 1d). VE captured fewer species than FREQ.

COVER ESTIMATION – PF VERSUS VE

For species jointly captured by PF and VE, the two cover estimation methods were highly correlated (Tau=0.64, p<0.001) and, for cover values above 0.7% (according to VE), not significantly different (see Table 1 for details). When each species was tested separately, the cover values of PF and VE differed (paired t-tests, p<0.001) for all but one species (data not shown). With decreasing cover, agreement between the two procedures decreased (Figure 2a). As the PF cover estimation approaches its smallest possible value of one hit (corresponding to a cover estimation of 0.8%) and zero hits, the VE values drift apart and their ranges become large (see Figure 2b: PF=0.8%, range of VE values: 0.005% to 3%, median: 0.4%; zero hits (PF), range of VE values: 0.001% to 2.5%, median: 0.1%). To assess the possible usefulness of PF in alpine vegetation monitoring, we calculated the probability of detecting a species using PF. Below 1% VE cover, the probability to detect a

species by PF drops below 80%. Below 0.25%, the probability is below 50%. Only with covers of more than 2.5% does the probability to detect a species by PF exceed 90% (see Figure 3 and Table 2).

TIME REQUIRED TO COMPLETE FIELD WORK

The three methods for recording species presence/absence and cover estimation showed significant differences in the time required for field work (PF<VE<FREQ, all comparisons p<0.01). PF was always the shortest (5 - 20 min), FREQ was the most time consuming (15 - 133 min), and VE was in between (12 - 63 min) (Figure 4a). Time consumption between the three methods was not correlated, i.e. quadrats requiring more time using VE did not require more time using PF or FREQ (data not shown).

With increasing species number, values increased significantly for VE and FREQ, but not for PF (Figure 4b). Similarly, when compared to total vegetation cover, PF and FREQ showed a significant increase of time required as total cover increased, while VE did not (Figure 4c).

Discussion

Our results showed that the different methods have advantages and disadvantages when comparing species capture capacity, precision of cover estimation, and time required for fieldwork.

SPECIES NUMBER

PF does not capture all species present in the quadrat: it missed 40% of species occurrences. This is the prevalent conclusion of other authors dealing with PF in a comparable plot size to point number relationship, although the numbers vary (Sorrells and Glenn, 1991; Dethier et al., 1993; Brakenhielm and Liu, 1995; Vanha-Majamaa et al., 2000; Leis et al., 2003; Symstad et al., 2008). The reason is that FREQ and VE scan the quadrat very carefully, the former even more carefully than the latter (see also Carlsson et al., 2005), while PF does not consider any vegetation beyond the points. Increasing the number of points in sagebrush steppe vegetation (Floyd and Anderson, (1987) showed that little precision could be gained at increasing sample sizes within a reasonable increase of time.

FREQ and VE were significantly different in terms of species capture efficiency (also found by Carlsson et al., 2005), but agree on 91% of species occurrences. In principle, both approaches should record every single species present. Departure from this is attributed to observer error, which can be divided into the error of missing a present species and

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misidentification (for errors see also Hope-Simpson, 1940; Clymo, 1980; Floyd and Anderson, 1987; Carlsson et al., 2005).

Thus, for species numbers in the quadrat, VE and FREQ are more efficient methods than PF; when used in combination, they deliver a precise account of the species present.

RARE SPECIES – PF VERSUS VE

Compiling a simple list of the rare species not detected by PF seems to solve the problem of recording all species in the quadrat. However, such a list gives no indication of the abundance of each of these species. Especially rare species and their cover might be of particular interest for comparing change over time in long-term monitoring. Cover estimations of PF and VE are similar for high cover values, but differ greatly for low covers (see Figure 2a). The ranges of VE cover values at PF = 0 or 1 are fairly large for sensitive monitoring (Figure 2b). One reason for this range is the often-mentioned high inter-observer variation in VE (Kennedy and Addison, 1987; Tonteri, 1990; Klimeš, 2003; Cheal, 2008). Some authors even suggest that cover changes of up to +/- 20% should be attributed to observer variability (Kennedy and Addison, 1987), while others propose that calibration and training will leave the variability small (Brakenhielm and Liu, 1995). In this study, templates were used to more reliably estimate the small covers, so therefore VE was more useful than PF in those ranges. Nonetheless, proper observer training and calibration are essential and, where possible, more than one observer should agree on the cover value (see also Klimeš, 2003; Vittoz and Guisan, 2007).

Based on our numbers, a 90% chance of detecting a plant using PF requires a cover of 2.4%. Depending on the type of vegetation being studied, this might be a relatively common cover value. In the case of low-density alpine and subnival plant assemblages with a highly scattered species arrangement and when most species have covers below this value, PF is not a suitable method.

COVER ESTIMATION OF HIGH COVER VALUES– PF VERSUS VE

Cover estimations between PF and VE were similar for large covers. At this level they correlated well (see also Brakenhielm and Liu, 1995) and might be convertible. VE covers above 0.7% were not significantly different than those recorded by PF (Table 1). Although PF has been praised as "one of the most trustworthy and most nearly objective methods" (Goodall, 1952) of vegetation cover sampling and recommended in many books (see e.g. Mueller-Dombois and Ellenberg, 1974; Greig-Smith, 1983), our findings support the VE method in alpine environments. A potential disadvantage of VE is that it is said to be influenced by total cover (Klimeš, 2003). However, it is more robust when different leaf shapes and life forms are present in one quadrat (see Brakenhielm and Liu, 1995 for

drawing), or when vegetation differs in the size and distribution of individuals (Mueller-Dombois and Ellenberg, 1974; Floyd and Anderson, 1987). Dethier (1993) claims that VE delivers more accurate estimates although PF seems more objective.

SUBPLOT FREQUENCY

Subplot frequency supplies a data set that cannot be converted to cover estimation. However, it provides a spatially explicit account of the quadrat, useful for finding supposedly lost species in re-surveys. Additionally, as shown here, it provides the most complete record of species present in the quadrat (Figure 1c). Some argue that it is a more objective method than visual estimation (Ringvall et al., 2005), but the amount of time spent on it can be the limiting drawback (Figure 4).

TIME TAKEN

PF was the most rapid of the three methods tested, and FREQ took the longest time, with VE somewhere in the middle. This was also found by Floyd (1987), although he used cover classes instead of precise percentage estimations, and by Symstad (2008) and Leis (2003), who compared VE and PF. Our results contradict those of Sorrells (1991), Brakenhielm (1995), Dethier (1993), Vanha-Majamaa (2000), Seefeldt (2006), and Vittoz (2007). Surprising, although the environments in which the studies were conducted vary extremely, PF is considered the slowest method. This, however, depends very much on the arrangement and number of points (Symstad et al., 2008). An alpine environment is often dominated by bare ground and rocks rather than shrubs or meadows, so PF is much more quickly completed.

With increasing vegetation cover, FREQ and PF increased in time taken for each quadrat (Figure 4d), but the latter only slightly. FREQ and VE took longer with increasing species richness. This was also reported by Symstad (2008). It was not unexpected because each species is recorded and considered separately by the latter two methods. In the PF method, on the other hand, the pin is lowered regardless of the cover, and whatever is present is noted down.

CONCLUSION

For studies assessing higher covers and larger areas without focusing specifically on rare species, PF is the most suitable method (Klimeš, 2003), especially because it is faster and less dependent on total cover. However, for long-term monitoring in alpine environments when focusing on the full array of species including rare ones, VE is far more useful, in particular when improved by applying scale templates. Here, PF should only be considered as an additional control method.

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Figure 1

FIGURE 1: a: Species numbers captured by visual estimation (VE), point-framing (PF), subplot frequency (FREQ); b: agreement in species capture between the methods; c: comparison of species capture in VE versus PF; d: species capture in VE versus FREQ. Dashed line represents y=x, points are jittered.
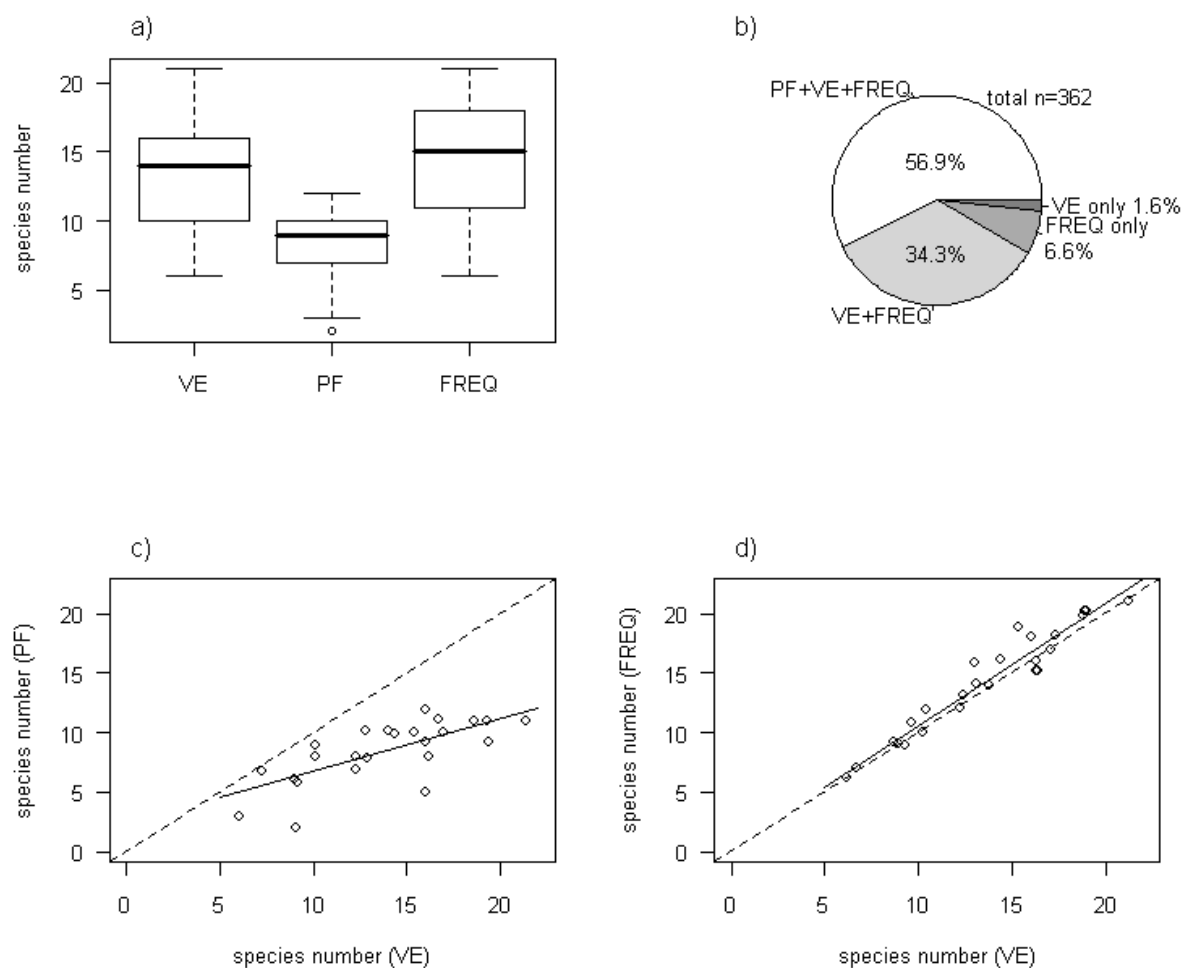
Figure 2

FIGURE 2: a: Comparison of cover estimation of PF (point-framing) and VE (visual cover estimation). Dashed line represents y=x, points are jittered. b: range of VE cover values for rare species, left boxplot: cases where PF hits 1 of 121 points (equivalent to a cover of 0.8%) and right boxplot: cases where plants are not detected by PF.

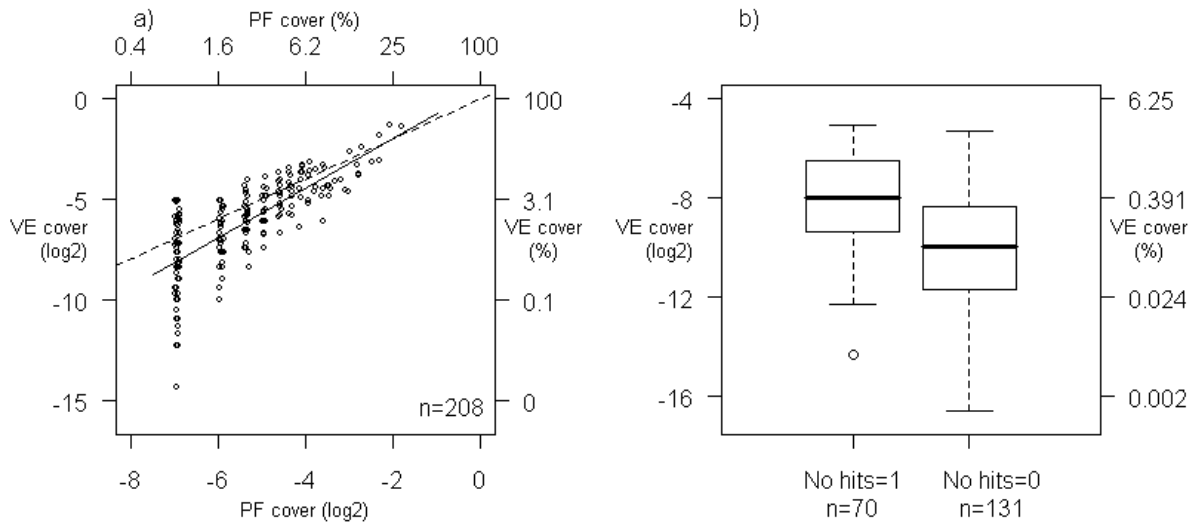Paper 4 – Methods for monitoring in alpine vegetation

Figure 3

FIGURE 3: Probability of detecting a species with PF (point-framing) in relation to its visual cover estimation (VE), y-axis: species detected (1) or not detected (0) by PF; n=364 (some points hidden by others due to equal values on x-axis).
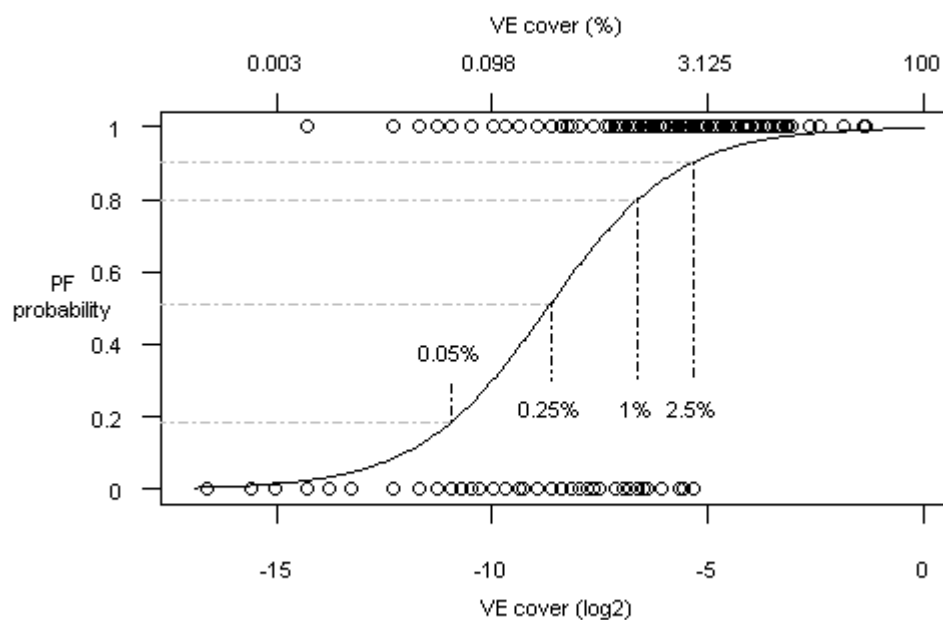
Figure 4

FIGURE 4: Time requirement compared for the three methods: point-framing (PF), visual estimation (VE), subplot frequency (FREQ) (a). Time requirement compared to species number found by each method (b) and cover sums of VE for each quadrat as a measure of total vegetation cover (c).
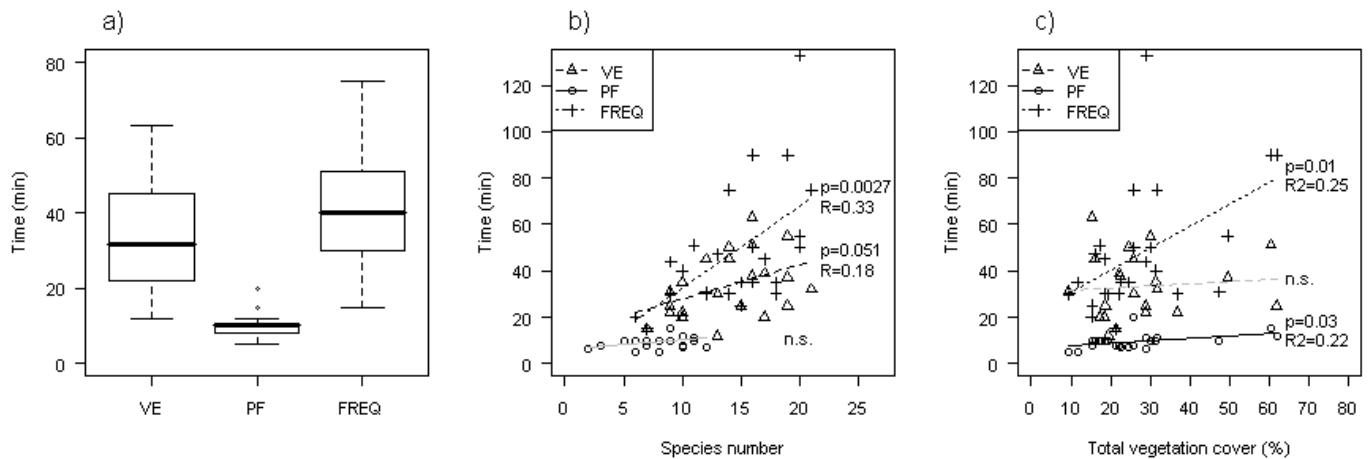

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Table 1

TABLE 1: Stepwise (in terms of VE cover) comparison of VE and PF cover values. n: number of cases compared (i.e. detected by both VE and PF). Additionally, the number of species not detected by PF is listed.

VE cover (%)	n	Number not detected by PF	significance level (p-value)
≥0.001	208	131	<0.001
≥0.01	207	119	<0.001
≥0.1	198	73	<0.001
≥0.2	187	53	<0.001
≥0.3	173	31	<0.001
≥0.4	168	30	<0.001
≥0.5	165	23	<0.001
≥0.6	156	18	<0.01
≥0.7	143	16	0.08
≥0.8	141	16	0.12
≥0.9	138	15	0.17
≥1	136	14	0.22
≥2	92	4	0.73
≥5	39	0	0.08
≥10	11	0	0.22

Table 2

**TABLE 2: probability of detecting species using PF compared to using VE. n=339. %
refers to the number of cases within the 25 quadrats that had a cover value lower
than the number listed in column "VE cover"**

VE cover (%)	probability of detection by PF	% of cases with cover less than VE cover
0.001	0.01	0.00
0.01	0.05	3.83
0.1	0.30	20.06
0.2	0.46	29.20
0.3	0.55	39.82
0.4	0.62	41.59
0.5	0.67	44.54
0.6	0.71	48.67
0.7	0.74	53.10
0.8	0.76	53.69
0.9	0.78	54.87
1	0.80	55.75
2	0.88	71.68
5	0.95	88.50
10	0.97	96.76

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2005-present	Tutor in English, Maths, Latin for asylum seekers and refugees
04/2004-present	Caritas (NGO) migrant help, night and weekend shifts in a home for asylum seeker
Summer 2007	WF (valuable acreage) mapping for Carinthia (part of nature conservation program of federal government ÖPUL)
Summer 2007	Habitat mapping in Salzburg (Rauris) for E.C.O. (Klagenfurt)
Summer 2006	Habitat mapping in Salzburg (Felbertal) for E.C.O. (Klagenfurt)
Spring 2005	Data acquisition in Grisons, Switzerland (Chur) for the re-dynamisation of the vineyard flora for Camenisch&Zahner (Switzerland)

Summer 2004/2005/2006	Vegetation studies in Grisons, Switzerland (Engadin), Salzburg and the Hochschwab massive, Data acquisition for dissertation
Summer 2003	Travel escort of a Chinese VIP delegation through Europe
Summer 2002	Internship at Bayer Healthcare Company in Beijing: Compiling and implementing a program for employee training about microbiology in the work environment
11/2001-03/2002	Assistance at the herbarium of the University of Uppsala. Database management
Summer 2000	Internship at Bayer Healthcare Company in Beijing: Water quality control of the headquarters and plant.
11/1999	Travel escort of a Chinese VIP delegation through Germany and Austria
Summer 1999	Internship at the catering company „Greenhouse" in Beijing
Summer 1995	Internship at Elin, Beijing, China

LANGUAGES

German	mother tongue
English	fluent
Swedish, Chinese, French	good level
Russian	basic knowledge

COMPUTER SKILLS

MsOffice, S-Plus, ArcView, SPSS, R, Sigma Plot

SIGNATURE

Lebenslauf (German)

BARBARA FRIEDMANN GEB. HOLZINGER

Geburtsdatum: 22.05.1979
Geburtsort: Wien, Österreich

AUSBILDUNG

Seit 2004	Dissertation bei Prof. Grabherr in Vegetationsökologie
2003-10/2004	Sprachkurse an der Universität Wien (Tschechisch)
07/2001-07/2002	Ein Jahr ERASMUS Austausch in Uppsala, Schweden. Unterrichtssprache: Schwedisch
1999-2003	University of Edinburgh School of Life Sciences Abschluss mit dem Bachelor of Science with Honors in Plant Sciences
Juli 1999	Absolvierung des HSK Tests (Hanyu Shuiping Kaoshi). Sprachlich Zulassungsgrad zum Individualstudium an einer Chinesischen Universität erreicht.
3/1999-7/1999	Beijing Tiyu Daxue (Sportuniversität Peking), Fortsetzung des Studiums der Chinesischen Sprache, zusätzlich Kurse zur Erlernung der Chinesischen Kampfsportart WuShu
9/1998-3/1999	Beijing Renmin Daxue (Volksuniversität Peking) Intensivkurs zur Erlernung der Chinesischen Sprache und Beijing
1995-1998	International School of Beijing, Beijing, China. Abschluss mit dem International Baccalaureate (IB) Unterrichtssprache: Englisch
1986-1995	Deutsche Schule Peking, China, 2. bis 10. Klasse nach dem Deutschen Schulsystem. Erfolgreicher Abschluss der Mittleren Reife.
1985-1986	Volksschule Bischof-Faber Platz, 1180 Wien, 1. Klasse (mit Unterbrechung durch Aufenthalt auf den Philippinen, dort Unterricht von Mutter)

ARBEITSERFAHRUNG

Seit 10/2007	Datenanalyse und Public Relations bei GLORIA (Global Observation Research Initiative in Alpine Environments, www.gloria.ac.at)
02/2008-10/2008	Mutterschutz und Karenz
Seit 2005	Nachhilfeunterricht Englisch, Mathematik, Latein für Asylwerber und Flüchtlinge
Seit 04/2004	Caritas Migrantenhilfe, Nacht- und Wochenenddienst in einem Flüchtlingswohnheim, 1070 Wien
Sommer 2007	WF (wertvolle Flächen) Kartierung für das Land Kärnten (ÖPUL Naturschutzmaßnahmen)
Sommer 2007	Biotopkartierung in Salzburg (Rauris) für E.C.O. (Klagenfurt)
Sommer 2006	Biotopkartierung in Salzburg (Felbertal) für E.C.O. (Klagenfurt)

Frühling 2005	Datenbeschaffung in Graubünden (Chur) im Bereich Redynamisierung der Weinbergflora für Camenisch&Zahner (Schweiz)
Sommer 2004/2005/2006	Vegetationsstudien in Graubünden (Engadin), Salzburg und auf dem Hochschwab, Datensammlung für Dissertation
Sommer 2003	Reisebegleitung einer Chinesischen VIP Delegation durch Europa
Sommer 2002	Praktikum bei Bayer Healthcare Company in Beijing: Zusammenstellung und Durchführung eines Moduls zur Weiterbildung der Mitarbeiter über Mikrobiologie im Arbeitsleben
11/2001-03/2002	Assistenztätigkeit im Herbarium an der Universität Uppsala. Updating und Katalogisierung der Datenbank.
Sommer 2000	Praktikum bei Bayer Healthcare Company in Beijing. Verantwortung für Wasserqualitätsprüfung innerhalb des Standorts.
11/1999	Reisebegleitung einer Chinesischen VIP Delegation durch Deutschland und Österreich
Sommer 1999	Praktikum bei der Catering Firma „Greenhouse" in Beijing
Sommer 1995	Praktikum bei Elin, Beijing, China

SPRACHKENNTNISSE

Deutsch	Muttersprache
Englisch	fließend, verhandlungssicher
Schwedisch	gut
Chinesisch	gut
Französisch	gut
Russisch	Grundkenntnisse

COMPUTERKENNTNISSE

MsOffice, S-Plus, ArcView, SPSS, R, Sigma Plot

UNTERSCHRIFT