Abstract: The Alps still comprise the largest natural and semi-natural environments in Central Europe, but even the remotest alpine regions may face drastic changes due to human-induced climate warming. The glaciers of the Alps respond to the ongoing temperature increase of about 1-2°C since the 19th century with a drastic shrinkage. The high mountain vegetation is generally considered to be particularly vulnerable to climate change. Therefore, this vegetation can be used as a sensitive “ecological indicator” for climate change effects. An upward movement of high mountain plants was empirically determined at subnival and nival summits (most of them exceeding 3000 m), but no such evidence is available for the lower vegetation belts. Plants will respond to climate change in different ways even at their upper limits, due to different preferences to topographically determined habitats. This resulted from a transect study with detailed field records and fine-scaled distribution models. In addition, the ecophysiological constitution of alpine and subnival plants, their propagation ability, and their life history will be crucial for vegetation dynamics in future warmer climates. The risks of climate-induced upward migration processes of plants include drastic area losses or even extinction of cryophilous plants, a disintegration of current vegetation patterns, and impacts on the stability of high mountain ecosystems.
1. Introduction

The Alps still provide by far the largest part of natural or semi-natural environments in Central Europe, in spite of the long tradition in high mountain agriculture and the increasing pressure from tourism. On the other hand, high mountain ecosystems are generally considered to be particularly vulnerable to climate change. Therefore, this vegetation can be used as a sensitive "ecological indicator" for climate change effects. An upward movement of high mountain plants was empirically determined at subnival and nival summits (most of them exceeding 3000 m), but no such evidence is available for the lower vegetation belts. Plants will respond to climate change in different ways even at their upper limits, due to different preferences to topographically determined habitats. This resulted from a transect study with detailed field records and fine-scaled distribution models. In addition, the ecophysiological constitution of alpine and subnival plants, their propagation ability, and their life history will be crucial for vegetation dynamics in future warmer climates. The risks of climate-induced upward migration processes of plants include drastic area losses or even extinction of cryophilous plants, a disintegration of current vegetation patterns, and impacts on the stability of high mountain ecosystems.

Abstract - The Alps still comprise the largest natural and semi-natural environments in Central Europe, but even the remotest alpine regions may face drastic changes due to human-induced climate warming. The glaciers of the Alps respond to the ongoing temperature increase of about 1-2°C since the 19th century with a drastic shrinkage. The high mountain vegetation is generally considered to be particularly vulnerable to climate change. Therefore, this vegetation can be used as a sensitive "ecological indicator" for climate change effects. An upward movement of high mountain plants was empirically determined at subnival and nival summits (most of them exceeding 3000 m), but no such evidence is available for the lower vegetation belts. Plants will respond to climate change in different ways even at their upper limits, due to different preferences to topographically determined habitats. This resulted from a transect study with detailed field records and fine-scaled distribution models. In addition, the ecophysiological constitution of alpine and subnival plants, their propagation ability, and their life history will be crucial for vegetation dynamics in future warmer climates. The risks of climate-induced upward migration processes of plants include drastic area losses or even extinction of cryophilous plants, a disintegration of current vegetation patterns, and impacts on the stability of high mountain ecosystems.

J. Mt. Ecol., 7 (Suppl.): 9 - 12
2. Evidence of climate change-induced plant migrations

Historical data on the flora of subnival and nival summits of the Alps (most of them exceeding 3000 m), dating from between 1835 and 1953 provided unique reference material for the study of climate-related changes of the vascular plant distribution. Evidence of an already ongoing upward movement of vascular plants within the uppermost vegetation zone was empirically determined by a comparison of these historical data with recent investigations from the same mountain peaks (for methods and details of the results see Gottfried et al., 1994; Grabherr et al., 1994, 1995, 1999; Pauli et al., 1996, 1997). Overall, 70 per cent of the 30 summits investigated showed a distinct increase in species richness as a result of invaders from lower altitudes. The number of species at the remaining nine summits was the same or slightly lower as recorded in the historical investigation.

The rates of upward movement were highly related to the geomorphological shape of the summit areas. The peaks with the highest increase in species richness have solid and structured ridges with numerous stable microhabitats for plants to establish. Furthermore, these peaks have more or less uninterrupted corridors, colonised with plants, stretching from the alpine grassland belt upwards to the summits. In contrast, most summits with a stagnating or slightly decreasing species richness are dominated by unstable scree, where permanent habitats are reduced by the high frequency of disturbance events.

For the subalpine and alpine belt of the Alps, no empirical evidences on recent upward migrations are available – due to the lack of appropriate historical reference data. The timberline was even lowered by 150-400 m with respect to its postglacial thermal optimum in response to human activities such as alpine pasturing. It has not moved upwards again, according to a case study in Switzerland (Hättenschwiler and Körner, 1995). Holtmeier (1994) suggests, that at least 100 years of thermal conditions more favourable than at present would be needed for a timberline advance.

3. Vegetation patterns of the high Alps in future climates

An extensive transect study at the transition zone between the closed alpine grassland and the open and scattered nival vegetation (the alpine-nival ecotone; at Schrankogel, Tyrol) showed that vascular plants close to their altitudinal limits are not randomly distributed: they follow distinct ecological gradients. Species as well as plant assemblages can be related to topographically determined gradients of disturbance (such as debris falls and substrate movements) and snow cover. Particularly species of alpine and subnival grassland (i.e. of Carex curvula-swards and pioneer swards), being able to create a closed vegetation cover and so enhance soil formation, are sensitive to both disturbance and a long lasting snow cover. Therefore, migration corridors for climate warming-induced upward migrations of alpine grassland species will be restricted to "stepping stones" at stable and rocky ridges. These alpine plants will only have a chance to establish at new unstable sites, when both snow cover and disturbance are reduced as a consequence of climate warming. The latter, however, may even be enhanced at many high sites of the Alps due to an increased frost weathering because of permafrost degradation (Haeberli, 1995). Frost-sensitive but disturbance-tolerant snow bed species, on the other hand, may suffer area losses due to a climate change-induced reduction of the snow cover period (for further details see Pauli et al., 1999b).

A spatial distribution model of vascular plant species and assemblages at the alpine nival ecotone, based on field observations at Schrankogel and on a fine-scaled Digital Terrain Model, yields similar patterns (Gottfried et al., 1998). The modelled distribution patterns show that sward-forming alpine grassland species are concentrated at the ridges, whereas typical species of the uppermost vegetation belt extend into the unstable scree area; snow bed species are restricted to scree-dominated sites.

This spatial distribution model was used to calculate distribution scenarios for predicted temperature regimes, by assuming an altitudinal temperature gradient of -0.95°C per 100 m (resulting from recent temperature measurements at Schrankogel; Gottfried et al., 1999). The model predicts a disintegration of the cryophilous subnival flora into small patches "trapped" in habitats with extreme terrain conditions, by the invasion of alpine species. Apart from topographically determined habitat preferences, the fate of the alpine and subnival plants as winners or losers in future habitat conditions with increased temperature and elevated atmospheric CO₂ will also depend on the ecophysiological responses of individual
species. Körner (1995) mentioned that the indirect effects of rising temperature (e.g. the length of the snow free period) are more important than direct temperature effects on life processes. For elevated CO₂, there is still no evidence that late successional alpine species will grow faster, but it can be expected that elevated CO₂ will increase the C/N ratio in the biomass. This would lead to reduced food quality for herbivores and to alterations in decomposition processes (Körner, 1995). In addition, an increased deposition of soluble nitrogen in alpine ecosystems will stimulate growth of some species and discriminate others, hence species composition is likely to change (Körner, 1995).

Overall, the life history strategies of alpine and subnival plants (e.g. ecophysiological constitution, propagation ability) will be crucial for vegetation dynamics in future warmer climates. Although studies on plant adaptations in alpine climates (e.g. Larcher, 1983; Körner and Larcher, 1988), experimental studies on plant responses to atmospheric changes (e.g. Körner et al., 1997; Arnone and Körner, 1997) as well as studies on the propagation of alpine plants (e.g. Hartmann, 1957) are available, a satisfying classification of species or species groups based on key functional traits is still lacking.

4. Risks of climate change-induced impacts on the vegetation of the Alps

A drastic decrease of the distribution area or even extinctions of cryophilous species can be the consequence of migration processes towards higher altitudes. Rates and patterns of these dynamics, however, will be highly dependent on the habitat preferences of particular species and their key functional traits. Due to the slow growing nature of many alpine species, particularly of sward-forming grassland species like Carex curvula All., a remarkable time lag between climate warming and migration responses can be expected (compare Grabherr, 1989; Grabherr et al., 1995).

Therefore, serious threats for the subnival biodiversity may not become evident within the next decades. Nevertheless, many endemic species of the Alps are concentrated in relict areas of isolated lower mountain ranges of the outer Alps (Pawlowski, 1970). Endemics with a narrow altitudinal distribution area close to the summits (e.g. Draba saturei Hoppe, D. stellata Jacq.) may be among the first species pushed into the greenhouse trap for ever (Grabherr et al., 1995).

In addition, migration processes will cause a disintegration of the present vegetation patterns (Gottfried et al., 1999). This could seriously impact the stability of alpine environments, at least in a long term perspective, for example by generating unstable transition zones with largely unpredictable behaviour. Therefore, the current signals of an already ongoing response to climate warming should be treated as serious warnings. Further research initiatives in high mountain environments, with international and interdisciplinary cooperation (e.g. Becker & Bugmann, 1997; Pauli et al., 1999a), including long-term monitoring, ecophysiological and phenological studies, as well as predictive modelling, are needed to establish an effective early warning system.

5. Acknowledgements

The comparison study on the flora of high summits in the Alps and the transect study at the alpine-nival ecotone of Schrankogel was financed by the Austrian Academy of Sciences within the framework of the International Geosphere-Biosphere Programme. Additional support came from the Austrian Federal Ministry of Science and Transport. Thanks to Max Abensperg-Traun for linguistic remarks on the manuscript.

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