EFFECTS OF CLIMATE CHANGE ON MOUNTAIN ECOSYSTEMS - UPWARD SHIFTING OF ALPINE PLANTS

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SUMMARY

Ecosystems at high latitudes and altitudes are particularly sensitive to climate change. As an effect of global warming, upward shifting of plant species in high mountain systems was predicted for the near future. In consequence the habitats of the alpine and nival vegetation could be restricted drastically, which might result in extinctions, particularly of summit floras. Evidence of upward movement of vascular plants in high mountains was recently empirically determined in the European Alps. In 1992 and 1993, data on the flora of 30 high summits were collected. A comparison of the recent investigations with historical records from the same peaks indicated a distinct increase of species richness at 70% of the summits. A stagnation or a slight decrease of species richness was recorded at 9 summits, but one of them showed an increase in species abundance. The change of species richness is correlated with the geomorphological situation, whereas no significant difference could be found by comparing siliceous and carbonate summits.

Approximate moving rates for common alpine plants were calculated to be between zero and 4 meters per decade.

This evidence of upward shifting of high mountain plants may already be a "measurable" result of global warming since the 19th century.

INTRODUCTION

From the ice age climax 18,000 years before present, when the central European Alps were fully ice-covered, to the Holocene climate, the surface temperature in central Europe shifted by 4 to 5°C (Grassl, 1994). During the past 100 years, the annual mean air temperature in Austria has increased by about 2°C, with a change of 1.2°C over the last 30 years, as was demonstrated based on recently updated climatological data (Auer, et al., 1996). A global warming of the atmosphere of 2-4°C by the end of the 21st century is predicted as a result of increased concentrations of greenhouse gases (Cubasch, et al., 1992).

Ecosystems at their altitudinal and latitudinal temperature-limits are considered to be particularly sensitive to climate change (Markham, et al., 1993; Oechel, 1993). Responses are demonstrated by fluctuations of the snowline and glaciers at high altitude levels (Barry, 1992; Haeberli, 1994). At Mt. Sonnblick (3,106m), a peak in the eastern European Alps, the average number of days with snow cover during May to September decreased from 82 days for 1910-25 to only 53 days for 1955-70 (Böhm, 1986). At high altitudes, vegetation is stress-dominated in the sense that abiotic factors, particularly climate, prevail over biotic ones. Therefore, effects of climate change could be more pronounced on vegetation above the timberline than on lowland vegetation (Körner, 1994).

Temperature distributions are determined by the altitude according to a well-known gradient. Atmospheric temperature decreases by 0.55°C per 100m on average, in summer by about 0.7°, in winter about 0.4°C (Ozenda and Borel, 1991). An expected warming of 3°C would cause an upward shifting of plant species or entire vegetation belts in high mountain systems like the European Alps of 400-600m (Nilsson and Pitt, 1991; Holten, 1993; Ozenda and Borel, 1995). Species from alpine tundras could encroach on space-limited habitats of less productive plants in the uppermost or nival zone of the Alps. On the other hand, the alpine swards may become overgrown by today's subalpine heaths and forests. These extensive migration dynamics, predicted for the near future, would drastically restrict the habitats of alpine and nival vegetation. Particularly summit floras of isolated mountain systems with a distinct flora could be eliminated. For example, endemic species at the exterior ranges of the Alps, where most of the summits do not exceed 2,500m, might become extinct due to the absence of higher, adjoining mountains to provide an area to re-establish (Grabherr, et al., 1995).

Did the more or less continuous warming during the past 100 years lead to ecological impacts in the present alpine vegetation? If mountain plants are already responding by a trend of upward moving, it could signal, that the above-cited scenario is currently under way. Scientific efforts to obtain evidence of climate-change-induced dynamics of alpine vegetation suffer from a lack of historical reference data. Most of the permanent plots established for monitoring global warming impacts do not allow a time span of more than a few years to be observed. Nevertheless, in spite of this unfavorable starting point for research activities, detailed records on the flora of several high summits of the European Alps, some of them dating back to the 19th century, are available. Furthermore, preliminary observations of summit floras in geographically restricted areas of the Swiss Alps showed increased species richness compared with previous data (Braun-Blanquet, 1957; Hofer, 1992).

The aim of this paper is to compare 30 historical summit records stemming from a considerable part of the Alps, with recent investigations carried out in 1992 and 1993.

Results derived from investigations at high siliceous peaks have already been published (Gottfried, et al., 1994; Grabherr, et al., 1994; Grabherr, et al., 1995). The current paper includes six high calcareous summits and compares changes of species richness between mountains with contrasting bedrocks. A general synthesis is given by presenting data from all investigated summits.

THE STUDY SITES

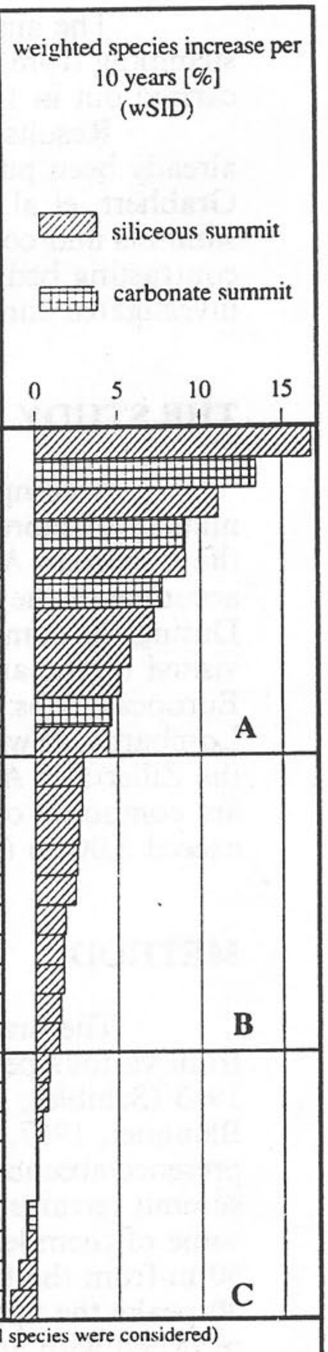
A comprehensive study of the literature revealed a remarkable number of more than 300 old records of summit floras from various parts of the European Alps. A total of 132 summit studies were selected based on the accuracy of the localizations, thus allowing useful recent investigations. During the summers of 1992 and 1993, 30 of these historical study sites were visited by the authors. The peaks are spread over three areas in the central European Alps: 1) the Rätische Alpen in Graubünden and northern Lombardia (Switzerland, Italy); 2) the Ötztaler Alpen (Austria, Italy); and 3) the Zillertaler Alpen and Rieserferner Gruppe (Austria, Italy). Six mountains are composed of carbonate and 24 of siliceous bedrock; most of the peaks exceed 3,000m (see Figure 1).

METHOD

The historical investigations yield records of different accuracy and from various periods of time. All 30 records, dating from between 1895 and 1953 (Schibler, 1898; Rübel, 1912; Klebelsberg, 1913; Braun, 1913; Braun-Blanquet, 1957, 1958; Reisigl and Pitschmann, 1958), provide complete presence/absence lists of the vascular plants occurring at the uppermost summit terrains. Most of the records consider the uppermost 15 or 30 m, some of them less (minimum of 2 m) and some of them more (maximum of 50 m from the highest summit point downwards); (see Figure 1). At 12 of the 30 peaks the uppermost position of each species within the summit area was recorded with an accuracy of one meter isolines (Braun, 1913; Braun-Blanquet 1957, 1958). One mountain, Piz Linard in eastern Switzerland, was researched 6 times during the last 150 years. A map of Piz Linard, the best known peak for high alpine summit studies, was drawn for the 1947 record (Braun-Blanquet 1957) and shows distributions and abundances of all vascular plant species found in the uppermost 30 m.

During the summer of 1992 and 1993 the historical investigations were repeated in the same manner as the original record. In addition, the

summit	altitude [m]	bedrock	year of historical record	year of present record	interval [m]	historical number of species	present number of species	no. of species in both records	weighted no. of species not found again	weighted no. of new found species	wSI [%]	wSID [%]
Piz dals Lejs	3042	sil.	1907	1992	30	11	34	10	0.7	16	143.0	16.8
Piz Laschadurella	3046	car.	1919	1992	30	7	17	6	0.7	7.25	97.8	13.4
Hohe Wilde [1)]	3480	sil.	1953	1992	20	11	19	11	0	4.75	43.2	11.1
Piz Tavrü	3168	car.	1927	1993	15	5	14	5	0	3	60.0	9.1
Stockkogel	3109	sil.	1953	1992	9	12	19	12	0	4.25	35.4	9.1
Piz Foraz	3029	car.	1921	1993	30	9	19	9	0	5	55.6	7.7
Napfspitze [2)]	2888	sil.	1912	1992	3	31	53	30	0.7	18.3	57.3	7.2
Monte Vago	3059	sil.	1905	1992	30	28	51	27	0.7	14.75	50.7	5.8
Piz Nuna	3124	sil.	1919	1992	30	19	34	19	0	7.25	38.2	5.2
Piz Uertsch	3268	car.	1911	1993	30	2	5	2	0	0.75	37.5	4.6
Großer Lenkstein	3236	sil.	1912	1992	2	4	6	3	0.7	2	35.1	4.4
Wilde Kreuzspitze	3135	sil.	1907	1992	3	8	10	6	1.4	3.25	25.0	2.9
Piz Kesch	3418	sil.	1902	1992	30	8	13	8	0	2	25.0	2.8
Munt Pers	3207	sil.	1906	1992	11	15	19	14	0.7	4	22.4	2.6
Hint. Spiegelkogel [3)]	3426	sil.	1953	1992	15	15	19	15	0	1.45	9.7	2.5
Piz Forun	3052	sil.	1903	1992	30	48	69	47	0.7	11	21.6	2.4
Gorihorn	2986	sil.	1895	1992	7	14	18	12	1.4	3.75	17.5	1.8
Festkogel	3038	sil.	1953	1992	35	58	63	54	2.8	6.5	6.5	1.7
Hint. Seelenkogel	3470	sil.	1953	1992	12	11	13	11	0	0.75	6.8	1.7
Flüela Schwarzhorn	3146	sil.	1902	1992	50	34	43	32	1.4	6	13.8	1.5
Piz Stretta	3104	sil.	1903	1992	30	20	28	20	0	2.5	12.5	1.4
Liebenerspitze	3399	sil.	1953	1992	20	2	3	1	0.7	0.75	2.9	0.8
Piz Plazer	3104	sil.	1918	1992	30	16	19	14	1.4	2.25	5.5	0.7
Piz Sesvenna	3204	sil.	1918	1992	30	17	19	17	0	0.5	2.9	0.4
Piz Blaisun	3200	car.	1911	1993	20	5	6	4	0.7	0.75	1.1	0.1
Piz Julier	3380	sil.	1900	1992	30	9	10	8	0.7	0.75	0.6	0.1
Piz Nair	3010	car.	1918	1993	10	22	22	20	1.4	0.5	-4.2	-0.6
Piz Linard [4)]	3411	sil.	1947	1992	30	10	10	8	0.75	0.5	-2.9	-0.6
Piz Trovat	3146	sil.	1907	1992	24	8	7	7	0.7	0	-9.1	-1.1
Radüner Rothorn	3022	sil.	1897	1992	5	8	6	5	2.1	1	-15.5	-1.6



1) recalculated values (in Gottfried et al. 1994, Grabherr et al. 1994 and 1995 only 10 historical species were considered)
2) abundance values of 9 new species were assigned a weight of 0.7
3) abundance value of 1 new species was assigned a weight of 0.7
4) weighted with respect to available historical abundance values

Figure 1 Change in species richness at 30 nival summits in the European Alps; wSI weighted species increase, wSID weighted species increase per decade abundance of each species inside the study area and the local distribution of the highest specimens found were recorded. Finally, a detailed reconnaissance of the summit terrain was made to describe the relief of the study site.

The analysis was carried out by comparing each new record with the historical investigation (in the case of Piz Linard the latest record, dating from 1947, was considered).

Table 1 Changes of species richness at Piz Linard; presence and abundance: p present, c common, i intermediate abundance, r rare, ia increased abundance

species	1835	1864	1895	1911	1937	1947	1992
Androsace alpina	p	p	p	p	p	c	c, ia
Ranunculus glacialis		p	p	p	p	c	c, ia
Saxifraga bryoides			p	p	p	c	c, ia
Saxifraga oppositifolia			p	p	p	c	c, ia
Poa laxa				p	p	c	c, ia
Draba fladnizensis				p	p	c	c
Gentiana bavarica				p	p	i	i
Cerastium uniflorum				p	p	i	r
Tanacetum alpinum		p			p	i	
Saxifraga exarata					p	r	
Cardamine resedifolia							r
Luzula spicata							r

The species values were weighted for abundance. This weighting was taken into account because the possibility could not be excluded that the historic author overlooked one or the other rare species (Gottfried, et al, 1994). For the new values, weighting was carried out in the following manner: weight for common species = 1, for rare species 0.25 and for species with intermediate abundance 0.5. The historical records do not give abundance assessments; therefore the values of species that were not found again were weighted by 0.7. This corresponds to the mean of all new abundance values. Those species present in both the old and the new record were not weighted.

According to the weighting for abundance, the present number of species is calculated by the historical number of species plus the weighted number of new species minus the weighted number of species not found again. Based on this calculated value, a weighted species increase (wSI) was determined, which is defined as percent species increase. Furthermore, values are standardized by a 10-year interval because of the different time spans between old and new records (wSID):

$$wSID = (wnS - wmS)/(eS + wmS)*100/[(pY - hY)/10]$$

where: wSID = weighted species increase per decade, wnS = weighted number of new found species, wmS = weighted number of species not found again (missing species), eS = number of species found in both records (equal species), pY = year of the present investigation, hY = year of the historical investigation.

RESULTS

The historical and present data of all 30 summits are shown in Figure 1. The absolute number of species in past and current records, the number of equal species (eS) and the weighted data of missing (wmS) and new found species (wnS) are given along with the resulting values of the weighted species increase (wSI) and the weighted species increase per 10 years (wSID). The mountains are ordered according to the values of wSID, which describes the changes of species richness in various time spans in the most comparable way.

Changes of Species Richness in Three Distinguished Groups of Summits

A distinct increase of species richness was found at 21 (70%) of the summits. At 11 of those peaks, the weighted number of species rose by more than 35%, with a maximum of 143%. At 9 (30%) of the mountains, a stagnation of species richness was observed, with 4 of these showing a slight decrease. According to the wSID values, 3 groups can be distinguished (Figure 1). Group A is characterized by a clear increase of species richness (wSID is more than 4%, with a maximum of 16.8%), which indicates high rates of migration. Group B shows a moderate increase, and the third group (C) is determined by almost no increase or even a slight to moderate decrease (maximum negative wSID of -1.6%).

A careful reconnaissance of the geomorphological shape of summit terrains showed that almost all summits in group A - the siliceous as well as the carbonate ones - are composed of solid and structured ridges. Such a rocky environment with comparably little erosion and many crevices provides numerous micro-habitats for vascular plants to set roots. In addition, the peaks of group A have more or less uninterrupted, vegetated corridors at the south-facing slopes and ridges, stretching down to the more populated alpine grassland zone.

In contrast, most of the summits of group C, those without significant increase or even slight to moderate decrease, are dominated by crumbling rocks and scree. Space for permanent habitats of flowering plants is reduced by the high frequency of erosion events. The peaks of group B, showing moderate increases of 1.4 to 2.9% per 10 years, are characterized by an intermediate position concerning the geomorphological situation.

Special Cases of Stagnating Species Numbers

The siliceous summit terrain of Piz Linard (3,411m), the classical mountain of high alpine summit research, has shown a stagnation of species richness (group C) according to the most recent investigation in 1992. In contrast to the present results, a drastic increase of the species number between 1835 and 1947 was demonstrated by Braun-Blanquet (1957). In 1835 only one species was found (Heer, 1866), and until 1947 the number of flowering species rose gradually up to 10 (Table 1). In 1992, 8 of them were found again, along with 2 new species, although just a few individuals of the latter were present. Considering the results since 1835, Piz Linard is not a group C-mountain, but a typical summit of group A. However, new species were unable to find a permanent habitat during the recent decades. On the other hand, some species that had already been present at the peak increased in abundance, and they currently grow at new sites as well (Table 1). This was obvious by a comparison with the map of populations, drawn up by Braun-Blanquet in 1947.

A similar situation may be true at Piz Nair (3,010m), a carbonate peak first investigated by Braun-Blanquet in 1918. Compared with the results of 1993, the number of species remained stable at 22, and the species composition was nearly the same. Yet, based on the geomorphology, this peak is not representative of group C. Solid ridges with crevices are available for plants to establish.

Siliceous versus Carbonate Peaks

The alpine and nival vegetation at mountains with different bedrock - like siliceous and carbonate peaks - is contrasted by a distinct flora, with more acidophilus species on siliceous and more basophilous species on calcareous substrates. In this regard, a comparison of past and present records revealed no clear differences in changes of species richness. The 24 siliceous peaks are spread over all 3 groups, with 7 summits in A, 10 in B and 7 in C. From the 6 mountains composed of carbonate bedrock, 4 peaks were assigned to group A and 2 to group C (see Figure 1). Carbonate sites show a higher percentage of group A-peaks and are missing in B, but due to the lower number of samples, this cannot be interpreted as an obvious difference.

Table 2 Species listed in historical and present records of two representative summits of group A with different bedrock (values weighted)

Hohe Wilde (3,480 m), siliceous bedrock (interval 20 m)			**Piz Laschadurella** (3,046 m), carbonate bedrock (interval 30 m)		
species	1953	1992	species	1919	1992
Androsace alpina	1	1	*Achillea atrata*	-	0.25
Carex curvula	-	1	*Androsace helvetica*	-	0.5
Cerastium uniflorum	1	1	*Arabis alpina*	-	0.5
Draba fladnizensis	1	1	*Arabis caerulea*	1	1
Erigeron uniflorus	-	0.25	*Arenaria ciliata*	-	0.5
Festuca halleri	-	0.25	*Campanula cochleariifolia*	-	0.5
Gentiana bavarica	-	1	*Cerastium latifolium*	1	1
Luzula spicata	1	1	*Draba ladina*	-	0.5
Minuartia sedoides	1	1	*Draba tomentosa*	1	1
Poa laxa	1	1	*Festuca alpina*	-	1
Potentilla frigida	1	1	*Festuca pumila*	0.7	-
Primula glutinosa	-	0.5	*Minuartia gerardii*	-	1
Primula minima	-	0.25	*Moehringia ciliata*	1	1
Ranunculus glacialis	1	1	*Poa minor*	-	1
Saxifraga bryoides	1	1	*Saxifraga aphylla*	1	1
Saxifraga exarata	-	1	*Saxifraga oppositifolia*	1	1
Saxifraga oppositifolia	-	0.5	*Taraxacum alpinum*	-	1
Silene exscapa	1	1	*Trisetum distichophyllum*	-	0.5
Tanacetum alpinum	1	1			
weighted species number	**11**	**15.75**	**weighted species number**	**6.7**	**13.25**
wSI	**43.2%**		**wSI**	**97.8%**	
wSID	**11.1%**		**wSID**	**13.4%**	

Data of 2 representative summits of group A, with different bedrock and different species composition, are shown in Table 2. Mt. Hohe Wilde (3,480m), which was investigated by Reisigl and Pitschmann in 1953, represents a siliceous mountain. The species number has changed from 11 to 19 (15.75 in weighted values), while species richness (wSI) rose by 43.2%.

Similar, but even more obvious results were obtained at Piz Laschadurella (3,046m), a carbonate peak first researched by Braun-Blanquet in 1919; here, the change of species number is equivalent to almost a 100% increase of species richness.

This demonstrates a clear change of species richness in spite of the differences caused by the bedrock.

Rates of Upward Shifting

The detailed historical records for 12 siliceous summits, investigated by a meter-by-meter approach, enabled the authors to assess approximate migration rates within the researched summit areas. Migration rates of the 9 most common species were calculated by comparing the uppermost past and present occurrences (Grabherr, et al., 1995). The observed upward movements showed maximum migration rates of least 4 m per 10 years for 2 species, whereas most of the values were between zero and 1.5 m for the other common species. Obviously, those species, that inhabited the highest summit points both during the historical and the recent investigations, also had to be given zero values. In addition, the rates of new found species were minimal, because the historical upper limit was applied to the lower boundary of the research site, and not to the unknown highest historical occurrence. The investigated migration rates do not represent the real rates of upward movements of specific alpine vascular plant species, but do provide the first empirical approximations of the dimension of migration processes on mountain ecosystems. Furthermore, species with different moving rates were distinguished.

According to the increase of the annual mean air temperature in Austria by 2°C (Auer, et al., 1996), a hypothetical upward movement of temperature isolines would be roughly between 10 and 20 m per decade. In this light, the values of the empirically determined migration rates of alpine plants of maximally 4 m per 10 years are comparatively low.

CONCLUSIONS

The present paper provides an evidence of an increased species richness at mountain peaks, based on a comparison of past and current records from 30 high summits in the European Alps. The result is consistent with earlier publications that show increased species richness at mountains in restricted areas of the Alps (Braun-Blanquet, 1957; Hofer, 1992).

The increased species richness cannot be explained by chance alone, and it may be related to an upward migration of plants due to the climate warming since the 19th century.

The upward movement seems to be dependent on the morphological character of the mountain, with high rates at summits with little erosion and solid, structured ridges. In addition, migration corridors from the summit terrain downwards to the alpine grassland zone are crucial for migrations of vascular plants. A stagnation of species richness, observed at some peaks, can be explained by high erosion, which reduces permanent habitats and interrupts the connection to the vegetation below.

The reason for the stagnation at Piz Linard, which has shown drastic increases in the past, can be suggested hypothetically to reflect a saturation of species richness by the mid-20th century. The habitat conditions at the summit are still unsuitable for species from lower vegetation belts, but not for the nival flora, which already appeared around 1940. The abundance of these species has increased. The constant number of species at Piz Nair might be due to a similar saturation of the flora.

Upward shiftings of vascular plants are evident for siliceous as well as for carbonate peaks. Summits composed of the two contrasting bedrocks are characterized by different geomorphological relief-structures and different substrate, which determine a distinct flora and different vegetation patterns. Despite an expected difference in changes of species richness, however, these clearly differentiated environments may be affected in quite the same way. On the other hand, the frequency of erosion events plays an important role in determining the actual plant migration in each specific high alpine ecosystem.

Alpine plant species show different rates of migration due to rapid climate warming, leading to changing vegetation patterns.

The migration rates of vascular plants approximated here are far below the hypothetical rates of upward movement of temperature isolines. This indicates a remarkable time lag between the temperature increase and an obvious ecological response.

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