

# POTENTIAL IMPACT OF CLIMATE CHANGE ON VEGETATION IN THE EUROPEAN ALPS: A REVIEW

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**Abstract.** Based on conclusions drawn from general climatic impact assessment in mountain regions, the review synthesizes results relevant to the European Alps published mainly from 1994 onward in the fields of population genetics, ecophysiology, phenology, phytogeography, modeling, paleoecology and vegetation dynamics. Other important factors of global change interacting synergistically with climatic factors are also mentioned, such as atmospheric CO<sub>2</sub> concentration, eutrophication, ozone or changes in land-use. Topics addressed are general species distribution and populations (persistence, acclimation, genetic variability, dispersal, fragmentation, plant/animal interaction, species richness, conservation), potential response of vegetation (ecotonal shift – area, physiography – changes in the composition, structural changes), phenology, growth and productivity, and landscape. In conclusion, the European Alps appear to have a natural inertia and thus to tolerate an increase of 1–2 K of mean air temperature as far as plant species and ecosystems are concerned in general. However, the impact of land-use is very likely to negate this buffer in many areas. For a change of the order of 3 K or more, profound changes may be expected.

## 1. Introduction

In recent years, attention has focussed on the possible impact of atmospheric and climatic changes on plants and vegetation. According to Beniston (1994), Guisan et al. (1995), Beniston et al. (1996), Kienast et al. (1998) or Cebon et al. (1998), high mountain systems such as the Alps (see Aeschimann and Guisan (1995) or Theurillat et al. (1998) for an introduction) are likely to be particularly vulnerable to climate change. Much uncertainty still exists as to the possible effects of such change on ecosystems and soils in the Alps, which could have severe biological and economic consequences. It is impossible to draw up a unique scenario valid for the entire Alpine chain, simply because of the diverse meso-climates, with all possible gradations between oceanic, continental and Mediterranean influences (Beniston et al., 1997) and also because climate change is very likely to affect differentially the organisational levels of ecosystems, from population to landscape (e.g., Theurillat et al., 1998). For millennia, the entire range of the European Alps has been subject to human pressure (grazing, agriculture, forestry), even in remote areas, modifying species' distribution such as larch (*Larix decidua*) (e.g., Ozenda, 1985). Therefore,



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it is uncertain whether the present vegetation of the Alps is in a natural equilibrium between climate and ecological factors, and this is why palaeoecology is an important tool to understand vegetation equilibrium under reduced human impact.

The present review aims to summarize the main trends in assessing the impact of climatic and atmospheric change on vegetation in the European Alps. Such trends have been obtained from proven test cases during recent years in fields such as population genetics, ecophysiology, phenology, phytogeography, modeling, palaeoecology and vegetation dynamics. The review is based on conclusions drawn from previous work in the general field of climate and atmospheric change impact assessment in mountain regions (e.g., Tegart et al., 1990; Peters and Lovejoy, 1992; Gates, 1993; Körner, 1992, 1993, 1994, 1995; Markham et al., 1993; Körner et al., 1996; Schächli and Körner, 1996; Beniston et al., 1996; Theurillat et al., 1998), but only synthesizes results relevant to the European Alps.

However, other important factors of global change may interact synergistically with climatic factors. These, such as atmospheric CO<sub>2</sub> concentration, eutrophication, ozone or changes in land-use, are also mentioned.

A summary of some of the major trends in mountain ecoclimatology relevant for the European Alps is given in Box 1 in order to clarify the following discussion on the results of impact studies.

## 2. Potential Responses of Plant Species

There are three basic ways in which mountain plants may respond to a climatic change (see also Guisan et al. 1995a; Bazzaz, 1996): (i) persistence in the modified climate, (ii) migration to more suitable climates or (iii) extinction. Three types of persistence are possible: gradual genetic adaptation of populations, phenotypic plasticity (i.e., individual variation in the properties produced by a given genotype – genetic character – in conjunction with the environment) or ecological buffering (edaphic climax, i.e., where it is the soil processes that essentially control the final stage of plant succession, as opposed to climatic climax, where climate is the main determinant of the final stage). However, other influences, such as fragmentation or plant/animal interaction, must be taken into account in conjunction with climate change, as they can greatly affect plant species' populations in the near future.

### 2.1. IMPACT ON GENERAL SPECIES DISTRIBUTION

Evidence gleaned from past climate changes tends to indicate that species are more likely to respond by migration rather than by adapting genetically (Huntley, 1991). However, there is also a body of evidences that at particular places (nunataks, i.e., high elevation zones which remained snow- and ice-free above the ice-sheet even at the glacial maximum) cold resistant high elevation species (orophytes, i.e., high mountain plants) – both some Early Tertiary relict species and more recent Late

Box 1: Selected features of mountain ecoclimatology.

The following parameters should be taken into account when assessing the ecological impact of climate change in the Alps (see also Theurillat et al., 1998):

- In the Alps, mean air temperature decreases regularly as elevation increases, at a mean rate of about 0.558 K per 100 m difference.
- Conversely, precipitation (water + snow) tends to increase as elevation increases, with different local and regional patterns (Sevruk, 1997, 1998).
- The regular decrease of mean air temperature determines vegetation belts which are altitudinal sections characterized by a given vegetation and a given climate, i.e., bioclimatic zones. In the European Alps, vegetation belts have an altitudinal extension of approximately 700 m and, conventionally, they are named, from bottom to top, colline, montane, subalpine, alpine and nival belts. Vegetation belts being determined by climate, their elevation varies according to variations of the mesoclimate within a range. The subalpine belt is the upper forest belt; it corresponds mainly to coniferous forests. Its lower, respectively higher limit can vary from 1200–1300 m to 1900–2000 m asl. in the northern, colder and wetter Alps, to 1600–1700 m to 2300–2400 m asl. in the internal, warmer and drier Alps.
- Mean air temperature is directly linked to the plant growth season, and the sum of temperature (degree-days) influences plant phenology linearly. Late frosts interact with temperature, either increasing or decreasing (chilling effect) the amount of degree-days required for plant development (Schlüssel et al., 2000; Theurillat and Schlüssel, 2000).
- The decrease of mean air temperature with elevation appears to be in close correlation with the general decrease of species' richness with elevation (Grabherr et al., 1995; Schlüssel, 1999).
- Mean air temperature is also a determining factor for the water chemistry (e.g., pH) of remote alpine lakes. Aquatic ecosystems at high altitude might respond with extreme sensitivity to climate warming (Sommaruga-Wögerath et al., 1997; Sommaruga, 1999) and global change in general.
- Precipitation regimes determine oceanicity or continentality, which in turn influence plant distribution (see also Eggenberg, 1995; Zimmermann, 1996; Kienast et al., 1998; Pache et al., 1996).
- Periglacial phenomena (permafrost, gelifluction, cryoturbation) also affect plant distribution.
- Timberline is very likely growth-determined, with a lower thermal threshold defined by seasonal values of mean air temperature between 5.5 and 7.5 °C (Körner, 1998, 1999).
- Frequency of extreme climatic events (e.g., late frosts, avalanches) is an important factor determining timberline position.
- Winter snow cover is a key parameter for plants sensitive to frost, and for those requiring a low amount of heat for starting their development, for winter soil microbial activity and resulting carbon and nitrogen biogeo-chemical dynamics (Brooks et al., 1997; Williams et al., 1998), and for the activity of periglacial phenomena.
- Edaphic factors can locally compensate for climatic factors; soil may induce either a positive or a negative feedback loop in the response of plant to climate change.

Tertiary species (preglacial relicts) – have survived probably uninterruptedly *in situ* since the Late Tertiary, (e.g., Merxmüller, 1952–1954; Hantke et al., 2000; see also Stehlik, 2000; Stehlik et al., 2000). According to Scharfetter (1938), during the warmest interglacial periods, forests climbed higher towards the summits of low mountains (1800–2300 m), thereby reducing many high elevation orophyte populations. Many isolated orophytes now living in such refugia as the peaks of

low mountains in the Alps would also be threatened, because it would be almost impossible for them to migrate higher (to the present nival belt), either because they are unable to move there rapidly enough, or because the nival zone is absent (Grabherr et al., 1994, 1995; Gottfried et al., 1994). They include some endemics, i.e., plants indigenous to and restricted to a particular geographic region. With the help of fine-scale, local modelling at the nival belt, Gottfried et al. (1999) predict that some nival species will lose area and be more restricted with an increase of 1–2 K (see also Guisan and Theurillat, 2000). On average, most alpine and nival species could tolerate the direct and indirect (e.g., competitive exclusion) effects of an increase of 1–2 K (Körner, 1995; Theurillat, 1995), but not a much greater change (3–4 K; Theurillat, 1995; Theurillat et al., 1998).

Grabherr et al. (1994) published the first evidences of ongoing upward migration of alpine plant species in the Alps, including late successional species such as *Carex curvula* (Grabherr et al., 2001). The colonization over the last 60 years of the subalpine-alpine ecocline (i.e., the gradual change between the subalpine forest and the alpine swards and low heaths) by Arolla pine (*Pinus cembra*) at 2400–2500 m in the western Piemonte (Italy) is attributed by Motta and Masarin (1998) to recent warming. Similarly, Norway spruce (*Picea abies*) has colonized the subalpine-alpine ecocline (1850–1950 m) in Kärnten (Austria) for some 90 years, and in particular the last 60, according to Stützer (1999), who predicts an additional elevation of 50 m in the near future. According to Wagner and Reichegger (1997), moderate warming would favour an upward and northward colonization by two important sedges in the eastern Alps, *Carex firma* on limestone, and *C. curvula* on siliceous substrate (see also Section 2.2).

The present altitudinal range, distribution area, population size, conservation status (endangered/threatened or not), ecology (cool, wet *versus* dry, warm; light-exposed *versus* shady habitats), and genetic and phenotypic diversity, are thus primary parameters to take into consideration when assessing the general response of a species, or of a particular population, to climate change. Overall, species having a great potential for adaptive responses through genetic diversity, phenotypic plasticity, high abundance, or significant dispersal capacities are least at risk of extinction (Holt, 1990).

## 2.2. IMPACT ON POPULATIONS

Without taking other factors into consideration, moderate warming (1–2 K) may favour many species, in particular alpine species, by promoting seed production and seed size, as shown experimentally by Wagner and Reichegger (1997) for *Carex curvula* and *C. firma*. Preliminary results from Erschbamer (1999) on *Trifolium pallescens* show a similar tendency (see also Guisan and Theurillat, 2000). In general, moderate warming would be advantageous for late flowering species ('seed riskers'; Molau, 1993) such as *Saxifraga biflora* (Gugerli, 1997a), which could benefit from a longer growing season for seed maturation. However, this does not

hold for early flowering species ('pollen riskers') which would simply experience an earlier start to the growing season without further benefit. At the subalpine and alpine belts, milder winters or early springs are very likely to occur with warming, which can cause snow melt leading to a premature dehardening in plants, or a prevention of rehardening, especially if diurnal temperature is already high. For the blueberry (*Vaccinium myrtillus*), dieback may occur, as observed by Ögren (1996), and the alpenrose (*Rhododendron ferrugineum*) may undergo injury due to frost (Neuner et al., 1999). Although Tolvanen (1997) showed experimentally that the blueberry can recover vegetatively from occasional, moderate late frost injuries, he does not establish the result of several years of continual frost damage, which could be a more realistic consequence of early snowmelt because of climate change.

### 2.2.1. Persistence and Acclimation

Partial persistence is likely to occur where there are cryogenic processes and permafrost, steep slope, active, and unstable screes or cliffs. This is shown indirectly by monitoring the slow colonization on machine-graded ski runs (Delarze, 1994; see also Urbanska, 1995). The presence of ancient Tertiary relict species on montane and subalpine cliffs in the southern and south-eastern Alps, especially on limestone, is a well-known example of persistence. In addition, persistence may be facilitated by the great longevity (several tens to hundreds of years and more) of many alpine plants (especially clonal plants, i.e., plants that, through vegetative growth, form more or less extensive patches of modular parts), as e.g., 2000 years for the sedge *Carex curvula* according to Steinger et al., 1996, or several hundred years for alpenrose (*Rhododendron ferrugineum*) according to Pornon and Escaravage (1999) (see also Escaravage et al., 1998). Moreover, clonal plants, in particular with a 'phalanx' growth strategy (i.e., producing short internodes hence dense mats) can resist and outcompete invading species, e.g., alpenrose (see Pornon and Doche, 1994; Escaravage et al., 1998).

In the context of climate change, persistence of plant species through seed banking in the soil is rendered very unpredictable and unreliable. This is particularly so for rare species. Persistence is highly variable: it is species and habitat specific, later reestablishment is often disturbance-dependent, the species' pool may only partially reflect current vegetation, and species' frequency between the seed bank and present vegetation is often very different. The few studies available show that the diversity of the seed bank and the present vegetation in alpine and subalpine grasslands may be more or less in accord (Hatt, 1991; Erschbamer et al., 1999) or may be quite different (Diemer and Prock, 1993; Bernhardt, 1996; Prock et al., 1998; Urbanska et al., 1998). In species rich dry grasslands at lower elevation, many species cannot persist in the diaspore bank (Poschlod et al., 1998; see also Stampfli and Zeiter, 1999).

Phenotypic plasticity will determine the short term ecological response of species to climatic changes and, in some cases, might directly buffer the effect of such change. In this respect, one of the most important factors for high alpine orophytes

may be their potential to acclimate their respiration at night (dark respiration) to a higher temperature (see Larigauderie and Körner, 1995; Körner, 1995). For *Ranunculus glacialis*, Arnone and Körner (1997) showed that acclimation occurs for leaves.

### 2.2.2. Genetic Variability

In the past, glaciations lead to tremendous fragmentation of populations, and disappearance of species throughout the Alps. However, glaciations also generated rejuvenation and evolution of the Alpine flora. Populations of many cold-adapted Tertiary species, prevalingly diploid, were pushed downwards from high elevations. On the Alpine margins, especially in the eastern Alps, these populations were brought into contact with populations from other regions, such as the Balkans, under new ecological conditions, and hybridization occurred between these different biotypes of the same species or, more rarely, between species themselves (Ph. Küpfer, in litt.). This led to polyploidy (i.e., individuals having more than two sets of chromosomes as is the case in diploid individuals), which is considered to be a mechanism for rapid adaptation to new ecological conditions. At the end of glaciation, the newly formed, and better adapted polyploids get the chance to expand and colonize vast new territories (e.g., Küpfer, 1974; Stebbins, 1984; Favarger and Galland, 1996). At present, warming acts in the opposite way, i.e., increasingly it isolates high elevation populations. Although climate change can rapidly provide new ecological conditions, it is very unlikely, due to dispersal barriers, that different populations from low elevations could rapidly occupy the potentially available new territories at higher elevations, nor make contact in order to promote hybridization and new polyploids. However, for related species close enough to allow a successful hybridization, climate change may provoke an isolation of hybrids' habitat from parents' habitat, thus allowing evolution into distinct species by escaping parental back-cross (genetic isolation) and competition (ecological isolation) (Gugerli, 1997b).

Certain evidence suggests that strong selection like that induced by a climatic change may create very rapid genetic differentiation within plant populations (e.g., Theurillat et al., 1998). Genetic diversity is an important prerequisite for adapting to new environmental conditions. The present distribution of many regional endemic species has been explained by a genetic impoverishment which prevented a greater expansion (e.g., Niklefeld, 1972) (but see Section 2.2.3). According to recent results, observed genetic variation along an ecological gradient can result from selection, e.g., in *Picea abies* along an altitudinal transect in the Swiss Alps (Bergmann, 1978) or in *Anthoxanthum alpinum*, a widespread grass growing in the subalpine and alpine belts (Felber et al., 1997; Theurillat et al., 1998). For Norway spruce, Oleksyn et al. (1998) showed additional evidence for the existence of altitudinal ecotypes for several traits such as growth rate, biomass partitioning, needle nitrogen content, and rates of photosynthesis and respiration. In addition, the genetic diversity of a species itself can vary between distinct populations in separated

geographical areas of its range. For instance, populations of Norway spruce (*Picea abies*) in northern Italy show a lower genetic variability than those in Switzerland and south Germany (Müller-Starck, 1994). On the contrary, no significant variability is shown between populations of silver fir in Switzerland nor when they are compared with populations from glacial refugia in central Italy (Hussendörfer, 1997; see also Hussendörfer and Müller-Starck, 1994; Müller-Starck et al., 2000). However, silver fir shows clear local and regional differentiations, as a consequence of different environmental conditions, which could lead to an even greater differentiation under heterogeneous environments (Hussendörfer, 1997), thus possibly enabling this species to cope with climate change. In the same way, the arctic-alpine *Saxifraga cernua*, a rare, relictual species, shows no genetic variability either within or among the seven populations across the Alps although these populations present some genetic differentiation (Bauert, 1994; Bauert et al., 1998).

Furthermore, some species in submontane, semi-dry calcareous grasslands in the Jura range show a significant genotypic variation to CO<sub>2</sub> changes (Stöcklin et al., 1997, 1998), so that in the future species-specific responses to elevated CO<sub>2</sub> could differ from those observed today (see also Steinger et al., 1997; Stöcklin and Körner, 1999). On the contrary, Lüscher and Nösberger (1997) and Lüscher et al. (1997) found no intraspecific differences in the response to elevated CO<sub>2</sub> for six main species from permanent, managed lowland meadows.

### 2.2.3. Dispersal

During interglacial periods dispersal has always been a key issue for plants in order that they overcome natural barriers and move beyond their refugial areas ('massifs de refuge'), especially for regional endemics (e.g., Merxmüller, 1952–1954; Favarger and Galland, 1996). For instance, *Primula glaucescens* and *P. spectabilis* Tratt., two related, vicariant alpine endemic primroses on limestone in the south-eastern Alps, are very unlikely to expand their present, contiguous area, nor to come into contact because of lithological barriers and forest spread (Ravazzi, 1999). However, climatic factors, in particular the gradual change from east to west, contributing to competitive exclusion, have been opposed recently to historical factors and the pre-eminence of dispersal limitation in order to explain the restrictive present distribution in refugial areas of many regional endemic species during glaciation (Pils, 1995; Dullinger et al., 2000).

At the high alpine and nival belts, pioneer wind-dispersed species should be able to reach new sites at higher elevations, according to observations on moraines by Stöcklin and Bäumler (1996) (see also Erschbamer et al., 1999). However, according to Grabherr et al. (1994), the speed of upward progression may not be rapid enough to keep pace with warming. Certainly the very low seedling recruitment observed for some alpine and subalpine clonal plants, as monitored for *Carex curvula* (Grabherr, 1997) or the alpenrose (Pornon and Escaravage, 1999), makes it difficult to understand how these plants can occupy such vast areas other than by colonization following disturbance. The monitoring of machine-graded ski

runs, which show a lower species richness and a different density when compared to adjacent grasslands (Urbanska and Fattorini, 1998a,b; Urbanska et al., 1998, 1999), confirms the slow colonizing rate in the alpine belt. The hypothesis is that the limiting factor may be a very high mortality of seedlings because of the low occurrence of safe sites (Urbanska et al., 1988) as shown on glacier foreland by Stöcklin and Bäumler (1996) and Erschbamer et al. (1999). In dry grasslands at lower elevation there is substantial limitation to natural dispersion as well, and the availability of safe sites is also an important limiting factor (e.g., Stampfli and Zeiter, 1999).

In the Alpine landscape, natural dispersion is presently limited at lower elevation by forests, landscape fragmentation (roads, built-up areas) and changes in traditional agricultural land-use, such as abandonment of secular transhumance (Poschlod et al., 1998) which had replaced previous dispersion by wild animals. At the alpine and nival belts, at least for species which are not wind dispersed, natural dispersion is limited mainly by natural (e.g., orographical, geomorphological, lithological) barriers. However, one should not forget that man is responsible for the present distribution of many species, especially trees, and that this may prove to be an even greater factor in the future, especially at the timberline.

#### 2.2.4. Fragmentation

Fragmentation of population is of particular importance for endemics and orophytes. For these species, a marked fragmentation of their populations is to be expected, as a result of a decrease of the alpine and nival belts' surface area and due to an increase in steep slopes, as evidenced by Figure 1. Those distributed throughout the Alps would not be expected to disappear, nor would those inhabiting rock fissures in montane and subalpine zones. If they cannot persist or adapt, species showing a disjointed (north–south, east–west), or fragmented distribution may see their range become even more fragmented, with local disappearances. Some categories of plants would appear to be more vulnerable. For instance, isolated arctic relict species living only in a restricted range of habitats, e.g., which are pioneers in wet habitats may very well disappear since these habitats are very rare and many of them have already been destroyed by the implantation of artificial lakes for hydro-electric plants. Alpine endemics restricted to tops of low mountains (i.e., those lacking nival belts, mainly in the eastern and lower external Alps) or those distributed over a limited area because of pedological and/or lithological barriers (e.g., massive limestone) are likely to be severely endangered by extinction.

Even though largely distributed species or species living at lower elevations than orophytes, which are supposed to be able to move upward, may not risk disappearance through climate change, they may nevertheless face fragmentation of their populations, because of land use, which can lead to reduced fecundity and offspring performance, as Kéry et al. (2000) showed for *Primula veris* and *Gentiana lutea*, two common species of nutrient-poor calcareous grassland.



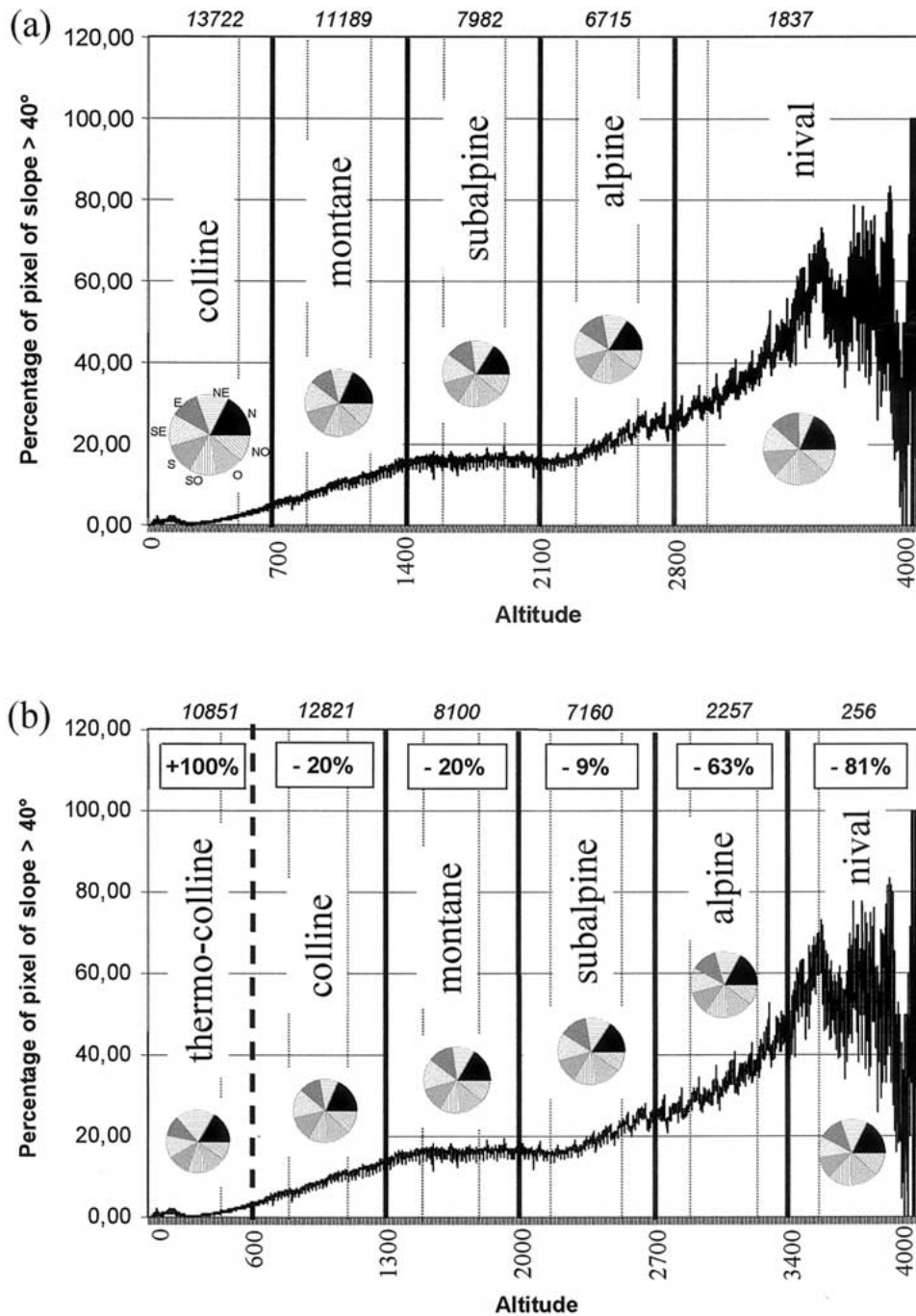


Figure 1. On dividing Switzerland into pixels of 25 m by 25 m, proportion of square kilometers of slope steeper or equal to 40 degrees as a function of elevation. Pie charts indicate the proportion of the height classes of slope orientation in each belt. (a) Vertical lines indicate limits of present vegetation belt along the elevation gradient. The total number of square kilometers in each belt is provided on top of the graph. (b) Displaced limits of vegetation belts, considering a +3.3 K annual mean temperature warming. Numbers in frames give, for each belt, the percent increase or decrease of surface area after the 3.3 K temperature rise. See Subsection 3.1 for details.

#### 2.2.5. Plant/Animal Interaction

By selectively reducing plant species' populations, herbivores also reduce plant dispersal potential, and consequently their ability to cope with climate change. In addition, selective pressure cannot always be taken into account in modeling. Herbivores can modify semi-natural ecosystems such as forests by selective pressure. This is presently the case in the Alps with the increase of red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) which, even at low density, selectively damage or browse silver fir (*Abies alba*) (Motta, 1996; Ammer, 1996). In the past, such selective pressure also occurred due to the pasturing of sheep and goats, which eventually lead to the regional or local disappearance of silver fir (*A. alba*) and the dominance of other species, especially Norway spruce (*Picea abies*) (e.g., Lingg, 1986; Ott et al., 1997; see also Subsection 4.2). The increase of atmospheric CO<sub>2</sub> is generally considered to produce a 'nitrogen dilution effect' (i.e., an increase of the carbon:nitrogen ratio) in plant tissue, which leads to increased grazing by herbivores seeking an equivalent amount of nitrogen. In alpine grasslands, if the selective pressure by grasshoppers on the dominant, slow-growing species *Carex curvula* increases, it may produce a replacement of the sedge by less palatable species (Blumer and Diemer, 1996). In experimentally investigated calcareous grasslands, no change was observed in herbivore pressure by snails and grasshoppers (Ledergerber et al., 1997, 1998) but a change was observed in feeding preferences for slugs (Peters et al., 2000).

Locally or regionally, warming in coming decades may weaken dominant species through severe defoliation due to pest outbreaks, and may alter their potential to respond to climate change. This is what happened to the web-spinning sawfly (*Cephalcia arvenis* Panzer) of the Norway spruce (*Picea abies*) in the Italian Prealps (Marchisio et al., 1994): Warmer and drier conditions occurred over several years, thus improving the quality of food (higher sugar level in the needles) while reducing the insect's mortality and speeding up its development. In the same way, pine shoot beetles (*Tomicus piniperda* L., *T. minor* Htg.) and other pests may strongly affect the extended Scots pine (*Pinus sylvestris*) forests in the Valais in combination with other factors, in particular drought (Rigling and Cherubini, 1999). On the other hand, warming in late winter and early spring followed by late frosts may break the recurring outbreaks of the larchbud-moth (*Zeiraphera diniana* Gn.) in the subalpine belt in the more continental regions, and therefore modify the present equilibrium between Arolla pine (*Pinus cembra*) and larch (*Larix decidua*) (Baltensweiler, 1993; see also Baltensweiler and Rubli, 1999; Weber, 1999).

Climate change and atmospheric CO<sub>2</sub> increase may affect the relation between plants and pollinators. According to Erhardt and Rusterholz (1997) and Rusterholz and Erhardt (1998), elevated CO<sub>2</sub> may affect flowering (time, number of flowers), nectar quality (amino-acids) and quantity of the rich meadows characteristic of intermediate elevations (montane, subalpine) and, as a consequence, detrimentally affect plant-pollinator interactions. However, pollinator insects are mainly temperature limited (degree days) and their upward shift with warming should not be a

problem as insects appear to be more sensitive than plants to climate change, and therefore react earlier (Hodkinsin and Bird, 1998).

#### 2.2.6. *Species Richness and Conservation*

With a warmer and drier climate, local species' richness may increase, as shown by Kienast et al. (1997) for Swiss forests using a GIS-based static comparative model at a resolution of 1 km. Identically, in modeling regional plant species throughout Switzerland, Wohlgemuth (1998) comes to the conclusion that regional richness is likely to increase with warming, especially in mountainous areas. Regionally and locally, physiography (e.g., slope, see Figure 1) will be the first factor in determining the distribution of many widespread species. Lischke et al. (1998) give an example using a static distribution model (see also Guisan et al., 1998) for the two dominant sedges *Carex curvula* and *C. sempervirens*, the former showing a marked decrease, and the latter a slight decrease only under a moderate climatic change scenario (+1.5 K). Using a simple conceptual model, Kienast et al. (1997, 1998) evaluated the potential for Swiss protected areas to host migrating species. Due to their limited altitudinal range, 40–50% of all reserves investigated would not constitute adequate refuges for a moderate warming (1–1.4 K), and 70–80% in case of a stronger one (2–2.8 K).

### 3. Potential Responses of Vegetation

#### 3.1. ECOTONAL SHIFTS?

One widespread hypothesis is that global warming will shift – in a more or less regular pattern – the climatic ranges of species (e.g., Peters and Darling, 1985) or even whole vegetation belts (e.g., Ozenda and Borel, 1991, 1995) upward along altitudinal, thermally defined gradients. Although a shift of a whole vegetation belt is hardly likely, one can nevertheless project an initial estimate of the potential range of change that is to be expected. For Switzerland, an increase of 3.3 K in mean air temperature, corresponding to an altitudinal shift of 600 m, would reduce on average the area of the alpine vegetation belt by 63% as shown in Figure 1. Interestingly, the colline and montane vegetation belts would be reduced on average by only 20%, and the subalpine vegetation belt by even less (–9%).

Yet, area is not the only point to take into consideration. In the assessment of vegetation shift, it should be remembered that physiographic factors, and especially slope, are not equally present at every elevation. As an example, the proportion of slopes steeper than 40° may play an important role because (1) they can hardly support a closed vegetation, (2) they may act as barriers to upward dispersal of species and (3) they can provide a refuge for the species which are able to withstand such harsh ecological conditions, by insulating them, to a great extent, from the general climate. As shown in Figure 1 for Switzerland, there is a marked increase in the percentage of slopes > 40° with increasing elevation, especially above 2300 m (alpine

and nival belts). Thus, when shifting upwards in elevation, species and community will not find equivalent surface areas with similar physiographic conditions. In this respect, the alpine belt will undergo the greatest change among all vegetation belts as, on dividing Switzerland into pixels of 25 m by 25 m, ca. one third of all pixels will have a pendency greater than 40° (Figure 1b) instead of ca. one fifth at present (Figure 1a). Conversely, the subalpine belt will be less affected, with only a few percent increase of slopes steeper than 40°. Overall, this would lead to a marked decrease of communities bound to low pendency, like snowbed communities, some types of swards, as well as alpine fens, mires and springs. Interestingly, orientation (slope aspect) appears, globally, to be distributed equally throughout all vegetation belts, be they the current or the shifted belts. A closer look at Figure 1 shows that there are differences between belts, but that there is no clear trend. When orientations are separated into southern (SE, S, SO) and northern groups (NO, N, NE), slight differences appear. At present (Figure 1a), there is almost no difference in the percentage between northern and southern orientations in each belt, with the highest difference (8%) for the colline belt (41% vs. 33%) and no difference for the nival belt (each 35%). With the 3.3 K scenario, there will be a slight increase in the northern vs. southern orientations for the alpine belt (39% vs. 32%) and in the nival belt (42% vs. 31%). For the new, emerging thermo-colline belt, the difference will be a little greater between northern and southern orientations with 47% and 30% respectively. Therefore, orientation may not generally affect the upshifting of vegetation and flora. However, this should be examined on a finer regional scale, especially in the external calcareous Alps where the orientation of the geological layers can contrast regular, gentle southern slopes with abrupt northern slopes. In addition, the nature of the layers (soft marl vs. hard limestone) and the variation in their sequence and thickness will play a role in the response of flora and vegetation (Theurillat et al., 1998).

As a result, today's alpine belt would show a mosaic of subalpine elements (isolated *Arolla* pine, fragments of heaths and of swards) in the warmest and most stable places, and alpine elements in the coldest and most unstable ones. In turn, part of the present high alpine vegetation would have to shift into the upper nival belt, where such a belt exists. For the treeline to expand upslope, even where it has been artificially lowered by man, it would be necessary for a significantly warmer climate to last for at least 100 years (Holtmeier, 1994a,b). This is because on the treeline, extreme conditions, as well as edaphic and topographic factors already prevail, as in the alpine vegetation belt, and the establishment and growth of trees occur under harsh topoclimates (e.g., Holtmeier, 1994a,b).

For phanerophytes, (i.e., woody plants – trees, shrubs – which have surviving organs located more than 50 cm above the soil level), the subalpine-alpine ecocline (or 'kampfzone') represents a temperature-related boundary whose inertia compensates both positive and negative variations of climate, preventing a linear variation of the forest-limit (see Körner, 1998, 1999). Palynological and macro-fossil studies show that the forest limit did not climb more than 100–300 m

during the warmest periods of the Boreal and Atlantic periods of the Holocene (the Atlantic, 6000–5000 BP, was the warmest period of the Holocene) (e.g., Burga, 1988, 1991; Bortenschlager, 1993; Lang, 1993; Tinner et al., 1996; Wick and Tinner, 1997). Based on the general consensus that the mean annual temperature during these periods was 2–4 K higher than today, the forest limit could have been expected to climb 350–700 m higher (considering a decrease of 0.558 K per 100 m elevation), thus reaching the high alpine belt, in obvious nonconformity with palynological observations. Interestingly, however, these elevations match recent pedomorphological observations (i.e., of soil charcoal) on larch (*Larix decidua*) and Arolla pine (*Pinus cembra*) in the south-western Alps (Carcaillet et al., 1998; Carcaillet and Brun, 2000; Talon, 1997; Thinon and Talon, 1998). The apparent contradiction between the two results might be clarified by considering that charcoal of ‘trees’ from the alpine belt are very likely those from ‘krummholz’, i.e., gnarled, stunted trees or shrubs 0.5–8 meters in height (nano- and microphanerophytes), which rarely or never produce pollen under the conditions of the alpine belt. This could explain the absence of Arolla pine from alpine pollen profiles (Theurillat et al., 1998).

Therefore, an increase of 1–2 K in mean annual temperature may not shift the present forest limit upwards by much more than 100–200 m. In this respect, recent observations on the variation of solar activity and brightness (Parker, 1999) could uphold the 1–2 K thermal inertia of mountain ecosystems, as it quantifies the effect of temperature change due to periodical solar variation. Even greater inertia can be observed in edaphic climax vegetation. For instance, no change was observed in the subalpine belt in the contact zone between Scots pine (*Pinus sylvestris*) and Arolla pine (*P. cembra*) despite an increase of 0.8 K of the mean summer temperature over 30 years (Hättenschwiler and Körner, 1995; Körner, 1995). In such a context, avalanches, snowslips and snowcreep play a very important part. Although mean air temperature has increased consistently by about 1 K over the last 50 years, no long-term trend in change in snow depth nor in extreme snowfall has been observed during the century at high elevation in the Swiss Alps. Therefore, the number of destructive snow avalanches has not decreased (Schneebeili et al., 1997). Yet, over the same period, Beniston (1997) showed that periods with low snow accumulation and duration in the Swiss Alps are linked to the presence of high surface pressure fields from late fall to early spring over the Alps bringing mild winters with little snow which significantly affect regions up to 2000 m asl. These high pressure periods are strongly correlated with a positive and high North Atlantic Oscillation index. Thus, it is not regional factors which determine the amount of snow in the Alps, but large scale forcing, hence the influence of climate change.

However, it is inconceivable that the inertia of the temperature-related forest limit, either climatic or edaphic, will withstand a 3–4 K increase, which is equal to the temperature range of an entire vegetation belt. With such an increase, the ‘kampfzone’ would be very likely to invade the alpine belt, with a consequent shift of the forest limit into the low alpine belt. If a temperature increase of more than

2 K persists for several centuries, it is possible that forests could develop at even higher elevations than those observed since the last glaciation.

### 3.2. CHANGES IN THE COMPOSITION OF THE VEGETATION

In their response to climate change, climatic climax plant communities (i.e., zonal vegetation) and edaphic climax plant communities may behave differently (Theurillat et al., 1998). For climatic climax communities, new plant communities are likely to develop and, partially or totally, replace present ones (e.g., Tallis, 1991; Theurillat et al., 1998). However, provided that there is no immigration of new species, and if rapid dispersion of new invaders is limited, the species' pool should not be very different and plant communities should still belong to the higher phytosociological classification units (alliances, orders, classes) known for the Alps, in particular in the montane belt and above. Physiographic and edaphic factors will still play a determinant role (regionally and locally). For instance, a climatic community may persist in places with suitable edaphic conditions, and so withstand the new climate as an extrazonal, edaphic climax. In the alpine belt, it is very likely that plant communities on moderate slopes (e.g., snowbeds with *Salix herbacea*, alpine swards with *Carex curvula*) would shrink, or even disappear in some places. For edaphic climaxes, plant communities could sustain a climatic change provided that their limiting factors were not modified.

Brzeziecki et al. (1995) and Kienast et al. (1995, 1996, see also 1998) provided an estimation of change for Swiss forests with a Geographic Information System-assisted sensitivity model. For 1–1.4 K increase in temperature, 30–55% of the forested pixels of Switzerland would show a change of classification types. This figure reaches 55–89% with an increase of 2–2.8 K. Analysis of the adaptation potential for the dominating tree species with a diameter at breast height 12 cm shows an increase of poorly adapted pixels from 25–30% in today's situation, to 35–60% for the 2–2.8 K scenario. However, this is reduced to 8–15% for the 2–2.8 K scenario when trees with a diameter < 12 cm are included in the analysis.

Forests found in the colline to subalpine belts will respond to climatic change according to predictions of both dynamic, temporally explicit models (e.g., Kräuchi, 1994; Fischlin et al., 1995; Fischlin and Gyalistras, 1997; Lischke et al., 1998) and static, spatially explicit models (Kienast et al., 1995, 1996, 1997, 1998). Both approaches predict a shift of montane forests, dominated by deciduous trees, toward a higher elevation, which would force subalpine coniferous forests to shift into the alpine belt. However, according to the ForClim dynamic gap model (e.g., Bugmann, 1999; Fischlin and Gyalistras, 1997; see also Fischlin et al., 1995; Lischke et al., 1998), some subalpine forests, such as the Arolla pine-larch forest (*Pinus cembra*, *Larix decidua*) in continental parts of Switzerland, appear to be very sensitive to climate change, showing unexpected new trees combination under climate change, and can even experience a catastrophic change through competition. According to static modeling, it is expected that beech-dominated forests

(*Fagus sylvatica*) would be replaced by oak-hornbeam forests (*Quercus robur*, *Q. petraea*, *Carpinus betulus*) in the colline-submontane belt in the northern Alps; in the southern Alps, changes are less likely to occur due to mitigation of the temperature increase by an increase in precipitation. Yet, recent findings showing the preponderance, in the past, of silver fir (*Abies alba*) in the colline and low montane belts, before being eliminated by early human activities, especially fire, around 5000 BC (Tinner et al., 1999, 2000; see also Gobet et al., 2000), give new insights on forest potentiality at these elevations under the humid Insubrian climate. Interestingly, dynamic models predict an increase of silver fir in the northern Alps, from colline to low subalpine belt (Bugmann, 1999). In the southern Alps, however, the invasion in recent decades of the understorey of thermo-colline oak-chestnut forests by naturalized exotic laurophyllous species, i.e., with leaves of the laurel type ('laurophyllisation') will gain ground and replace the present tree layer (Gianoni et al., 1988; Klötzli et al., 1996; Walther, 1999, 2001, in press; Carraro et al., 1999). In a less humid climate, the present Mediterranean-type vegetation in the warmest areas of the lowest elevations of the southern border of the Alps may very likely expand, particularly on limestone. In the dry, continental part of the Alps, dynamic modeling predicts that the colline downy oak forest (*Quercus pubescens*) may be severely affected by drought. However, these results should be accepted with reservation, as models, in particular dynamic models, do not include parameters of potential adaptation or acclimation such as change in reproductive success, growth forms, genetic variability, chilling effect or dark respiration, nor parameters such as forest management coppice, pest outbreaks, selective pressure or dispersal or species sensitivity to fire. Moreover, parameterization of temperature response at the warmer range limit has been criticized (Loehle, 1998; see also Bugmann, 1999). According to Loehle, it is unlikely that there will be a sudden dieback if net moisture stress remains constant (see also Subsection 4.1; Keller et al., 1997).

### 3.3. STRUCTURAL CHANGES IN VEGETATION

As regards the dynamic change of communities, it is unlikely that every component will change simultaneously. In addition, the upper (northern) and lower (southern) limits of a species are generally not limited by the same ecological factors. For colline to subalpine species, especially trees, temperature is often the limiting factor at the upper limit, and moisture at the lower limit (see Sholes, 1994). For many alpine species, light is very likely to be an important limiting factor through competition with taller plants, as Guisan et al. (1998) showed for the alpine sedge *Carex curvula*. Therefore, one of the first effects of warming will be to modify competitive relationships between plant functional types, i.e., species grouped according to some of their functional traits (mainly life-forms). For instance, at the lowest elevations, sclerophyllous, i.e., having tough, persistent leaves, or laurophyllous phanerophytes in the understorey may overrun the

deciduous tree layer (see Subsection 3.1). In the subalpine belt, deciduous trees may overrun coniferous ones. And finally, in the alpine belt, chamaephytes (i.e., plants which have surviving organs lying close to the ground up to 50 cm) may overrun hemicryptophytes (i.e., plant which have surviving organs lying at the soil surface), and low shrubs may overrun chamaephytes in subalpine-alpine heaths. Also, not all structural components of plant communities will be modified at the same rate. In particular, some of them could persist in new communities as long as the conditions of their microhabitats (especially humidity) are not substantially modified. This could be the case for some shade tolerant herb synusiae or for mosses synusiae. (A synusia is a functional unit within a distinct layer of a plant community composed of plants of similar requirements.) In the subalpine and alpine belts, structural differences between different types of heaths and different types of swards (Schlüssel and Theurillat, 1996; Schlüssel, 1999) might lead to differential ecosystems responses. Thermophilous heath ecosystems, with their gradually intergrading dominant synusiae along an elevation gradient, exhibit a better adaptation to warming than the mesophilous heath ecosystems with their uniform, dominant synusiae along the same gradient. The former appear better adapted to warming than the latter, which depend primarily on the duration of the snow cover period and would be unable to endure its reduction.

In addition to climate, an increase in CO<sub>2</sub> concentrations is likely to produce structural changes in vegetation through differential response between species. For alpine swards dominated by the sedge *Carex curvula*, Schächli (1996) found that an elevated CO<sub>2</sub> concentration is going to decrease the sedge's competitive performance by reducing tiller density and by stimulating the population growth of dominant forbs (*Leontodon helveticus*, *Trifolium alpinum*). An increase in CO<sub>2</sub> concentration and nitrogen deposits would also modify the distribution and dominance of species in Norway spruce-forest understorey (Hättenschwiler and Körner, 1996, 1997). In particular, CO<sub>2</sub> may compensate for low light, allowing fewer shade-tolerant species to develop in shady habitats, whereas nitrogen deposition may enhance the growth of shade-tolerant species. According to Hättenschwiler and Körner (1997), 'past increases of atmospheric CO<sub>2</sub> concentration and N deposition have already induced shifts in species composition in spruce-forest understorey communities'. Recent investigations show that semi-natural, submontane semi-dry calcareous grasslands in the Jura range exposed to elevated atmospheric CO<sub>2</sub> concentration exhibited an indirect increase in soil moisture as well as differential species' responses in biomass, and thus in vegetation structure (Stöcklin et al., 1998; Leadley et al., 1999; see also Leadley and Körner, 1996; Lauber and Körner, 1997; Rötzel et al., 1997; Stocker et al., 1997; Niklaus et al., 1998a,b; Volt et al., 2000). Increase in soil moisture, together with increased C input to soil, will promote microbial activity which will in turn release N<sub>2</sub>O (nitrous oxide), a potent greenhouse gas (Arnone and Bohlen, 1998). Therefore, increasing atmospheric CO<sub>2</sub> may generate a positive feedback loop in such grasslands, thus intensifying the estimated warming due to greenhouse effect.



According to experimental investigations (Bungener et al., 1999a,b), tropospheric ozone may also promote a differential species' response in grasslands both for foliar injuries and biomass. For instance, some species are adversely affected (less biomass) at low ozone concentration (e.g., *Trifolium repens*), some are favoured (more biomass) when ozone concentration is increased (e.g., *Bromus erectus*), some only up to a certain point (e.g., *Trisetum flavescens*), and some appear to be insensitive (no change in biomass) (e.g., *Arrhenatherum elatius*). In addition, foliar injuries vary with humidity. Some species show more injuries under humid conditions (e.g., *Trifolium repens*, *T. pratensis*, *Trisetum flavescens*), a few species under dry conditions, like *Arrhenatherum elatius*, and others show no difference (e.g., *Dactylis glomerata*). High levels of tropospheric ozone will also negatively affect forests at low elevations in the foothills of the southern Alps, especially in north Italy and in Ticino, provoking an early senescence of leaves and eventually the death of the most sensitive individuals as well as a genetical impoverishment of populations (Cherubini and Moretti, 1999; see also Fuhrer et al., 1997).

#### 4. Changes in Growing Season, Ecosystem Productivity and Growth

##### 4.1. PHENOLOGY AND GROWING SEASON

Phenology offers promise as a tool for assessing climate change's impact on plant growth and development, and many studies have been carried out recently with this aim in mind (e.g., Diekmann, 1996; Fitter et al., 1995; Molau, 1996; see also Moore, 1995). Analysing data from the International Phenological Gardens, a network covering Europe from Macedonia to Scandinavia (42–69° N) in latitude and from Ireland to Finland (10° W–27° E) in longitude, Menzel and Fabian (1999) come to the conclusion that since early 1960 the average annual growing season has lengthened by 10.8 days (six in spring, 4.8 in autumn), and that this change is the result of an increase in the mean air temperature. According to Houghton et al. (1992), during that time the mean annual surface temperature over the northern hemisphere increased by 0.5–0.6 K. Interestingly, 100 m of elevation results in a difference of 0.55 K and, according to Schröter (1923–1926), in a difference in the growing season, on average, by nine days over the year (six in spring and three in autumn). These figures are very close to the prolongation observed by Menzel and Fabian (1999) and the annual temperature increase over the northern hemisphere. The timing of budburst is an important phenological event, often involving low temperatures (chilling effect) for breaking winter dormancy in spring, but also for inducing it in the autumn. For three important low elevation species: vine (*Vitis vinifera*), downy oak (*Quercus pubescens*) and chestnut (*Castanea sativa*), Chuine and Cour (1999) show that the summer temperature of the previous year does not affect budburst in the following spring.

## 4.2. GROWTH AND PRODUCTIVITY

Warmer and wetter conditions are very likely to increase productivity and biomass formation (e.g., Menzel and Fabian, 1999). Yet, changes in productivity cannot be dissociated from eutrophication and the 'fertilization effect' of increasing atmospheric CO<sub>2</sub> (e.g., Melillo et al., in Houghton et al., 1996) nor the opposite effect of stratospheric ozone (e.g., Fuhrer et al., 1997; Ashmore and Marshall, 1999).

### 4.2.1. Grasslands

Modeling the productivity of managed grasslands in the Swiss Alps, (Riedo et al., 1997a) showed that, with a doubling of CO<sub>2</sub> concentration, an increase of temperature (2 K) and of precipitation, both downscaled to a regional level, net primary production would increase 20–70%. However, different management styles (e.g., grazing vs. cutting) as well as regional differences should be taken into account (Riedo et al., 1997b, 1998). Such an increase of primary production would probably have an impact on land use (next section). For subalpine mires, warming may increase the growth rate of peat mosses (e.g., *Sphagnum capillifolium* (Ehrh.) Hedw.) as shown by Gerdol et al. (1998), providing that there is no drawdown of the water table, for instance due to a decrease of precipitation or an increase of evapotranspiration. In the alpine belt, four seasons of *in situ* CO<sub>2</sub> enrichment on a *Carex curvula* sward in the Swiss Alps have shown that an increase in the productivity of alpine swards may not be forthcoming (Schäppi and Körner, 1996; Diemer, 1997; Körner et al., 1997; Diemer and Körner, 1998), even for a symbiotic N<sub>2</sub> fixing species like *Trifolium alpinum* (Arnone, 1999). However, litter quality and decomposition rate for *C. curvula* decreased (Hirschel et al., 1997).

### 4.2.2. Trees

In a non-linear transfer function, explorative modeling studies of radial tree growth using Artificial Neural Networks based on ten sites in southern Alpine and Mediterranean France, Keller et al. (1997; see also Tessier et al., 1995; Keller et al., 2000) show that only larch (*Larix decidua*), at its upper distribution, and Scots pine (*Pinus sylvestris*), at its lower Mediterranean distribution, may be affected by a 2–3 K increase of mean annual temperature and moderate precipitation increase if the temperature increase occurs mainly during winter (February). Larch will increase its radial growth with higher temperatures, and Scots pine will reduce it because of water limitation. Interestingly, other populations of larch at a lower, subalpine elevation may not react because temperature is less of a limiting factor at lower elevation. A comparative study of the radial and apical growths of Norway spruce (*Picea abies*), larch (*Larix decidua*), Arolla pine (*Pinus cembra*) and mountain pine (*P. mugo* subsp. *uncinata*) at the upper subalpine belt on two aspects (north and south) and two substrates (calcareous and siliceous) in four climatically different regions of the French Alps (oceanic to continental), Rolland et al. (1998) shows that radial growth has increased significantly since the middle of the 19th century and

is clearly linked to a warmer climate, although each of the four species has its own growth strategy (Petitcolas et al., 1997). Radial growth appears to be similar for Norway spruce and Arolla pine, the strongest growth for all species being under the more oceanic, colder climate and then varying according to species, aspect, substrate and climate, being greater for Norway spruce and Arolla pine on southern aspect and siliceous substrate, and being less dependant in this respect for larch and mountain pine (see also Badalotti et al., 2000). Apical growth is higher on northern aspect and calcareous substrate. Although these results should be treated with caution, because of the limited number of sites studied and especially because of the dominant sampling strategy used (see Cherubini et al., 1998, 1999), they nevertheless show the importance both of the general and regional climate, in particular hygric continentality, on tree growth and forest ecosystems and consequently the potential impact of climate change. Another study (Desplanque et al., 1999) on Norway spruce (*Picea abies*) and silver fir (*Abies alba*) in the same region confirms that radial growth is limited by both climatic and environmental factors, with climate being the main factor, in particular summer temperature, at the subalpine belt, and drought at lower elevations. For silver fir, critical factors are especially drought in May (i.e., the growing season) and in August of the previous year, warmth in April and September, and cold in February and November of the previous year (Rolland et al., 1999; see also Bert, 1993). In the most continental region of the French Alps, detailed investigations on mountain pine (*P. mugo* subsp. *uncinata*) by Rolland and Schueller (1996) (see also Schueller and Rolland, 1994) reveal that tree-ring growth is limited by low precipitation or high temperature (hygric stress), especially in June, and in August and September of the previous year, but also by the environmental factors such as elevation (i.e., growing period), substrate and aspect, the influence of climate being stronger at low elevation, on calcareous substrate, and on southern aspect. Other investigations on tree-ring growth at the montane and subalpine belts confirm that tree growth benefits from warmer temperatures in autumn to form late wood in mountain pine (*Pinus mugo* subsp. *uncinata*), Scots pine (*P. sylvestris*) (Camerero et al., 1996, 1998; see also Rolland and Schueler, 1995) and Norway spruce (*Picea abies*) (Gindl, 1999). Monitoring growth (cumulative height and diameter) of Arolla pine (*Pinus cembra*) over 25 years in experimental plots (afforestation) on a south oriented slope at the subalpine belt in the Austrian Alps showed that growth is positively related to the length of the growing season, and negatively to wind speed, especially at the highest elevation (Kronfuss, 1994; Kronfuss and Havranek, 1999). Another experimental afforestation carried out over 20 years on the timberline in the Swiss Alps confirms the preceding results for growth (height) of Arolla pine, and shows that mortality through an infection by *Ascolyx abietina* Lagerb., a parasitic fungus and the major factor of mortality, was positively related to the duration of snow cover. However, mortality, to a lesser extent, due to another fungus, the snow blight (*Phacidium infestans* Karst.) was negatively related to the duration of snow cover.

On the contrary, larch (*Larix decidua*) showed a much higher survival rate than Arolla pine.

200 years of observation of the tree rings of the Arolla pine in the Austrian Alps reveal that their width has increased over the last 100 years, possibly related to a CO<sub>2</sub> increase rather than to temperature according to Nicolussi et al. (1995; see also Körner, 1995). For Norway spruce (*Picea abies*), an increase of CO<sub>2</sub> would be unlikely to improve productivity on poor soil, but in all likelihood a rise in nitrogen deposits would be beneficial (Hättenschwiler and Körner, 1997). According to Overdieck (1996), the biomass of beech (*Fagus sylvatica*) is unlikely to increase with increasing CO<sub>2</sub>, but that of sycamore maple (*Acer pseudoplatanus*) may do so. However, beech will respond differently according to the substrate, with biomass increasing on calcareous soils but not on acid soils with elevated CO<sub>2</sub>, an increase in biomass on acid soils occurring only with increased nitrogen, which has no effect on calcareous soils (Egli and Körner, 1997; Maurer et al., 1999).

## 5. Changes in Landscape and Interaction with Human Activity

Landscape may respond very noticeably and differentially to climate change as it integrates all ecological and historical factors. In natural landscapes, differential responses may be observed within the same region, as shown by pollen profiles from the foothills of the northern Alps in southern Bavaria (Küster, 1990). The arrival of Norway spruce (*Picea abies*) was delayed by as much as 700 years between three sites only three kilometers apart, with no physical barrier between them. Significant delay also occurred later during the expansion of European silver fir (*Abies alba*) and beech (*Fagus sylvatica*). However, landscape has been strongly defined by human activity for millennia in the Alps. In such a cultural landscape, the response of vegetation to climatic change may be very different when the effects of anthropic factors are taken into account (e.g., Di Castri and Hansen, 1992; Grime, 1993). In this respect, land use is a very important factor which may either accelerate (afforestation, discontinuing grazing, eutrophication) or counteract (traditional use) vegetation's response to climate change (Theurillat et al., 1998; see Subsection 2.2.3).

In the Alps, landuse started as early as the Atlantic period with burning and pastoral activities, even in the high alpine zone (e.g., Theurillat et al., 1998). This led to modification of species' distribution and diversity, and of the vegetation in general. For instance, during Roman times, selective cutting of silver fir (*Abies alba*) for timber significantly reduced populations in several parts of the Alps but fir recovered afterwards (Küster, 1994; Nakagawa et al., 2000). In the Romanche valley, in the north-western Alps, a second deforestation phase occurred in the 5th and 6th centuries when silver fir and beech (*Fagus sylvatica*) were non-selectively exploited. At that time, fir did not recover. In the 12th century a third deforestation occurred and this time beech did not recover (Nakagawa et al., 2000). Intensific-

ation of forest use and grassland expansion took place in the medieval period up to the end of the 19th century (e.g., van der Knaap et al., 2000). Yet, grassland expansion at the expense of forest was beneficial for many species, in particular orophytes in the alpine belt (e.g., Ravazzi, 1999). According to Wiersema (1989), the lowering of the upper limit of the forest extended the habitat of the ibex (*Capra ibex* L.) downslope and greater grazing pressure may have helped to extend the area of high alpine swards at the expense of low alpine heaths. Therefore, extensive grazing of alpine swards over millennia played a significant role in shaping the distribution of plants and plant communities of the subalpine-alpine ecocline.

From the middle of the 20th century, important changes occurred in traditionally managed meadows, especially in the southern and central Alps (e.g., Studer-Ehrensberg, 1995). Many traditionally mown or cattle-grazed montane grasslands were (1) either abandoned, leading to their disappearance through invasion by shrubs and trees, or (2) subjected to higher selective pressure through sheep pasturing, which leads to a substantial decrease in the diversity of sensitive species and an increase in unpalatable ones such as *Brachypodium pinnatum*, a clonal plant (e.g., Stampfli and Zeiter, 1999; see also Ellenberg, 1996; Schläpfer et al., 1998), or (3) intensively fertilized and/or more frequently cut, leading to strong decrease in plant species' richness (e.g., Stöcklin et al., 1999; Gigon, 1999). Leaving certain lands fallow due to an increase in grassland productivity may also affect landscape, although e.g., Swiss farmers today report that they would not abandon such land, but use it more extensively for milk, or find an alternative use for it (Riedo et al., unpublished). In the upper subalpine belt, declining grazing pressure is speeding up the recolonisation of pastures and formerly pastured larch forests by Arolla pine (*Pinus cembra*), as observed by Holtmeier (1994b) in Engadin (Switzerland) and Motta and Masarin (1998) in the western Piemonte (Italy), and by Norway spruce (*Picea abies*) in Kärnten (Austria), as observed by Stützer (1999).

Physically, the Alpine landscape will change with the advent of warming as glaciers may shrink within decades, and the permafrost limit may rise by several hundred meters leading to increasing instability of frozen slopes at high elevations thus generating more screes, stone-falls and landslips, and also affecting water cycles (Haeberli and Beniston, 1998). With global warming, however, it is very likely that settlement and all other kinds of human activities, especially recreational ones, will continue to increase, in both the upper subalpine and the alpine zones.

## 6. Conclusion

'Rapid climate change could not be happening at a worse time' (Soulé in Peters and Lovejoy, 1992), because ecosystems have already been profoundly modified and even destroyed by other factors of global change, mainly land-use and eutrophication, key elements in the decrease and modification of biodiversity everywhere. These are very likely to become even more wide-spread in the near future (e.g.,

Matson et al., 1997; Nobel and Dirzo, 1997). Hence, even if high mountains such as the European Alps appear to evince a natural inertia and thus to tolerate a climate change of the order of 1–2 K as far as plant species and ecosystems are concerned, the impact of land-use (especially afforestation, grassland management, urbanization) is very likely to negate this buffer in many areas. Thus, the perpetuation of traditional land-use is a key factor to offset climate change over the following decades in order to preserve species' diversity and sensitive ecosystems. Yet, climate change is expected to be of the order of 3 K or more over the century or so and such an increase prevents an accurate assessment by expert knowledge or modeling. Obviously, no land-use can compensate for such a major change, (the equivalent of a whole vegetation belt moving upwards), and restoration ecology could only intervene selectively. Therefore, deeper understanding is needed on key issues if we are to improve our comprehension and modeling. These key issues are persistence, acclimation and dispersal of rare, dominant, keystone or flagship species, taking into account limitation by factors other than climate and main regional differences. Although the European Alps are certainly the most studied of all the high mountain ranges in the world, long-term observations on vegetation and species' distribution are rare. Moreover, there are no comparative surveys covering the Alps. Therefore, long-term comparative monitoring and experimental manipulation, including land-use, should be rapidly developed. Such actions will provide data on composition and structural changes, growth, and productivity of important vegetation types, especially extensively used ecosystems, for example, subalpine and alpine grasslands and heaths, as well as sensitive habitats.

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