5

Sensitivity of Plant and Soil Ecosystems of the Alps to Climate Change

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5.1 CLIMATE AND VEGETATION

Climate is a major determinant of the distribution of ecosystems on earth (e.g., Woodward 1987), as the latitudinal zonation of the vegetation biomes, such as evergreen rain forest, boreal forest, and tundra, as belts or zonobiomes from the equator to the poles illustrates. Climate fundamentally influences the distribution of both plant species and vegetation (e.g., Walter 1984, 1985; Walter and Breckle 1991; Ellenberg 1986, 1988, 1996). In high mountains, climate influences not only ecosystems' latitudinal distribution but also their altitudinal distribution. Indeed, altitudinal zonation characterizes the vegetation of all high mountains that form separate biomes, called orobiomes, that occur within the zonobiomes. Thus, an orobiome consists of all the vegetation zonation from the bottom to the top of the mountain range. The gradual decrease of mean air temperature with increasing altitude (0.55 K per 100 meters' elevation at middle latitudes) is about 1,000 times steeper in Europe and northern Asia (about 1 K per 200 kilometers) than the latitudinal decrease toward the poles (Walter 1984, 1985). This is half the gradient predicted for North America by Hopkin's law (MacArthur 1972). Hence, vegetation belts of orobiomes are 500 to 1,000 times narrower than the vegetation zones of zonobiomes, and a modest change in mean annual air temperature may significantly affect the altitudinal distribution of plants and vegetation (e.g., Halpin 1994a, 1994b; Ozenda and Borel 1991, 1994). Projections for global warming by the latter half of the next century should modify biomes' present ranges. According to Halpin (1994a, 1994b), high mountain systems such as the European Alps are likely to be particularly vulnerable to climate change, and this may have severe biological and economic consequences.

Considering the biological and socioeconomic importance of both the forests and the alpine zone of the Alps, several questions should be addressed concerning global warming's potential impacts:

- To what extent is climate influencing these ecosystems?
- In what ways are these ecosystems likely to respond to climate change?

- How may different components of these systems respond?
- What will be the rate of change and the limits of response of these ecosystems and their different components?
- What will be the mechanisms of response?
- How can we best assess the impacts of climate change on forests and alpine ecosystems?

It is an exceedingly complex task to assess climate change's potential impacts on ecosystems. More fundamental research is required before a reliable evaluation of the major trends can be made. Still, the defining features of the subalpine-alpine ecocline (i.e., relatively unmodified, marked visual difference between the upper subalpine forests and alpine meadows) make it a useful system for studying climatic change's potential impact on mountain ecosystems. This raises a further question: Is it possible to find markers in the biosphere and the pedosphere to monitor the evolution of climate change's impact on ecosystems?

A comprehensive review of the sensitivity to climate change of the diverse range of ecosystems in the Alpine region is beyond the scope of this chapter. For this reason, we focus mainly on the potential response of soil ecosystems and the alpine zone to changed temperature and precipitation regimes predicted for the coming century. Other important aspects of global change (enhancement of atmospheric CO_2 concentration, eutrophication, acidification, increase in UV-B, changes in land use) will be mentioned only where they interact synergistically with climatic factors.

Here we analyze the potential response of plants of the alpine zone to climate change, using published literature and studies in progress at two sites in the Alps of the Valais, where soils and vegetation (bryophytes, vascular plants) are being investigated at several levels of complexity. These studies are referred to as the "Ecocline project." Figure 5.1 renders the organizational levels and interactions considered in the Ecocline project.

In this chapter, we

1. briefly review the biodiversity of bryophytes and vascular plants in the European Alps
2. outline the main ecological and biological factors prevailing for both soils and vegetation in the subalpine and alpine zones of the Alps, emphasizing the importance of climatic factors
3. present an integrated assessment, based on examples from the past, of how alpine ecosystems may respond differentially to climate change and what the consequences of this may be for biodiversity.

Exploration of these points is coupled with a summary of key assessments of vegetation and soil ecosystems' response to climate change. The chapter concludes by proposing an integrated vision about the paradigm of species' individual response.

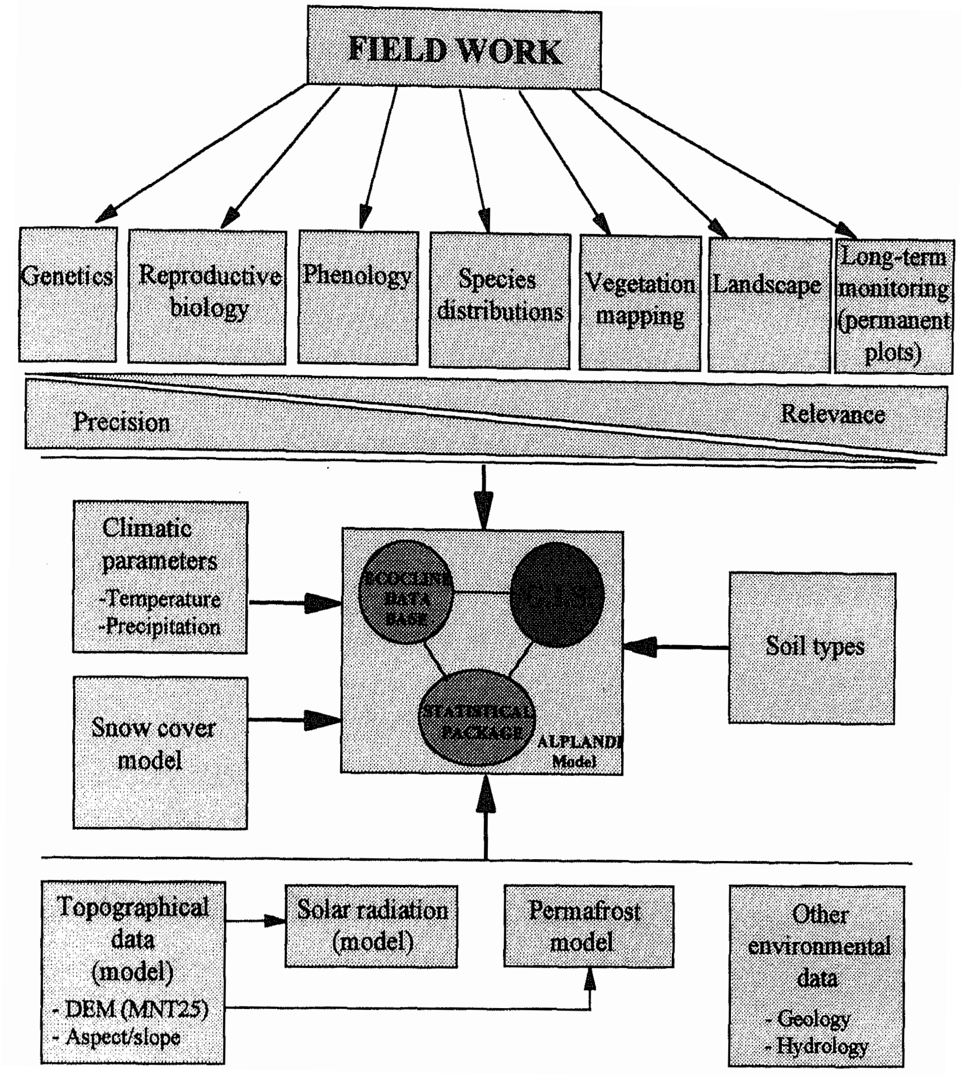


Figure 5.1 Domains and organizational levels of the biosphere in relationship to the fields of study, methods of investigation, and timescale. Relevance increases with both spatial scaling-up and time. Precision increases in the opposite direction.

5.2 THE DISTRIBUTION OF BRYOPHYTES AND VASCULAR PLANTS IN THE ALPS

5.2.1 Vegetation Belts, Forests, and Alpine Ecosystems of the Alps

Changes in elevation result in the formation of more or less homogeneous sections of vegetation extending over 700 meters in elevation called *vegetation belts* (figure 5.2). Given the regular temperature decrease with elevation, a vegetation belt corresponds to a range in mean annual temperature of around 3.8 K. According to Schröter (1923), 100 meters of elevation shortens the growing season by nine days, on average, annually (six in spring and three in autumn).

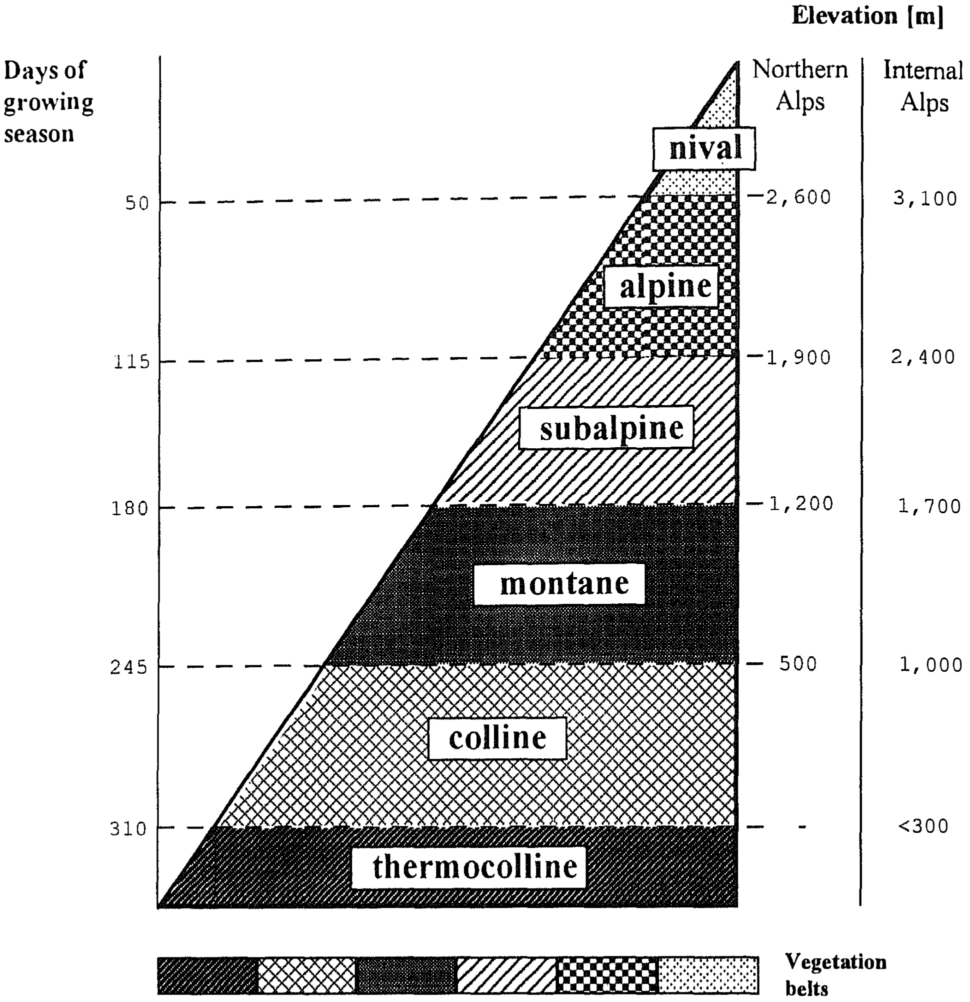


Figure 5.2 Vegetation belts in the temperate part of the Alps, with indications of the length of the growing season (days with mean daily air temperature of at least 5°C).

The highest belt where forest can potentially still grow is termed the *subalpine vegetation belt.* Generally, this belt's lower limit in the European Alps is between 1,200 and 1,700 m a.s.l., and its upper limit is between 1,900 and 2,400 m (Landolt and Aeschimann 1986; Landolt 1992; Favarger 1995b). Formations of phanerophytes (woody plants taller than 50 centimeters—trees and shrubs) characterize this vegetation belt, which supports boreal coniferous forests of species such as Norway spruce (*Picea abies* (L.) Karst.), larch (*Larix decidua* Miller), Arolla pine (*Pinus cembra* L.) and mountain pine (*Pinus mugo* subsp. *uncinata* (DC.) Domin). The subalpine deciduous forests, particularly beechwoods, grow in the lower part of this vegetation belt on the external border of the Alps and are subject to a more Atlantic climate (Pache, Michalet, and Aimé 1996). The subalpine vegetation belt's mean annual temperature is between 0.5°C and 4°C, and the vegetation growth period extends over 110 to 180 days (Ozenda 1985; Theurillat 1991).

The *alpine vegetation belt* begins at around 1,900 to 2,400 m a.s.l. and extends up to 2,600 to 3,100 m. Formations of swards and low heaths, the absence of phanerophytes, a decrease in abundance of annual plants (therophytes) and of bulbar plants (geophytes), and the presence of cushion plants characterize this belt (e.g., Landolt and Aeschimann 1986; Landolt 1992; Ozenda 1985; Favarger 1989, 1995a). All alpine plant communities can be considered "specialized" (i.e., limited to particular habitats; see section 5.4.3) with geomorphology, microrelief, and site exposure strongly determining their distribution. These factors determine the microclimate and the related length of snow cover (Thornwaite 1954).

Above 2,600–3,100 meters is found the *nival belt,* where the growing season is less than 50 days. At these elevations, snow remains on flat ground throughout the summer. These environmental conditions preclude the development of closed plant communities such as swards. Vascular plants of the alpine belt form loose plant communities in screes and rock fissures in the lower part of the nival belt. Higher up, these plants grow only sporadically in favorable, rocky places.

5.2.1.1 Forests The forests of the European Alps constitute a major ecosystem and fulfill several important functions. They regulate runoff, thereby moderating the hydrological regime and preventing erosion of steep slopes (Brooks et al. 1991). They protect human settlements from avalanches and landslides. They provide fuel, pulpwood, and timber for human use and, in conjunction with alpine meadows, are the dominant component of an attractive landscape for recreational activities. In addition to their economic roles, Alpine forests are among the most natural remaining ecosystems in the Alps, other than alpine ecosystems, and thus they play an important role in biodiversity conservation. On a larger scale, understanding Alpine forests' climate sensitivity may provide important insights into the potential responses of mountainous forest ecosystems throughout the world.

Forests and the atmosphere form an intertwined system in which temperature, precipitation, and winds influence the structure of forests, and forests in turn feed back to the climatic system via changes in albedo, surface roughness, and evapotranspiration (e.g., Woodward 1987; Running and Nemani 1991). On a regional scale, studies have shown the potential of these feedbacks to affect regional climate (e.g., Lean and Warrilow 1989; Pielke et al. 1994).

In the context of climate change, forests are important terrestrial ecosystems because they can fix, through photosynthesis, and store a significant amount of carbon. For instance, on a global scale, forest ecosystems store 80 percent of the above-ground and 40 percent of the below-ground nonfossil carbon, which amounts to 62–78 percent of all carbon stored in the terrestrial biosphere and 61–77 percent percent of all carbon in the world's biomass (e.g., Dixon and Turner 1991; Wisniewski et al. 1993; Dixon et al. 1994; Perruchoud and Fischlin 1995). Therefore significant changes in the extent of the world's forests could exacerbate changes in climate by releasing large amounts of carbon into the atmosphere (King and Neilson 1992; Neilson 1993; Smith and Shugart 1993; Watson et al. 1996).

5.2.1.2 Alpine and Nival Zones In a phytogeographical sense, the alpine zone, or alpine vegetation belt, is the area between the tree line and the snow line. About one-fourth (1,000–1,100 species) of the Alps' flora is found in the alpine zone, in conjunction with the upper forest zone and the nival zone. These species, called orophytes, can be considered the Alps' "primary diversity" that is, those species native to the Alps as opposed to those (mainly weeds, ruderal, and grassland species) whose natural distribution has been widely extended through human activity. Most orophytes evolved from the surrounding flora of the warm lowlands in the late Tertiary (Pliocene). Their distribution in the alpine zone is more a factor of microclimates generated by microrelief (topoclimates) than of the general climate. The distribution of these orophytes is also considered to be in equilibrium with natural conditions because the alpine belt's upper zone, at least, is considered to have experienced minimal impact from human use. In this respect, the alpine and nival belts are the largest relatively unmodified ecosystem in middle Europe.

The tree line, the contact between the forest and Alpine belt, is a striking bioclimatic boundary (e.g., Tranquillini 1979; Wardle 1983; Holtmeier 1989; Tallis 1991; Slatyer and Noble 1992). Where edaphic and orographic factors abruptly prevent the growth of trees, the treeline can be a sharp boundary (an ecotone); where climate determines the boundary, a transitional zone (an ecocline) of heaths, shrubs, stunted trees, and meadows can occur between the forest limit, or timber line, and the tree limit, or tree line. According to Tallis (1991) and Slatyer and Noble (1992), the tree line is determined by "trees" taller than two meters (i.e., microphanerophytes; see also sections 5.2.1, 5.4.6)

This subalpine-alpine ecocline is called the "kampfzone" or the "krummholz zone." Its distribution fluctuates in response to local factors such as topography and site exposure. The kampfzone now rarely exists under natural conditions in the Alps because human activities have lowered the upper limit of forest almost everywhere, thus broadening the subalpine-alpine ecocline (see also section 5.4.6).

5.2.2 Bryophytes

5.2.2.1 Characteristics Mosses, liverworts, and hornworts are collectively known as bryophytes, the second largest group of land plants, comprising some 23,000 species worldwide. They are poikilohydric plants, that is, plants whose water status completely depends on that of the aerial environment (Walter 1931, 1985; Walter and Breckle 1985, 1991). Such plants tolerate drought by reducing photosynthesis and respiration and withstanding complete tissue dehydration. In contrast to mosses, the homeohydric vascular plants have developed morphological adaptations and internal conducting systems that enable them to maintain relatively constant water contents independent of their environment. Poikilohydry provides the physiological ability to survive, to the point of desiccation, a high variation in water content. In dry conditions, bryophytes strongly resist frost and heat (Longton 1980). Growth is restricted to periods only when the moss is wet. Some bryophytes can photosynthesize at very low internal water contents (Proctor 1982), an important ability for competition, particularly with changing growth conditions.

Bryophytes live in microenvironments whose conditions may differ from those of the surrounding vegetation, determined by (macro)climate, and thus they show characteristic substrate specificity. Bryophytes can colonize bare soil after landslides or other disturbances (Slack 1988). In other situations, they constitute the edaphic climax (see section 5.4.3) on rocks, in crevices, and in screes, fens, and streams. Various bryophyte communities are present as synusiae in plant communities dominated by vascular plants.

In bryophytes, asexual reproduction is often a more important means of propagation than sexual reproduction (During and van Tooren 1987). They have a variety of modes of vegetative propagation. In harsh environments, bryophytes may persist at a vegetative stage for long periods. In dioecious taxa (those with sexes on separate plants), successful sexual reproduction depends on the simultaneous presence of both sexes, which geography may restrict (Longton and Greene 1969a). Genetic variability is especially high in mosses (Wyatt, Stoneburner, and Odrzykosski 1989; Wyatt 1994), as is their phenotypic plasticity (Longton 1974; Busby, Bliss, and Hamilton 1978).

Unfortunately, ecophysiological data are unavailable for alpine bryophytes, although extensive ecophysiological work has been carried out in polar regions. Because arctic (and antarctic) environments may to some extent be comparable to alpine conditions, these results may provide some insights relevant to the European Alps. In addition, the species investigated also occur in central Europe.

The productivity of bryophytes is low, but their aboveground production may be similar to that of vascular plants in arctic areas (Oechel and Sveinbjörnsson 1978). In Canada, Busby, Bliss, and Hamilton (1978) and Robinson, Vitt, and Timoney (1989) have studied bryophytes' response to microclimatic and edaphic gradients, especially water. Bryophytes' role in ecosystems' processes such as nutrient and water interception and retention is still poorly understood, at least for temperate and tropical regions (Longton 1992). Again, more data are available for polar regions (Longton 1984, 1988). Studies on nutrient cycling in the Alaskan taiga (Oechel and Van Cleve 1986; Chapin et al. 1987) showed that the bryophyte layer functions as a selective filter, acquiring some nutrients rapidly and losing them slowly.

Bryophyte tissue decomposes much more slowly than that of vascular plants because it has a high concentration of lignin-like compounds, thus accumulating acidifying organic matter in the soil (e.g., Hobbie 1996).

Herbivorous animals normally do not graze mosses because of their low digestibility.

5.2.2.2 Patterns of Distribution Bryophytes have an ancient origin, with their oldest fossils dating to the upper Devonian. Extant species have been found in Eocene deposits. In Great Britain and North America, fossil alpine species were discovered at sites far from the present distribution range (Miller 1983). For the European Alps, paleoecological data support the presence of bryophytes in postglacial deposits, as in peat profiles, but unfortunately without no further identification than just "mosses." However, we may assume that the present alpine bryophyte vegetation established itself in the early Holocene.

In terms of species, 1,154 mosses and 423 liverworts are known for Europe, including the Azores (Corley and Crundwell 1991; Grolle 1983). More than two-thirds of the European species are found in the Alps, of which about 40 percent can be considered orophytes, based on the Swiss flora, for which 776 mosses and 252 liverwort species are reported (Urmi et al. 1992). The highest-growing moss in the Alps is an indeterminate *Grimmia* Hedw. species at 4,638 meters a.s.l. at the top of the Dufourspitze (Monte Rosa) on the Swiss-Italian border (Vaccari 1911). *Grimmia recurva* Schwägr. (= *G.*, cf. *sessitana* De Not.; E. Maier, personal communication) is the highest-growing known species, at 4,554 meters a.s.l. at the top of Punta Gnifetti (Monte Rosa) in Italys Aosta Valley (Vaccari 1913).

In contrast to the abundance of vascular plants, there are very few endemic bryophytes in the Alps, with only the liverworts *Riccia breidleri* Steph. and *Herbertus sendtneri* (Nees) Lindb. recognized as such. Moss species once considered endemic have since either been discovered on another continent or reduced to synonymy after taxonomic revision. Many rare alpine species are more frequent in arctic regions. In contrast to the lowlands, where the significant human impact has consequently impoverished the diversity, the alpine bryophyte vegetation is still quite rich and well developed, mainly in subalpine forest and heath communities and in humid vegetation types such as fens, springs, and snowbeds, where the bryophyte layer may show considerable productivity and diversity.

The great majority of bryophytes have a large distribution range, circumboreal for the majority of alpine species. Throughout the Alps, each species' ecological requirements varies little compared to those of vascular plants. The results of bryoecological research are therefore applicable to large geographical areas.

In the Alps, some genera of bryophytes are highly diversified and also possess great phenotypic plasticity. Ecological modifications that reflect unfavorable growth conditions may hamper taxonomic evaluation, yet they may be useful for environmental monitoring. For example, Frisvoll (1988) has recently revised the complex of *Racomitrium heterostichum* (Hedw.) Brid., considered to date one species in central Europe, for the Northern Hemisphere. At least five well-delimited taxa, each with a particular ecology, are reported for the Alps. A similar program has been set up for the genus *Grimmia* Hedw, whose taxonomy in the Alps was poorly understood until recently. As knowledge on habitat requirements has improved, it has been suggested that some species might be used as indicator species (Maier and Geissler 1995).

5.2.3 Vascular Plants

5.2.3.1 Characteristics Orophytes (see section 5.2.1.2) are specifically adapted to cold conditions through physiological and morphological characteristics (e.g., Atkin, Botman, and Lambers 1996; Friend and Woodward 1990; Körner 1989, 1991, 1992, 1994, 1995; Körner and Diemer 1987; Körner et al. 1989; Körner and Larcher 1988; Larcher 1980, 1994). These species have developed several mechanisms of resistance to frost. They assimilate efficiently at temperatures near 0°C, despite the lower partial pressure of CO_2, exhibit a high mitochondrial respiration (dark respiration) rate in comparison to plants from the lowlands (see also section 5.4.2.1), and accumulate large amounts of soluble sugars. They also have a high nitrogen content and abundant secondary compounds. For example, they possess a high level of antioxidants, such as ascorbic acid, as an adaptation to the intense irradiation that may generate oxidative substances (Wildi and Lütz 1996). Plants in the alpine belt also exhibit morphological and anatomical adaptations to low temperatures and hereditary features such as thick leaves, small size, and slow growth. The tillers of the important alpine sedge *Carex curvula* All., for example, may grow on the order of 0.5–1 millimeter per year (Grabherr, Mähr, and Reisigl 1978). However, this occurs in conjunction with daytime canopy temperatures that may reach 20–30°C because of strong radiation. Alpine plants' inherently slow growth is related to a small leaf area per leaf biomass, a limited number of dividing cells at the growing points, and low night temperatures' inhibiting mitotic division and therefore cell growth. Based on the environmental conditions at the alpine belt, plant morphology, and plant longevity, orophytes are considered "stress tolerators" according to the "competitive—stress tolerant—ruderal" scheme Grime (1979) developed. However, closer observations in the high-alpine and nival belts indicate that orophytes do not completely fit the concept of stress tolerators, because they also show competitive and ruderal traits, such as supporting considerable herbivory by small mammals (Diemer 1996).

5.2.3.2 Patterns of Distribution The European Alps support a high level of plant biodiversity in a relatively small area, with about 4,500 vascular plant species, more than a third of the entire European flora (west of the Urals). Favarger (1972) identified 1,049 orophytic taxa in the Alps (about 23 percent of the Alps' entire flora). The highest growing vascular plant observed in the Alps is a saxifrage (*Saxifraga biflora* All.) at 4450 meters a.s.l. at the Dom in Valais (Anchisi 1985).

According to Pawlowski (1970), 397 taxa, in the narrow sense, are endemic to the Alps. In addition, there are 55 subendemic taxa (plants having their main distribution in the Alps but extending also to other mountain ranges). Among the endemics and subendemics, more than half are orophytes. Based on Pawlowski's figures, Favarger (1972) mentioned 331 (32 percent) endemics among his 1,049 species of orophytes. However, the status of endemic taxa remains unclear because of the lack of a precise assessment of the Alps' flora as well as taxonomic divergences. In a broader, conservative sense, only 15 percent of the plant species of the Alps may be endemics (Favarger personal communication).

Orophytes' distribution patterns result mainly from the integration of two dominant factors: climate and macrorelief. Glaciation during the Pleistocene played a key role in shaping the present distribution patterns of species according to intrinsic biological characteristics (dispersion capacity, competitive ability, adaptation, and persistance). Species' individualistic response to climatic vicissitudes makes it difficult to use their distribution to define phytogeographical regions in the European Alps, and no agreement exists between authors even for the major divisions (Theurillat et al. 1994). However, some general patterns exist (Ozenda 1985, 1988, 1994; Favarger 1989, 1995a, 1995b; Theurillat 1995).

Four main distribution patterns of orophytes can be distinguished:

1. Many species are distributed through the whole range
2. Many species occur only in the western or eastern part of the Alps, on either side of a line from Bodensee to Lago di Como, or a line from Lake Geneva to Lago Maggiore
3. Many species exhibit a north-south disjunction in their distribution as a result of the absence of limestone in the central part of the Alps
4. Several species, including both those distributed through the entire range of the Alps as well as eastern or western distributions, show wide disjunction or fragmented distributions, mainly due to glacial events.

In addition to these four patterns, several species possess chromosomic races (diploid, polyploid) that show a west-east distribution (phytogeographical pseudovicariance; Favarger 1962).

Glacial expansion had four other effects on the distribution of orophytes, in addition to those on general distribution patterns:

1. the ancestors of the Arcto-Tertiary flora were almost completely extirpated
2. many orophytes were limited to refugia in the northeastern, southeastern, and southwestern margins of the Alps, where they are now distributed; therefore, the main centers of endemism are the Maritime Alps, the southern Alps between Lago di Como and Lago di Garda, and the low eastern Alps

3. some orophytes moved to lowland areas surrounding the Alps, where they have persisted until the present

4. some orophytes moved to neighboring high mountains and the Arctic; according to figures derived from Jerosch (1903) for Switzerland, about 30 percent of orophytes also occur in the Arctic, and more than 50 percent occur in the mountains of central and southern Europe.

5.2.4 Summary

- Altitudinal vegetation belts, each spanning about 700 meters in elevation, can be distinguished in the European Alps. The subalpine belt is the highest potential limit for forest. The alpine belt above it is composed of low heaths and swards, and the nival belt above that of sparse vegetation.
- The subalpine and alpine vegetation belts are mainly composed of plants, called orophytes, that are specially adapted to cold conditions through several mechanisms.
- In the Alps, about 40 percent of bryophytes and about 25 percent of vascular plants are orophytes.
- Bryophytes tolerate almost complete dehydration, in contrast to most vascular plants.
- The microclimate of bryophytes' habitats usually differs significantly from the mesoclimate.
- Most bryophytes are distributed over the entire Alps, whereas vascular plants have a wider array of distribution patterns.
- Four main distribution patterns for vascular plants result from past climate change, orography, dispersal and/or competitive abilities: entire range, eastern-western distribution, north-south, and east-west disjunction.
- The Maritime Alps, the southern Alps, and the low eastern Alps are the main centers of endemism for vascular plants because of their role as refugia during Pleistocene glaciations.
- Only a few bryophytes are endemic to the entire Alps, whereas there is about 15 percent endemism among orophytic vascular plants in the Alps.

5.3 SUBALPINE AND ALPINE SOILS: GENERAL CHARACTERISTICS

Scientific understanding of subalpine and alpine soils in the European Alps is limited. In the Swiss canton of the Valais, for example, where the Ecocline studies are in progress, few studies have been published on the formation and evolution of soils (e.g., Paternoster 1981; Spaltenstein 1984; Keller 1991). Soil formation and evolution in the French Alps are slightly better known (e.g., Bottner 1972; Legros and Cabidoche 1977; Bartoli and Burtin 1979; Robert, Cabidoche, and Berrier 1980; Dambrine 1985), as are those of the eastern Alps.

The classical definitions of soil types distinguish two main categories according to the minerals in the parent rock: those on carbonate rock and those on acidic siliceous rock. This distinction is arbitrary because there are many intermediate types of rock (e.g., silica-rich calcschists). Furthermore, decarbonated loess can cover limestone and give rise to acidic soils. The soil's present physicochemical characteristics are likely to determine its reaction to climate change.

Eight main types of subalpine and alpine soils can be identified, outside of wet zones, based on their degree of evolution (table 5.1).

5.3.1 Time Scales in Soil Development and Evolution

Soils bring together many ecosystem processes, integrating mineral and organic processes; solid, liquid, and gas processes; and biological, physical, and chemical processes (Arnold et al. 1990; Yaalon 1990). Soil may respond more slowly to environmental changes than other elements of the ecosystem, such as, for example, the plant and animal components. In subalpine and alpine climates, the time needed to form and stabilize soil is estimated to be several thousand years. So how could soil development follow rapid climate changes, and how could we use soils to detect these changes?

This question belittles the complexity of soil, which develops through processes operating at differential rates. Only the soil's complete evolution, to the formation a stable soil "type," requires the entire period. Within the soil ecosystem, many processes operate much faster than the evolution of mature soil. Moulds begin to decompose Arolla pine needles internally, for example, only a few weeks after they fall, and podzolized soil layers can form in only a few centuries. These changes take place on a wholly different scale from the millennia required for soil ecosystems to form in situ.

The different timescales at which soil components evolve challenges another common misconception, namely that soils evolve more and more slowly as the climate becomes harsher. Soils in cold regions are assumed to take longer to change over time than those in hot regions, where the vegetation has a high rate of productivity and a rapid biogeochemical turnover. But this assumption neglects soil development's dependence not only on climate, but also on local conditions, including topography, which allows constant rejuvenation through colluvial movement; calcium content, which prevents acidification; and coarse soil texture, which promotes rapid water transit. Under these conditions, alpine soils can evolve rapidly and may help reveal climate changes at an early stage (Labroue and Tosca 1977). Keller (1992, 187) observed: "These ecosystems [at high altitudes], long thought of as little evolved, in fact constitute very active systems, which can be used as models to study the different biological and biochemical factors in the first stages of soil development."

Table 5.1 Comparison of eight subalpine and alpine soil types

Reference Baize and Girard 1992	Soil type Duchaufour 1977	Soil type Soil taxonomy 77	Horizonts Baize and Girard 1992	pH range (average)	Dominant processes	Humus forms	Vegetation (examples)
Cryosol	Cryosol	Pergelic Cryorthent	O-J-C	4.0–8.0	Frost	Moder, mor	Drabion hoppeanae Androsacion alpinae
Regosol	Régosol	Lithic Entisol	O-A-C	4.0–8.0	Rock alteration	Moder	Thlaspion rotundifolii Petasition paradoxi
Organosol	Sol lithocalcique	Lithic Cryumbrept	OL-OF-OH-(A)-R	3.5–6.0	Organic matter accumulation	Mor	Piceion abietis
Rankosol	Ranker	Lithic Humitropept	OL-OF-A-R	3.5–5.0	Weak humus-clay aggregation	Moder	Caricion curvulae
Rendisol	Sol humocalcique	Entic Cryumbrept	OL-OF-Aci-R	5.5–7.5	Humus-clay aggregation	Mull, moder	Caricion firmae
Neoluvisol	Sol brun lessivé	Typic Hapludalf	OL-OF-A-E-BT	4.0–5.5	Clay leaching	Mull, moder	Nardion strictae
Alocrisol	Sol brun acide Sol brun ocreux	Typic Dystrochrept	OL-OF-A-S-C	4.0–5.5	Brunification Weak podzolization	Mull Moder	Oxytropido-Elynion Festucion variae
Podzosol	Podzol humo-ferrugineux	Humic Cryorthod	OL-OF-OH-A-E-BPh-BPs-C	3.0–5.0	Cheluviation	Moder, mor	Rhododendro-Vaccinion

5.3.2 Organic Matter—A Key Indicator

Even if each soil type, such as those presented in table 5.1, shows different rates of response to climate change, humus layer A will always be a key indicator of these changes because of its mixed organomineral constitution. In fact, the evolution of organic matter appears to provide an important means of understanding the changes that can affect the soil. Many essential soil properties depend on it: structure, water retention, mineral fertility, strength, and diversity of animal life and microflora. Soil organic matter is complex and a key regulator of global carbon fluxes. It also regulates the nitrogen cycle, in which the organic matter forms the principal store of this important nutritional element (except in the nival zone, where snow pack appears to be the main reservoir for nitrogen; Haselwandter et al. 1983; Körner 1989).

Soil processes involving organic matter, in addition to those concerning water retention, are the most revealing among the possible descriptors of rapid soil change (on the scale of a year to a century). Changes in soil organic matter can also indicate vegetation change, which can occur quickly because of climate change (Almendinger 1990). In contrast, the soil's mineral evolution (weathering of rocks, new formation of silicate minerals, removal of carbonates) is typically slower, even though Dambrine (1985) provided evidence that these changes were happening faster than expected.

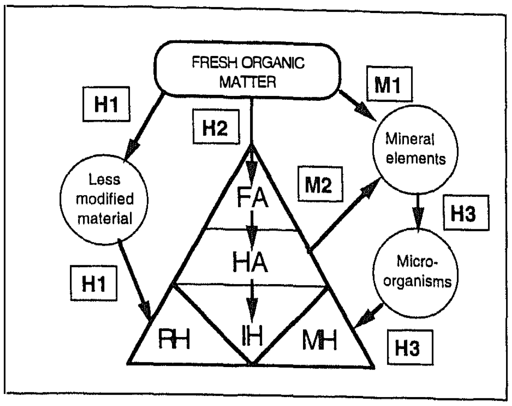
Whereas the total carbon content is a good indicator of rapid changes in some young lowland soils (Fierz, Gobat, and Guenat 1995), it does not seem particularly helpful in the subalpine and alpine zones, where its inertial mass is large. Here, secondary mineralization is very weak. Some humus components may be several thousand years old, as Balesdent (1982) showed for the soils of the Haut-Jura (Jura range).

Tracking changes in subalpine and alpine soils may provide a useful means of qualitatively understanding the dynamics of organic matter. This knowledge may be important on a global scale when considering the terrestrial and atmospheric carbon budgets. The "missing sink" (about 0.4–4 Gt C/yr; Gifford 1994) needed to balance these two budgets may well be in soils.

5.3.3 Humification and Podzolization

Two promising processes have emerged from the research within the Ecocline framework: the physicochemical evolution of the litter and its transformation to humus, and the intensity of podzolization.

During humification (see Duchaufour 1983; Stevenson 1982; Schnitzer and Kahn 1989), litter undergoes various transformations between fresh debris and stable humine, the last stage in the evolution of soil organic matter. The three possible humification routes are inheritance (recovery of components present in the vegetation), polycondensation (aggregation of crenic, fulvic, and humic acids), and synthesis by bacteria (secretion of polysaccharides)



Explanations

A. Transformations
M1 = Primary mineralisation
M2 = Secondary mineralisation
H1 = Inheritance humification
H2 = Polycondensation humification
H3 = Microbial humification

B. Organic matter categories
FA = Fulvic acids
HA = Humic acids
RH = Residual humine
IH = Insolubilisation humine
MH = Microbial humine

Figure 5.3 Dynamics of organic matter in soil. (After Soltner 1992, simplified.)

(figure 5.3). The first stages are particularly interesting because they take place at rates that can be readily measured (Gallet and Lebreton 1995). These phases of humification have a direct functional link with podzolization.

Taking into account the organic material's degree of chemical evolution requires models sensitive to subtle changes in organic carbon. A more refined modeling approach is essential to predict reliably the transfer of carbon among the categories of organic material, each of which corresponds to a certain carbon retention period. Ågren and Wirkström (1993, 343) have demonstrated the difficulties in constructing such models of allocation: "In view of the criteria that should be satisfied by C-allocation models, we conclude that today there are no allocation models that satisfy all requirements," Perruchoud and Fischlin (1995) emphasized the same point. Bryant and Arnold (1994) and Powlson, Smith, and Smith (1996) evaluate some models (SOMM, CANDY, CENTURY, and others) that try to consider the different parts of soil organic matter and to integrate nitrogen.

Podzolization is one of the fastest soil-generating processes (Guillet 1972; Boudot, Bruckert, and Souchier 1981). It occurs only in acid soils and involves organometallic compounds (chelates) migrating from the O or A layers to the spodic layers BP, where they precipitate as organic molecules (BPh) and as metal oxides (BPs). Podzolization also requires a wet climate, so that even short periods of chemical reduction liberate iron. In the Alps, this happens particularly when the snow melts. Therefore, changes in the rate of podzolization may be a useful indicator of environmental change. On steep slopes, however, solifluction may severely slow podzolization by constantly eroding the organic layers.

5.3.4 Summary

- Processes in soils operate at different rates, and many happen on a timescale of one year or tens of years.
- Organic matter, the key factor in soil processes, will be affected by climate change (directly or indirectly, qualitatively and quantitatively), changing main soil processes (humification, podzolization), and the nitrogen cycle.
- Podzolization, a fast soil-generating process on acid soils, is directly linked to the qualitative decomposition of organic matter (humification) in a wet climate.

5.4 ALPINE VEGETATION: THE DRIVING FACTORS

The vegetation of the European Alps is certainly the best known of those of all the high mountain ranges in the world (e.g., Ellenberg 1986, 1988, 1996; Favarger 1995a, 1995b; Mayer 1974; Mucina and Grabherr 1993; Mucina, Grabberr, and Ellmauer 1993; Mucina, Grabherr, and Wallnöfer 1993; Ozenda 1985, 1988). To understand how vegetation may respond to climatic changes, we review the relationships between climate and vegetation. "Vegetation" and "flora" are distinct terms. Flora is the set of all the plant taxa (species, subspecies, varieties) found in a given area. Vegetation is the set of all the plant communities resulting from ecological and competitive combinations between species. Flora and vegetation are closely linked, but two regions with almost the same flora may have different vegetation.

5.4.1 Complexity Levels in Vegetation

Vegetation is a key factor in ecosystem structure. Vegetation's physiognomy, one of its more obvious components, varies according to environmental conditions and human utilization. Vegetation's architecture determines many ecological parameters within a plant community, such as microclimate, energy budget, photosynthesis, water regime, surface runoff, snow gliding, and soil temperature (e.g., Cernusca 1976; Tappeiner and Cernusca 1991, 1994, 1996).

Vegetation can be classified according to its physiognomical characteristics into several types called *formations* (e.g., Ellenberg and Mueller-Dombois 1967; Mueller-Dombois and Ellenberg 1974). Within a formation, distinguishable variations in plant species composition result from the different ecological requirements, competitive abilities, and distribution of each species. Such variations can be used to distinguish plant communities or phytocoenoses within a formation.

A *plant community*, generally considered the fundamental organizational level of vegetation, is a more or less discrete entity. It is a part of an ecosystem (the microecosystem; Ellenberg 1973) and is defined by its plant combination (floristic structure) and ecological characteristics. There are several approaches for the study of formations and plant communities, including physiognomic, floristic, and ecosystemic approaches (e.g., Mueller-Dombois and Ellenberg 1974; Grabherr and Kojima 1993).

Because of their different life forms and ecological requirements, the species in a plant community do not occupy and use the habitat in the same manner. Therefore, a plant community may be divided into ecological compartments called *synusiae* (e.g., Gams 1918; Barkman 1980; Walter 1984, 1985; partial systems of Ellenberg 1973; microcoenoses). Synusiae constitute organizational levels at which the competition among the species within a single synusia is assumed stronger than among the species belonging to different synusiae. Because of their ecological specificities, synusiae may function independently. Hence, synusiae represent functional units for the microhabitats of plant communities, and they can be considered functional groups in the sense of Körner (1993b). The earlier concept of "guild" introduced by Root (1967) may be considered to be the equivalent of a synusia.

Landscape is the highest level of complexity. It integrates all the ecological factors and can provide strong variations in environmental gradients through its heterogeneity or patchiness (fine or coarse) and boundaries. In many ways, landscape can be considered the memory of the past in mountainous regions, preserving records of geological, geomorphological, and biological events, including human use. At the landscape level, plant communities are assembled into *vegetation complexes* (biogeocene complexes: Walter 1984, 1985) of several levels of complexity (Naveh and Liebermann 1984; Theurillat 1992a, 1992b, 1992c) relating to ecological gradients and geomorphology.

5.4.2 Climatic Factors

The vegetation ecosystems of the European Alps will doubtless change in response to changes in climate. However, as discussed in chapters 2 and 4, changes in climate are very likely to be complex, characterized by new combinations of temperature, precipitation, solar radiation, and other factors that will differ from one part of the Alps to another. Because mathematical complexity constrains present scientific understanding of the atmospheric system and many climate processes, it is impossible to predict changes in climate reliably at a spatial and temporal scale relevant to most plants. In the absence of this key knowledge, we limit our discussion of plant responses to climate change to the (in principle) potential effects of changes in temperature, precipitation, and the frequency of extreme events.

5.4.2.1 Temperature Temperature is a complex factor directly correlated to solar radiation, and both are key factors for plant growth. Given that climate change would not alter solar radiation intrinsically, the main effect of an elevation of temperature would be to extend the growing season length by sixteen to seventeen days per degree increase in mean annual air temperature. To some extent, this could enhance plant growth in general, particularly that of alpine species. However, as Körner (1994, 1995) indicated, photoperiod-sensitive alpine species might not benefit much from a longer growing season, as Prock and Körner (1996) showed for *Ranunculus glacialis* L. For other vegetation belts, plants—particularly trees—would be able to grow at higher altitudes because of a longer vegetation period only if all other requirements were fullfilled. For instance, the growing season of mountain pine (*Pinus mugo* subsp. *uncinata* (DC.) Domin) could be extended in autumn if the maximum temperature in August and September remained above a threshold level. Also, cold nights during September would influence bud and cambial initiation and thus influence growth in the following year (Rolland and Schueller 1995).

Elevation of temperature, would also stimulate mitochondrial respiration (dark respiration), an important physiological feature. If no acclimation occurred with the elevation of temperature, this catabolic process could lead to a negative carbon balance and a rapid exhaustion of the plant's carbohydrate reserves, eventually killing it. Larigauderie and Körner (1995) showed that some alpine plants such as *Cerastium uniflorum* Clairv., *Saxifraga muscoides* All., and *Saxifraga biflora* All. might have very low acclimation potentials, this may also be the case for plants from lower altitudes.

5.4.2.2 Precipitation Precipitation and cloudiness affect oceanicity and continentality, which in turn influence plant distribution (e.g., Holten and Carey 1992; Holten 1993; Pache, Michalet, and Aime 1996). For the two parameters, which represent opposite extremes of a common phenomenon, a hygric and a thermic aspect must be distinguished. The hygric aspect is the ratio of precipitation to altitude, and the thermic aspect is the amplitude of the variation among daily or seasonal temperatures. Elevated precipitations at a given altitude correspond to a high hygric oceanicity or to a low hygric continentality; an increase in temperature amplitude corresponds to a low thermic oceanicity and a high thermic continentality.

An increase in precipitation enhances hygric oceanicity. To some extent, this can slightly balance the increase in mean air temperature, because of water's high specific heat. However, if cloud cover also increases, this reduces solar radiation, resulting in a decrease in temperature and a reduction of temperature amplitude, which could lead to a higher thermic oceanicity. At the opposite extreme, a decrease in precipitation could increase solar radiation, with the increase in temperature increasing thermic continentality. A variation in hygric and thermic continentality or oceanity may shift the distribution of dominant tree species, particularly in transitional zones. According to Klötzli (1992, 1994), an increase in precipitation in the Alps to that of a peroceanic climate would enhance the development of cushion-like vegetation on alpine swards, and given simultaneous eutrophication, tall herbs and green alder (*Alnus viridis* (Chaix) DC.) shrubs would show greater development.

Changes in the timing of precipitation and in the variability in the depth of snow cover would affect vegetation and soil processes differentially. For instance, changes in snow cover would modify the contrasts between convexities or steep slopes and concavities or flat places. A decrease in snow cover would affect plant communities sensitive to frost, such as snowbed communities and some heaths. For example, blueberry (*Vaccinium myrtillus* L.) slowly loses its tolerance to cold during the winter through the diminution of soluble sugars as a result of respiration (Ögren 1996). Late frosts in spring could particularly affect dwarf shrubs (i.e., chamaephytes and nanophanerophytes). Snow cover allows microbial activity during winter by insulating the soil surface from the air temperature, maintaining a soil temperature slightly below 0°C. The resulting release of CO and N_2O account for more than 25 percent of the carbon and more than 10 percent of nitrogen fixed in annual aboveground production (Brooks, Schmidt, and Williams 1997). Changes in precipitation would also modify physical processes, especially periglacial phenomena for winter precipitation (see section 5.4.3.1).

5.4.2.3 Extreme Events Knowledge about potential changes in the frequency and duration of extreme events as a result of climate change is even more limited than that for temperature and precipitation. However, frequency and variability of extreme events exert a greater influence on the position of the timberline than do average values (Holtmeier 1994). If the frequency of extreme events like late frosts increases, because of warmer winters and earlier springs, it could slow the upward shift of the vegetation belts (Wigley 1985). In particular, trees are likely to be very sensitive in this respect, because air temperature is the most important factor regulating bud burst (e.g., Hänninen 1991). Moreover, late frosts could lead to a severe loss of needles by conifers, such as Arolla pine and Norway spruce. This could then start a positive feedback loop, with increasing sensitivity to winter cold because of reduced or even no summer growth due to a reduced photosynthetic capacity, even in a warmer climate. In return, this could make the supranival parts more sensitive to winter stress, as observed by Kullman (1996a) in the Swedish Scandes.

An increase in snow cover could increase the number of avalanches, snowslips, and snow creeping. This could counter the potential for subalpine trees and other biota to move upslope into the alpine zone where these phenomena occur, and, in some cases, could even lower the present timberline if these phenomena become more frequent and/or of greater magnitude. Snow accumulation may favor the development of parasitic snow fungi that can severely damage conifers. Stronger winds can also affect the elevation of the timberline, particularly in exposed zones.

Drought may not be a problem to native vegetation in the subalpine and alpine belts, as these ecosystems are not presently under water stress (Körner

1994; Körner et al. 1996). However, in lower elevations, it may affect the vegetation of dry places like the internal valleys (such as Vintschgau, Valais, Aosta, Maurienne, and Haute-Durance) and the Mediterranean part of the western Alps.

5.4.3 Edaphic and Orographic Factors

Where edaphic factors strongly influence the distribution of vegetation, the resulting vegetation forms specialized plant communities termed *edaphic climax communities* (pedobiomes; Walter 1984, 1985). On the opposite end of the spectrum, where climate is the main controlling factor, the resulting plant communities are termed *climatic climax communities.* Examples of edaphic climaxes are wetlands and vegetation on salty soils. When a climatic climax occurs in another climate different from the one where it is usually found because edaphic factors compensate for the general climate, such vegetation is called *extrazonal.* For instance, a plant community normally occurring in a dry climate as its climatic climax can also be found in a wetter climate as an edaphic climax in particular situations such as outcrops or well-drained soils (for example, oak woods with *Quercus pubescens* Willd., climatic climax in the Mediterranean or continental regions, and extrazonal, relict, edaphic climax only in very warm and dry places at low elevation in the suboceanic areas of western central Europe). The vegetation associated with cliffs is another example illustrating a compensation through edaphic factors. There, vegetation may be strongly influenced by geological substrate and slope, factors that influence water availability, and by aspect and slope, which influence temperature. As a consequence, the same type of cliff vegetation can be found in places with climates differing remarkably in their mean temperature and precipitation and at different elevations. Such vegetation is said to be *azonal.* Thus, relative to climate, many edaphic climaxes illustrate the Rubel's (1935) law of the replaceability of ecological factors, which is equivalent to Walter's law of the relative constancy of habitat (Walter and Walter 1953; Walter 1984, 1985).

5.4.3.1 Physical Processes Physical processes can mediate climatic change's impact on vegetation (e.g., Holten and Carey 1992). Their importance increases with elevation, and they typically dominate in the upper alpine belt.

From the alpine belt upward, the slopes become much steeper (figure 5.4). Beyond a slope of 40°, the environment becomes rocky, and downward transportation of altered material through erosion, runoff, snow creeping, solifluction, and landslips becomes prominent. These factors are of major importance in the development of soil. Active screes derived from cliffs may be another environment where factors other than the general climate more strongly influence vegetation. Because of their ability to free the plants growing in these habitats from the general climate, cliffs and screes are con-

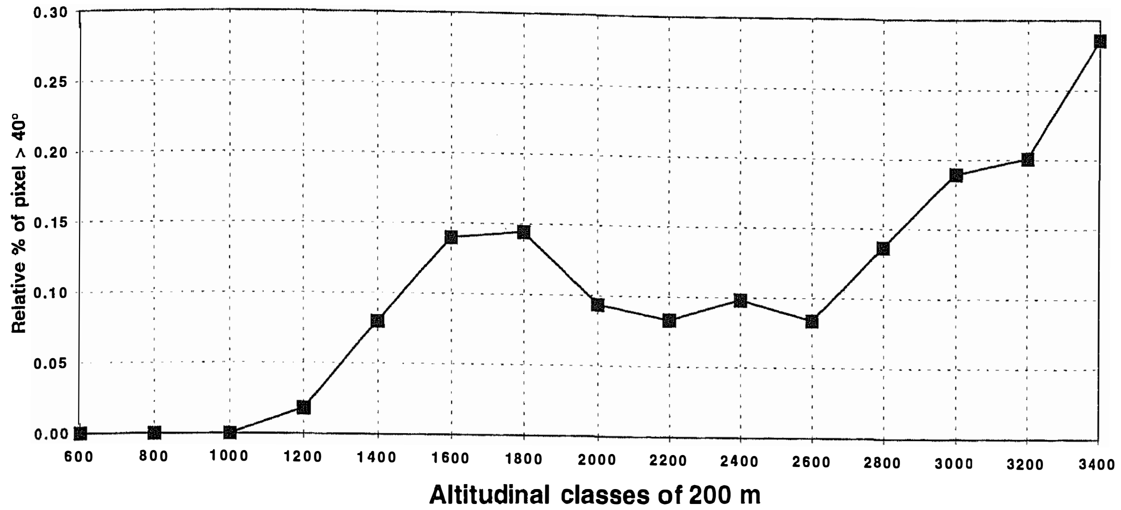


Figure 5.4 The increase in area of slope greater than 40° with elevation in the region of the Val d'Arpette (120 km^2) and Belalp (98 km^2) (Alps of the Valais). The relative percentage is calculated in both regions with the 25 m Digitized Elevation Model for Switzerland on the number of pixels greater than 40° in altitudinal sections of 200 m (i.e., 400–599 m a.s.l., 600–799 m, ..., 3,000–3,199 m), except for the last section, which comprises altitudes above 3200 m.

sidered to have played a key role in the persistence of the endemic Tertiary flora during the Pleistocene glaciations (e.g., Braun-Blanquet 1948; Rioux and Quézel 1949; Davis 1951; Pawlowski 1970; Snogerup 1971).

Geological factors play a role in the response of vegetation on limestone to climate change. The nature (soft marl vs. hard limestone), alteration processes, position, slope and orientation of the limestone layers may strongly influence the composition and distribution of plant communities (e.g. Béguin 1974; Béguin and Raemy 1995). These factors may greatly affect the altitudinal shift of vegetation zones, as they vary greatly with the sequence and thickness of the geological layers.

Periglacial phenomena, that is, those phenomena governed by frost and thaw in contact with glaciated areas, are important factors affecting vegetation and soils at higher elevations in the European Alps. Permafrost is potentially widely distributed (e.g., Keller 1994). In the upper alpine zone, persistence of permafrost influences the altitudinal shift of the vegetation of the lower alpine zone and the distribution of species. When permafrost melts, frozen slopes in the high elevations may become less stable, and this may generate more screes, stone falls and landslips, which could benefit pioneer vegetation.

Gelifluction (solifluction generated at thaw) and cryogenic processes (originated by frost) are other periglacial factors influencing vegetation that are closely linked to climate (e.g., Carbiener 1966; Veit and Höfner 1993). They occur in the upper subalpine zone. Their intensity and distribution increase in the alpine zone up to the transition to the nival zone. Gelifluction affects sediment transfer. Cryogenic processes (such as cryoturbation, the moving and sorting of material by frost) destroy closed vegetation such as alpine swards. The intensity of gelifluction and cryoturbation depends mainly on snow cover and winter temperature. Mild winters with early snow cover result in shallow frost penetration in soil and little or no gelifluction. Severe winters with late or shallow snow cover result in intense gelifluction and cryogenic processes. Therefore, the shift of the alpine belt into the nival belt through global warming may depend on winter temperature and precipitation, particularly snow cover (depth, regime). Periglacial processes regulated by winter climate could either speed up alpine vegetation's colonization of the nival zone or slow it down.

Brockmann-Jerosch's mountain mass elevation effect (*Massenerhebungs-Effekt*) or Merriam effect (e.g., Brockmann-Jerosch 1919; Ellenberg 1986, 1988, 1996; Flenley 1995; Grubb 1971) is responsible for vegetation's altitudinal distribution. In the highest massifs and large aggregations of mountains, the vegetation belts extend higher than in the lower and isolated massifs. Gams' water continentality index expresses the mass effect (Gams 1931, 1932). Correlated to the mass effect, the elevation effect (van Steenis 1961; Backhuys 1968; Hengeveld 1985; Ellenberg 1986, 1988) corresponds to potential, more or less temporary abyssal and upper distributions outside the normal range, if the massifs are high enough for a permanent zone of establishment. According to Backhuys (1968), species growing in massifs in the Swiss Alps' that are higher than 2,000 meters are distributed, on average, 600–700 meters below this altitude, in part because of the elevation effect. However, although the elevation effect does exist, Backhuys' data cannot prove his explanation statistically (Hengeveld 1985).

5.4.3.2 Effect of Soil

Variability in soils may limit vegetation's ability to respond to climate change. For example, a ranker (a poorly evolved, alpine soil on acidic rocks) could rapidly evolve into a podzosol (a well differentiated, evolved soil), progressing first to a cryptopodzolic ranker (or humic podzosol), then to a true podzol. Meadows whose soil undergoes such a transformation are very susceptible to colonization by acidifying heath plants and quickly disappear. On the other hand, a brown or ochre, acid soil (or alocrisol) resists transformation into a podzol longer, even if podzolization is already occurring in a diffuse form (Michalet and Bruckert 1986). Meadows with this type of soil may be less susceptible to colonization by heath vegetation. In addition, soils that formed under a vegetation different from that which they are currently supporting may accelerate recolonization by the initial vegetation, given the favorable pedological conditions. For example, in matgrass (*Nardus stricta* L.) pastures occurring on podzols formed under a heath, recolonization by heath will reinforce the initial soil conditions through a positive feedback through heath's acid litter. At present, however, pedological arguments alone cannot predict whether heath or meadow will prevail under a climatic change. One must also consider functional interactions among temperature, precipitation, carbon, and nitrogen (see section 5.6.5).

Complex scenarios involving the dynamics of soil-vegetation interactions must also consider the different inherent rates of change of the systems concerned. As a rule of thumb, on the phytocoenotic level, one can estimate that the vegetation has ten times less inertia than the soil as a whole. But at the lower organizational levels—synusia and soil layers—the vegetation strata and the pedological layers can have comparable responses.

It is a tenable hypothesis that the vegetation changes observed on limestone soils would essentially reflect climate changes, the internal changes in the soil being relatively insignificant because of their chemical buffering capacity. On acid soils, vegetation changes would occur through both climatic change and changes in soils induced by the vegetation itself.

As described in section 5.6.5.5, changes in soils' nitrogen supply may strongly affect vegetation. In synergy with climate change, this could accelerate or slow the vegetation's response to climate change.

5.4.4 Biological Factors

In addition to climatic and physical factors, biological factors also play a role in the distribution of species and plant communities. Interestingly, some biological factors are correlated with climatic factors, at least with temperature. Biological factors can act either in synergy with climatic and physical factors or against them. Factors not related to temperature, such as precipitation or wind, are not easily or reliably quantified at the relevant level of the microhabitat. Hence, because of their great variability, their effects are difficult to evaluate qualitatively, and they are too complex to model based on current available data.

Biological features such as competition, life strategies, and the ability of plants to adapt could also interact either positively or negatively with climate change. Competition among species limits their physiological possibilities. Therefore, the ecology of a species does not necessarily reflect its physiological optimum (that is, the conditions under which its best development would occur in the absence of competition with other species) or its physiological amplitude, and vice versa. Under new environmental conditions, competitive interactions among species change, possibly changing their ecology.

To some extent, clonal plants in heaths and swards are likely to be able to resist invading species under global warming, owing to characteristics such as their longevity, competitive ability, and rapid response to changed environmental conditions (Callaghan et al. 1992). Closed subalpine heaths like alpenrose (*Rhododendron ferrugineum* L.) heaths are a good example of resistance to trees' and shrubs' colonization. Their architectural characteristics, high biomass accumulation, and high humus accumulation present obstacles to seeds of other species and to their germination (Doche, Pommeyrol, and Peltier 1991; Pornon and Doche 1995b), as in the inhibition model of Connell and Slatyer (1977). Clonal, dominant species of alpine swards may also persist and withstand climate change, as evidenced for *Carex curvula* All. A clone of this sedge in the Swiss Alps was found to be around 2,000 years in age (Steinger, Körner, and Schmid 1996). Long-lived dominant species like trees may also not react immediately and therefore persist. Moreover, the physiological and morphological plasticities, as well as genetic adaptations, will increase ability to persist. Physiological factors, mainly plants' response to an increase in the atmospheric concentration of CO_2, may also modify climatic change's effect. These factors have been discussed by Woodward (1992), Woodward, Thompson, and McKee (1991), Körner (1993a), Schäppi and Körner (1996), and Körner et al. (1996). Körner (1994, 1995) reviewed atmospheric changes' potential ecophysiological effects on alpine vegetation (e.g., thermal acclimation, growth strategies, developmental processes, water relations, mineral nutrition, and carbon dioxide effects).

5.4.5 Phenology: A Link between Climate and Plant Development

The growth and development of plants are controlled by both internal factors (such as plant physiology, plant morphology) and external factors (such as nutrients and water availability, temperature; e.g., Odland 1995). Temperature is a key factor in plant development, influencing the timing of such key life history traits as bud burst, flowering time, growth, and length of vegetative period. "Phenology is generally described as the art of observing life cycle phases or activities of plants and animals in their temporal occurrence throughout the year" (Lieth 1974, 4). Phenological observations allow an assessment of many aspects of the development of plants and ecosystems. Many have published studies on the phenology of vascular plants (see, e.g., Dierschke 1990; Lieth 1974; Orshan 1989; Rathcke and Lacey 1985; Schnelle 1955).

Phenology also holds promise as a tool for assessing climate change's impacts on plant growth and development (e.g., Defila 1991; Diekmann 1996; Fitter et al. 1995; de Groot, Ketner, and Ovaa 1995; Hunter and Lechowicz 1992; Lechowicz and Koike 1995; Kramer 1994; Molau 1993, 1996; Moore 1995). Indeed, the existing correlations between phenophases (distinguishable phases in the life cycle such as flowering, bud burst) and climatic variables permit the use of phenological observations to derive climate data (e.g., Schreiber 1968; Schreiber et al. 1977; Bucher and Jeanneret 1994).

Grimme (1903) demonstrated that the sexual organs of bryophytes in central Germany may mature one to two months earlier than in Scandinavia, where Arnell (1875) studied the same species. Since these early accounts, few phenological observations have been published, and little information is available on bryophytes' reproductive adaptations to alpine environment. Climate affects formation and distribution of sex organs and development of the sporophyte generation (Longton and Schuster 1983), in contrast to vegetative propagation, which occurs throughout the growing season. Some species show distinct seasonal patterns of reproductive development, whereas others are more variable (Miles, Odu, and Longton 1989).

In the Ecocline project, phenological investigations in the subalpine and alpine belts with several species of bryophytes and vascular plants indicate how the decrease of temperature with elevation influences phenophases. These observations show also the close relationship between air temperature (or temperature at the surface of the vegetation canopy) and phenophases. For example, each of the flowering and fruit-setting stages of alpenrose (*Rhodendron ferrugineum* L.) can be correlated to a mean daily temperature of the air at two meters above ground level (figure 5.5; Schlüssel and Theurillat 1998). In the south-facing transect of the Val d'Arpette, there was a mean difference of 3.3 days in the developmental stages of plants for each 100 meters in elevation for the years 1993–96, which is in accordance with the observations of Puppi Branzi et al. (1994) on comparative phenology between grassland and heaths in the Apennines. In the east-facing transect of Belalp, there is a mean difference of 6.3 days for every 100 meters in elevation, in this case in accordance with the shortening of the growing season following thawing (six days per 100 meters). Contrary to some authors' opinions, phenology of alpine plants is not always more strongly determined by soil temperature than by air temperature. As Hegg (1977) has already observed, and according to our observations in the Ecocline project, soil temperature is not necessarily a determinant of phenology.

For bryophytes, the study of survival strategies (Lloret 1988; Longton 1994) of populations of *Pleurozium schreberi* (Brid.) Mitt. demonstrates that archegonia and antheridia (female and male sexual organs) are produced earlier at lower altitude, and that sporophytes occur less often at higher sites (Velluti and Geissler 1996).

Phenological observations permit an assessment of plants' habitat requirements in relation to temperature and other environmental parameters. Phenological data can also provide climatological information (Bucher and Jeanneret 1994). Global warming's first effect might be to lengthen the growing season. Not all plants may benefit, since many species commonly stop growing toward the end of summer (e.g., the dwarf Alpine willows *Salix herbacea* L., *S. reticulata* L., *S. retusa* L., and *S. serpyllifolia* Scop.). The same is true for plants in the arctic tundra (Bliss 1956). Wijk (1986) reported that August temperatures were not correlated to shoot elongation of the dwarf willow (*Salix herbacea* L.). For some species, phenology is determined more genetically than climatically (Körner 1994), and differential response to climatic parameters among populations of a single species can also be genetically determined (Rathcke and Lacey 1985). In bryophytes, phenological patterns can be determined both photoperiodically and climatically (Longton and Greene 1969b). The variety of phenological patterns observed plays a role in speciation and might be an expression of genetic differentiation (Stark 1985).

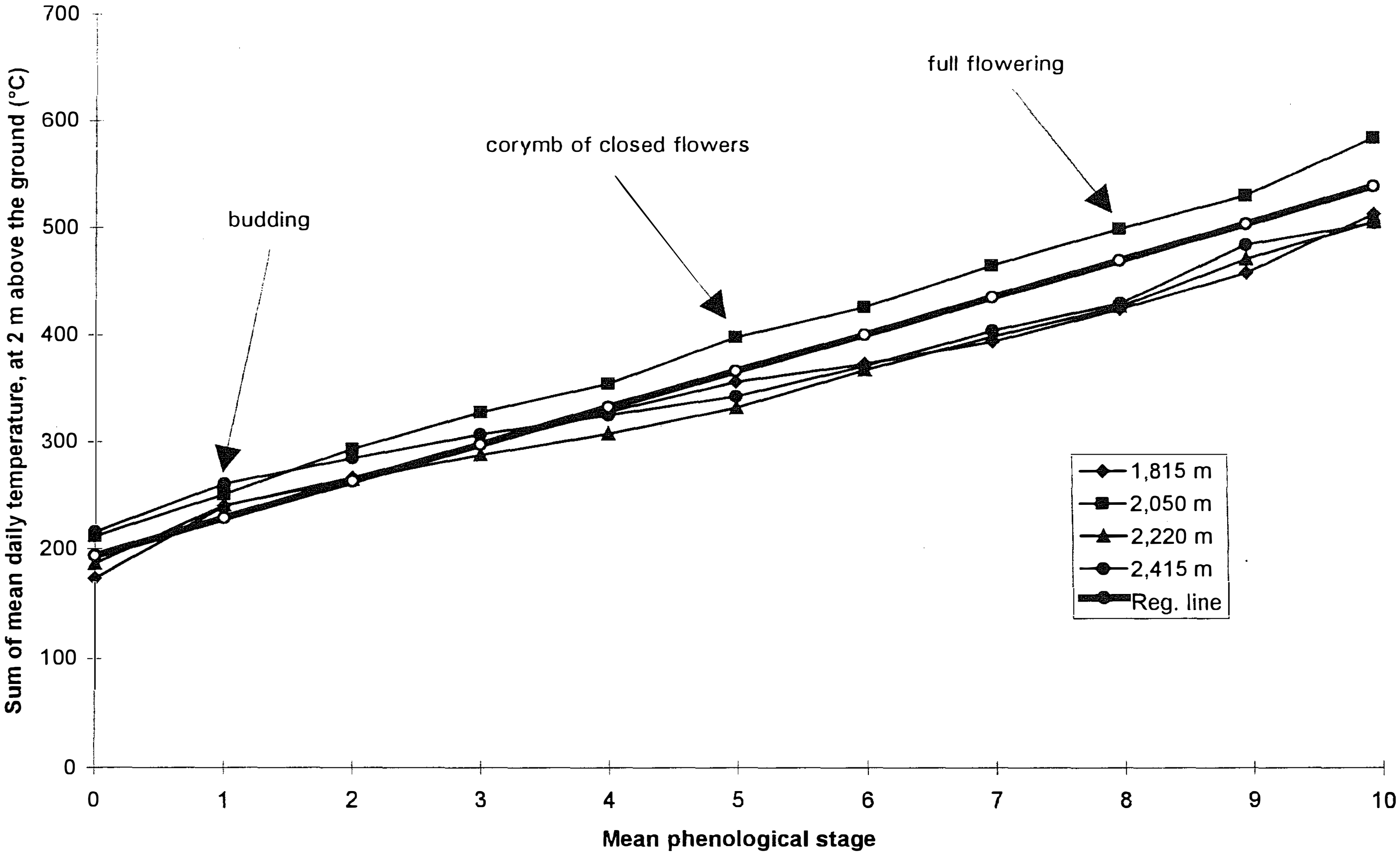


Figure 5.5 The relationship between mean phenological stages of alpenrose (*Rhododendron ferrugineum* L.) and the sum of mean daily air temperature (°C) at 2 m at four different altitudes (1,815 m a.s.l., 2,050 m a.s.l., 2,220 m a.s.l., 2,415 m a.s.l.) in the Val d'Arpette in 1995. Measurements were begun in each plot on the date of snow melt. The regression line over the four sites gives the overall correlation between temperature and phenophase. Phenological stages: 0: buds completely closed; 5: flowers closed and arranged in a corymb; 8: inflorescence with all flowers open.

5.4.6 Human Activities

Land use is a very important factor affecting ecosystems in the European Alps, where human activities have influenced every ecosystem for millenia, even the high alpine zone. To some extent, subalpine forests were transformed less, because of their protective value to human settlements. Man's transformations of the landscape enhanced the natural prehuman fragmentation of habitats in the Alps. Vegetation's response to climatic change may be very different when the effects of anthropic factors are included (e.g., Di Castri and Hansen 1992; Grime 1993). Very likely, the subalpine-alpine limit (ecocline) was one of the Alps' first ecosystems to be cleared and pastured during the Neolithic age, at the Atlantic period (6,000–5,000 yr BP). This is supported by the recent discovery of "Ötzi" in Tirol, on the Austrian–Italian border (e.g., Burga 1988; Bortenschlager 1993; Müller 1992; Pott 1993) and above all pedoanthracological investigations (that is, investigations of soil charcoal) in the alpine belt (Carcaillet, Barbero, and Talon 1996; Talon 1997). That clearing activities occurred above the present highest forest limit is also evidenced for the last thousand years by discoveries of macrofossils (trunks and branches) in alpine bogs (e.g., Tinner, Amman, and Germann 1996, for the Valais), and by toponymy (e.g., Mariétan 1929, for the Valais). Through the lowering of the upper limit of the forest by 200–400 meters and the development of heathlands and swards of replacement at the upper subalpine zone, the subalpine-alpine ecocline's climatic equilibrium has been modified (e.g., Holtmeier 1994).

Pollen analyses at the highest peat bog of the eastern Alps (2,760 meters) indicate that even the swards of the lower alpine belt may originate through pasturing, replacing low heaths (Bortenschlager 1993). Recent soil charcoal investigations in the southwestern Alps (Talon 1997) that show the regular presence of tree species like Arolla pine (*Pinus cembra* L.) and larch (*Larix decidua* Miller) up to 2,900 meters, 500 meters above the present tree line, support this hypothesis. These tree species, together with low heath species, were destroyed by fire at some point since the end of the Atlantic period (5,000 yr BP), very likely by human activities. Observations in the alpine belt in remnant undisturbed places—small, very infrequently grazed (or accessed) areas—currently support these findings, as does the ability of species at the tree line to tolerate climatic fluctuations by taking on a krummholz form (Kullman 1993, 1995; see section 5.5.3.1).

According to Wiersema (1989), the lowering of the forest's upper limit extended the habitat of the ibex (*Capra ibex* L.) downslope. Access to a greater forage supply very likely increased ibex populations, leading to greater grazing pressure that in turn may have helped extend the area of high alpine swards at the expense of low alpine heaths. Therefore, extensive grazing of alpine swards over millenia significantly shaped the distribution of plants and plant communities of the subalpine-alpine ecocline. Mass harvesting of medicinal plants probably also influenced this distribution, both locally and regionally. The harvest of the Celtic nard (*Valeriana celtica* subsp.

norica Vierh.) is exemplary. For centuries, the rhizomes (underground stems) of this small alpine plant were collected by the hundreds of kilos or even tons per year in some Austrian regions, where it was one of the major economic resources (Teppner cited in Jacquemoud 1989). No doubt this profoundly affected the vegetation where this plant grows.

Human activities can either assist or inhibit the upward shift of vegetation belts, in particular the elevation of tree line and the shift of subalpine forests into the alpine belt. Humans may try to accelerate this shift through, for example, afforestation to counter potential forest dieback, landslips or stone falls, or, at the tree line, by discontinuing grazing. On the other hand, humans may slow an upward shift of subalpine vegetation into the alpine belt by preventing the development of subalpine vegetation through more intensive pasturing of the alpine belt. Since the middle of this century, the alpine zone has been heavily altered in many places for skiing with the development of machine-graded ski runs. With global warming, recreational activities and settlement are very likely to increase in both the upper subalpine and the alpine zones. Hence, human activities may have a yet stronger impact, with more transformation of habitats and more habitat fragmentation.

5.4.7 Summary

- The structure of vegetation determines formations at the level of plant communities, and synusiae within plant communities.
- Mean air temperature is directly linked to growing season.
- Precipitation regime determines oceanicity and continentality, which in turn influence plant distribution.
- The frequency of extreme 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, for winter soil microbial activity and resulting carbon and nitrogen biogeochemical dynamics, and for the activity of periglacial phenomena.
- Edaphic factors can compensate for climatic factors.
- Geological factors are important determinants of the vegetation on limestone.
- Periglacial phenomena (permafrost, gelifluction, cryoturbation) affect plant distribution.
- Soil may produce either a positive or a negative feedback loop in the response of plants to climate change.
- Clonal plants can resist invading species and may persist longer under global warming.
- Many aspects of plant development, especially growth and flowering, are directly linked to temperature and can provide climatological information by way of observations of the developmental phases (phenology).

- Humans lowered the tree line and forest line by 200–400 meters through fire and pasturing activities as early as the Atlantic period.
- Man can either accelerate or counteract vegetation's response to climate change through his activities, especially at the human-determined subalpine-alpine ecocline.

5.5 THE ROLE OF PLANT GENETIC DIVERSITY

Species' response to climate ultimately can be reduced to the populations' genetic structure and the mechanisms that determine it, especially reproductive type and genetic variation, both key factors of microevolution. Geographic variation in a species' genetic structure and the possibility of an ecotypic differentiation imply that climatic changes may affect populations' ability to survive or adapt to new environmental conditions differentially. For example, previous climate changes, such as glaciation, provoked successive fluctuations in species' range, which might have favored differentiation among populations by adaptation to different environmental conditions or by random genetic drift (i.e., the random change of the genetic constitution of a finite population through generations). Thus, it is important to consider climate change's genetical impact, which modifies all the processes of selection within and among populations.

5.5.1 Genetic Variability

Genetic variability may be investigated at different scales and is often partitioned within and among population components, showing both spatial and temporal patterns (e.g., Baur and Schmid 1996). Genetic variability depends on several factors such as life history traits, population size, and population history.

The reproductive type of plants is the key factor for genetic diversity. Sexuality promotes population variability, whereas asexual reproduction decreases it (Eriksson 1993). Moreover, a plant's breeding system (autogamy, allogamy, apomixis) may alter populations' genetic structure. Self-pollination (autogamy) promotes within-population uniformity and favors between-population differentiation when compared to cross-pollination (allogamy) (Hamrick 1989). The reproduction by seeds of the maternal genome (apomixis) induces genetical uniformity even if several clones may coexist in a single population (Loveless and Hamrick 1984). This is not always the case, however. Bayer (1989) found higher diversity indexes in the obligate gametophytic apomictic *Antennaria rosea* Greene than in its diploid relatives with sexual reproduction.

For within-population diversity, the size of the plant population is an important parameter. Small populations may show effects of inbreeding together with genetic drift. In extreme cases, genetic drift may lead to a bottleneck—the absence of variability. However, rare plants' genetic structure may vary considerably according to the species (Cosner and Crawford 1994), and small, isolated populations or fragmented populations may still maintain a significant level of genetic variability (e.g., Foré et al. 1992; Ballal, Foré, and Guttman 1994; Holderegger and Schneller 1994; Young, Boyle, and Brown 1996).

One way to approach the genetic diversity within a population is to measure the mean number of alleles (i.e., the different forms of the same gene) per gene locus (the site on the chromosome where a given gene is located; a site with several possible alleles is called a polymorphic locus). The greater the mean number of alleles per locus within a population of a species, the better its ability to adapt to a change.

Another aspect of the allelic diversity parallel to the mean number of alleles at a gene locus is the degree of heterozygosity, that is, the proportion of individuals carrying more than one allele at one locus, one on each of the two homologous chromosomes for a diploid species, contrasted with being homozygous (i.e., having the same allele on both homologous chromosomes). Usually, a population's gene diversity is evaluated in terms of the expected heterozygosity under a random mating system. A loss of heterozygosity can reduce individual fitness and population viability.

Overall, species vary widely, and generalization about genetic diversity should be made only with caution. Nevertheless, tree populations usually show a very high genetic variability in comparison with other vascular plants based on their allelic diversity, both in the number of alleles per locus and in the degree of heterozygosity (e.g., Hamrick 1989; Hattemer 1994; Müller-Stark 1994; Slatkin, Hindar, and Michalakis 1995), to which longevity and stress resistance capacity are related (Hattemer 1994).

5.5.2 Genetic Differentiation of Populations

Two opposing forces regulate genetic differentiation of plant populations: selection, which favors different genotypes in a heterogeneous environment, and gene flow (the movement of alleles between populations), which acts as a unifying factor. These two mechanisms are not exclusive, and genetic differentiation may occur in the presence of gene flow (Endler 1977; Caisse and Antonovics 1978).

Genetic novelties may arise through mutation that are then transmitted if they survive to selection. Nevertheless, the common process of adaptation is the selection of new combinations of genes issued from the recombination of parental genetic material during meiosis. These changes might affect either genetic variability as a whole or the variation at a single genetic marker. Global genetic variability may be interpreted as an evaluation of a plant species' evolutionary potential, and high genetic diversity is a prerequisite to adaptation to new environmental conditions. Two main approaches can be used to determine genetic differentiation among populations: the ecological approach and the genetic approach.

5.5.2.1 Ecological Approach The first ecological experiments to demonstrate plant's ecotypic differentiation were comparative morphological analyses of plants collected in different habitats and cultivated in experimental gardens under uniform conditions (Clausen, Keck, and Hiesey 1940; Turesson 1922). Ecotypic differentiation of a species implies that populations differ in their survival and fertility as a function of the environment. Genetic differentiation may be detected in a common environment if the reaction norms (the relationship between phenotypic variation and environmental variation) do not overlap under the given ecological conditions. Common-garden experiments are convenient for demonstrating genetic differentiation (Böcher 1949a, 1949b), but differences in the inverse direction may be observed when the reaction norms intersect. Consequently, a higher value of a character in one population than in another may not necessarily reflect the natural situation.

5.5.2.2 Genetic Approach The ecological approach uses morphological and phenological traits to measure genetic differentiation. These characters are often polygenic, however, and environmental factors may influence their expression. They are consequently not necessarily reliable for evaluating genetic diversity. Recently, genetic variation at the protein and DNA levels has been increasingly emphasized. Enzymes and DNA markers are used extensively for monitoring genetic variability (e.g., Gottlieb 1981; Hamrick 1989; Nybom 1993; Lynch and Milligan 1994). However, the degree and type of variation depend greatly on which part of the genome is being investigated. Also, patterns of genetic diversity depend on the set of markers used, and generalizations are difficult to make. Therefore, comparison of the measure of diversity with isozymes or DNA markers may yield similar results (Heun, Murphy, and Phillips 1994) or divergent ones (Zhang, Saghai Maroofand, and Kleinhofs 1993). Nevertheless, a greater differentiation of populations may be found with DNA markers than with allozymes.

5.5.3 Genetics and Environmental Change

Numerous descriptions of genetic polymorphism illustrate that genetic variability is not random. Relationships between ecological gradients and genetic clines have been found regularly. For instance, Lumaret (1984) showed that a clinal variation occurs along both altitudinal and latitudinal gradients in *Dactylis glomerata* L. However, an individual plant's response to ecological change at the genetic level has two important aspects: phenotypic plasticity and the selection of adapted genotypes.

5.5.3.1 Phenotypic Plasticity and Selection An organism's *phenotype* is its appearance according to its genetic constitution (genotype) interacting with the environment. In new environments, an individual may change its appearance, expressing new phenotypes (phenotypic plasticity). Modifications may be adaptative (e.g., increase of survival or of reproductive success) or nonadaptative (e.g., Scheiner 1993). Phenotypic plasticity appears, however, to have a genetic determinism. Therefore, one can distinguish between "passive plasticity," that is, plasticity not regulated by the organism but resulting in the direct effect of environmental factors on cellular metabolism, and "active plasticity," that is, plasticity regulated on complex genetic-developmental mechanisms (Pigliucci 1996). An example of phenotypic adaptation to the environment is the occurrence of trees in high mountain regions. At the upper altitudinal limit of spruce (*Picea abies* (L.) Karsten) in the Scandes Mountains in Sweden, trees 4,700–4,800 years old survived climatic changes during the Holocene by taking on the krummholz form when temperature decreased (Kullman 1995). Similarly, Kullman (1993, 769) reaches the same conclusions about birches: "Possibly, birches with dead main stems may survive as copses of low growing sprouts more or less indefinitely."

Strong selection may create very rapid genetic differentiation within plant populations. Rapid genetic changes in plants are known from human activities that create many sharp disturbances of the environment. For instance, tolerance to heavy metals (Antonovics 1971) or to herbicides (Warwick 1991) provides several examples. Although they do not relate directly to climate changes, these examples suggest that climate change might induce measurable genetic changes. Another example is in the grass species *Anthoxanthum odoratum* L., where genetic differentiation in terms of plant height, yield, and susceptibility to disease was observed between adjacent meadows subjected to various fertilizer and liming treatments over a span of fifty years and over distances of thirty meters (Snaydon and Davies 1972). Many changes were already detectable within six years (Snaydon and Davies 1982). With the same species, differences in salt tolerances were observed in less than thirty years between a population located at the edge of a highway and those of the surrounding pastures (Kiang 1982).

5.5.3.2 Ecogeographical Gradients Gradual genetic variation along an ecological gradient can result from selection. For instance, selection was considered a possible explanation for genetic differentiation among populations of *Pinus ponderosa* Lawson along an altitudinal transect (Mitton, Sturgeon, and Davis 1980). Another convincing argument for selection is the study of acid phosphatase in *Picea abies* (L.) Karsten along a latitudinal gradient in Finland and an altitudinal transect in the Austrian Alps and in different populations in the Swiss Alps. In the three groups of populations, enzymic variation was consistent according to the climate gradients (Bergmann 1978). In the two sites of the Ecocline project, *Anthoxanthum alpinum* A. & D. Löve, a widespread grass growing in the subalpine and alpine belts, was tested for six enzyme systems including ten loci. When the populations were pooled, three enzyme systems, glutamate oxaloacetate transaminases (GOT), peroxidases (PX) and malate dehydrogenases (MDHB) showed a significant corre-

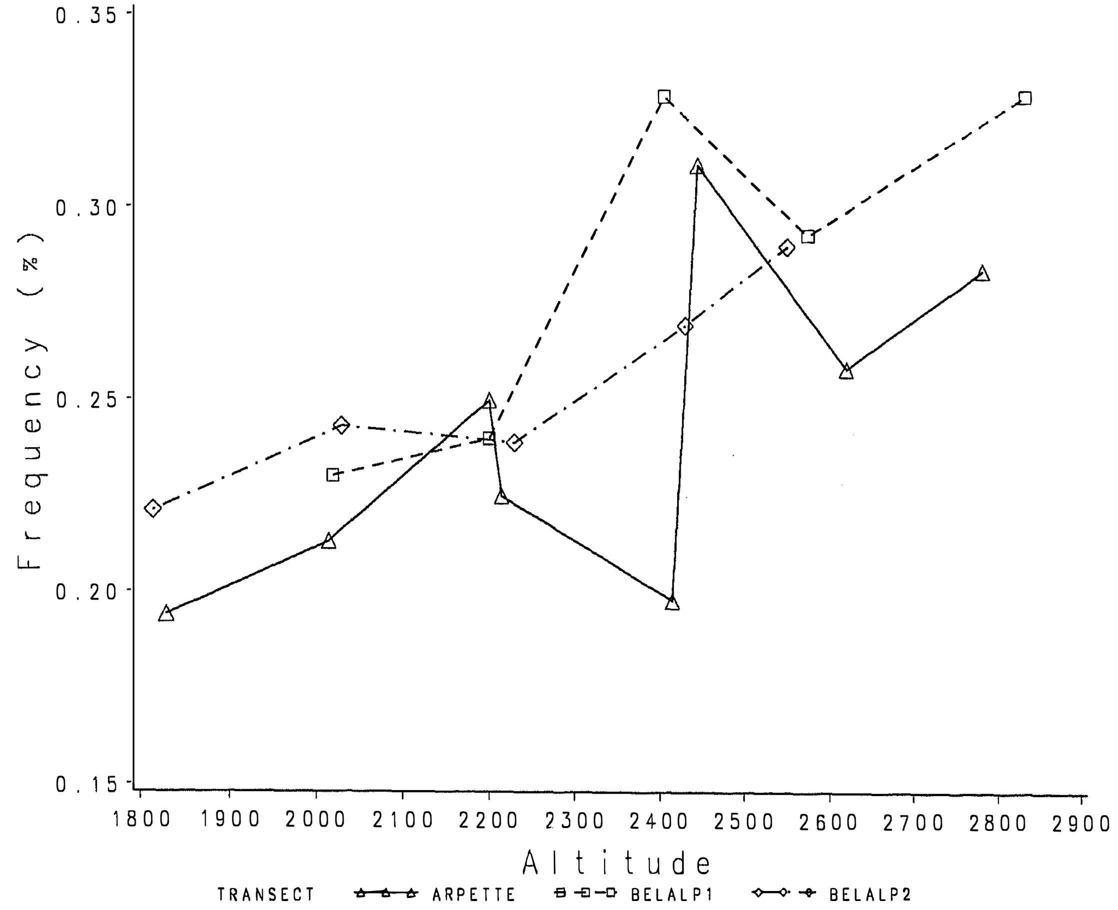


Figure 5.6 Variation of allele MDHB (malate dehydrogenase) in *Anthoxanthum alpinum* A. & D. Löve in relation to altitude in three transects at two sites in the Valais.

lation between one allele frequency and altitude. Figure 5.6 shows the increase of allele MDHB as a function of altitude.

On the other hand, interpretation of geographical clines is not straightforward because they may be caused either by the neutral diffusion of an allele during migration or by the action of selection on ecological gradients. Evidence of a selective effect may nevertheless be obtained by the demonstration of similar correlations at different locations or at different scales. In *Abies alba* Miller, geographical clines were explained by historical factors such as postglacial migration (Breitenbach-Dorfer et al. 1992; Hussendörfer and Müller-Starck 1994), and in *Pinus muricata* D. Don by recent contact with formerly isolated populations (Millar 1983). Enzymic variation in *Fagus sylvatica* L. was related either to climate or to geography, depending on the marker investigated (Felber and Thiébaut 1984; Cuguen et al. 1985).

5.5.3.3 Physiological Properties of Genetic Markers A parallel issue to the relationship between enzymes and environment is the variation in enzymes' physiological properties. It has been demonstrated repeatedly that alleles coding for enzymes may differ according to environmental conditions.

For example, differences in specific enzymes have been found in comparing related species occupying somewhat different thermal niches in the same area (Liu, Sharitz, and Smith 1978) or in comparing two clonal populations (Simons, Potuin, and Blanchard 1983; Simons, Charest, and Peloquin 1986).

Differences in function for the same enzyme have also been described in several widespread plant species at the population level (McNaughton 1974). Kinetic parameters of an enzyme can be associated with the climate the organisms experience, in that enzymes appear to function with the greatest efficiency or regulatory ability under the conditions an organism normally encounters.

Relatively small temperature differences among habitats may be associated with enzyme differences at the interspecific and intraspecific levels. Lumaret's (1984) study of polymorphism of the glutamate oxaloacetate transaminase (GOT1) of *Dactylis glomerata* L. found that the enzyme's relative temperature activity was consistent with the expected temperature in the clines of the natural populations based on the altitudinal and latitudinal gradients. Another example is that of isocitrate dehydrogenase (IDH) in European silver fir, *Abies alba* Miller. A latitudinal frequency cline was observed for the two forms of that system. Thermostability measurements demonstrated that the most frequent form in the South was more adapted to high temperature (Bergmann and Gregorius 1993).

5.5.3.4 Genetic Response to Climate Change—An Outlook Investigating genetic diversity in the context of projected climate change would present a number of opportunities. For example

1. Research could focus more strongly on assessing how plants react to natural or induced environmental changes. Phenotypic plasticity is a complementary approach to genetic studies. Phenotypic plasticity would determine species' short-term ecological response to climatic changes and would indicate how populations react to these according to elevation, and, in particular, if marginal populations differed from central ones. In addition, in some cases phenotypic plasticity might buffer the effect of climatic change.

2. Under the hypothesis that spatial scale mimics timescale, the variation of a single genetic marker might be investigated along environmental gradients paralleling the forecasted climate change. Correlations might be found between genetic markers and environmental variables, and their response to selection might be tested. Tools might be thus developed for monitoring a species' genetic response to climate change. However, correlation is not causality, and it would be important to test the response of markers to selection. If a genetic marker were directly subject to selection, physiological differentiation should be found in the different expressions of the genes (alleles). In that context, the activity of alleles could then be tested according to the suspected ecological parameter. Yet to be used, a genetic marker should not necessarily itself be submitted to selection but could just be tightly linked

to the selected gene. If recombination between the selected gene and the observed genetic marker were sparse, there would be no restriction on using such a marker. In that case, selection could be tested by reciprocal transplant experiments. However, an impressive number of genetic markers is available, and many dead ends might be encountered that could not be forecast. Therefore, more species differing in life history traits and distribution patterns would have to be analysed, and more genetic markers would have to be tested before generalizing.

5.5.4 Summary

- Genetic diversity is a prerequisite to adaptation to new environmental conditions; in general, big populations are less prone to genetic uniformity than small ones.
- Two opposing factors regulate genetic differentiation: selection (differentiating) and gene flow (unifying).
- Phenotypic plasticity is an important factor in the response to ecological changes.
- Adapted genotypes can be selected within a few years following an ecological change.
- Relationships between ecological gradients like climatic gradients and genetic clines have been regularly found.
- Genetic clines along ecological gradients may be correlated with physiological differences at the enzyme level(s).

5.6 THE RESPONSE OF THE SUBALPINE-ALPINE VEGETATION AND SOILS TO CLIMATE CHANGE: INTEGRATING ECOSYSTEM COMPONENTS ACROSS MULTIPLE SPATIAL SCALES

In the face of climate change, plants have three options: adapt in situ to the new conditions, migrate to more suitable habitats, or become extinct (Bazzaz 1996). Many contributions have considered the possible response of vegetation and ecosystems to the impact of climate change due to the doubling of the atmospheric CO_2 concentration and the increase of other greenhouse gases in the atmosphere (e.g., Bazzaz 1996; Bolin et al. 1989; Cramer and Leemans 1993; Gates 1993; Huntley 1991; Markham, Dudley, and Stolton 1993; Peters and Lovejoy 1992; Tegart, Sheldon, and Griffiths 1990; and Woodward 1992). The reaction of mountain and alpine plants and vegetation to climatic change has already been discussed several times, and various hypotheses and predictions have been proposed (e.g., Gottfried, Pauli, and Grabherr 1994; Grabherr, Gottfried, and Pauli 1994; Grabherr et al. 1995; Guisan, Theurillat, and Spichiger 1995; Halpin 1994a, 1994b; Hofer 1992; Holten and Carey 1992; Klötzli 1992, 1994; Körner 1992, 1993a, 1994, 1995; Markham, Dudley, and Stolton 1993; Ozenda and Borel 1991, 1994;

Theurillat 1995). Two main hypotheses have been put forward repeatedly concerning the migration of species:

1. Species will respond individually.
2. Species' response will not keep pace with the forecasted changes.

Thus, a climatic change might induce shifts in the abundance and distribution of species, extinctions, or adaptations to new ecological conditions (Holt 1990).

However, species also interact at different levels of complexity such as synusiae, plant communities, vegetation complexes, and landscapes. Because of their complex organization and structure and their relationship with abiotic factors, climate change can affect these levels differentially, and they may affect in return species' individual response. The following section attempts to evaluate such a differential response according to levels of complexity, using evidence from changes in the vegetation during the Holocene.

5.6.1 Synusiae

Climate change will directly affect synusiae of the dominant layers, like tree synusiae of forests, if they belong to climatic climax plant communities, although the impact may be gradual (see the example with *Fagus grandifolia* Ehr. and *Tsuga canadensis* (L.) Carrière below). In mixed forests, the dominance hierarchies may change if the species have different physiological amplitudes to temperature, for instance for bud burst, which initiates the growth period. These synusiae may be less affected if they belong to an azonal or extrazonal edaphic climax, where the habitat conditions could compensate for the new climate. Simulated distributions in response to climate change have been modeled for several important European tree species (e.g., Huntley et al. 1995; Sykes, Prentice, and Cramer 1996).

In the subalpine-alpine belts, some heath synusiae, determined by a few dominant clonal species, appear to be finely tuned to climatic factors, whereas others have a thermal inertia of at least 3 K based on their altitudinal amplitude. Investigations in the Ecocline project (Schlüssel and Theurillat 1996) show that the thermophilous ecosystem, with *Arctostaphylos uva-ursi* (L.) Sprengel, is composed of two systems of synusiae that intergrade into each other gradually. With a temperature increase the lower system would push the higher system upward, but without any change in the species composition, because the two systems' dominant synusiae have the same floristic composition. The synusial structure of the mesophilous ecosystem, with *Rhododendron ferrugineum* L. and *Empetrum hermaphroditum* subsp. *hermaphroditum* (Hagerup) Böcher, presents a great altitudinal uniformity for the dominant synusiae. Therefore, an increase in temperature alone would not modify the general structure of this ecosystem, whose driving factor is snow cover protecting species to sensitive late frost. However, a reduction in the length of snow cover could lead to an important change both in the synusial structure and in the species composition through frost damage.

Synusiae of the lower layers, like small herb synusiae or bryophyte synusiae of forests or shrub communities, may not react directly to climate change, but only indirectly through a change in the dominant synusiae of the phytocoenose, which in turn affects the conditions of the microhabitats such as microclimate, water and nutrient availability, and quantity and quality of light (e.g., Knapp, Smith, and Young 1989; Bahn et al. 1994; Svensson, Floderus, and Callaghan 1994). In particular, bryophyte synusiae may behave independently from synusiae dominated by vascular plants, implying that it may be useful to establish the present relationship of bryophyte synusiae to vascular plant vegetation. To our knowledge, no such analysis has been conducted in the European Alps since Frey 1922. Factors to consider may include changes in diversity, productivity, reproductive pattern, or interaction with other plants.

In the future, we could imagine a greater development of the cover of a dominant synusia with big leaves; such a development might cause the synchronal lower synusiae to disappear (Körner 1991, 1993a). Alternatively, lower synusiae or a part of them may well persist in new evolving phytocoenoses if the conditions of their microhabitats are left substantially unchanged. This would be the case for the lower synusiae developing before the others in early spring, in the absence of competition for light and nutrients at the time they grow, although these species might have a lower level of photosynthetic activity in an enhanced CO_2 environment (e.g., *Primula elatior* (L.) L.) compared to dominant species (Körner 1991, 1993a).

A historical example of an understory species' persistence may be the present distribution of the Compositae *Aposeris foetida* (L.) Less. at the foothills of the northeastern Alps (Bavaria, Austria). Its present distribution exactly matches the former distribution of the Norway spruce (*Picea abies* (L.) Karst.) before beech (*Fagus sylvatica* L.) replaced spruce a few thousand years ago in the region (Küster 1990).

Global warming would also modify competitive relationships among plant functional types, such as life forms (Körner 1992, 1993a). For example, deciduous dwarf shrubs (chamaephytes) such as bilberry (*Vaccinium myrtillus* L.) and bog bilberry (*V. uliginosum* L.) are unlikely to prevent low nanophanerophytes such as alpenrose (*Rhododendron ferrugineum* L.) from growing in mesophilous conditions with enough snow cover in winter, or dwarf juniper (*Juniperus communis* subsp. *alpina* (Suter) Celak) from growing in meso-thermophilous conditions if these nanophanerophytes can colonize open microsites. Alpenrose heaths are likely to be invaded by green alder (*Alnus viridis* (Chaix) DC.), however, if mean air temperature increases (i.e., there is a longer growing season). But alpenrose may not be completely outcompeted under the cover of the green alder or associated tall herbs unless precipitation and/or eutrophication increase strongly, because it can grow as an understory plant.

Another important effect of climate change at the synusial level would be that the exotic species would be likely to invade particular synusiae of plant communities, at least in the lowest vegetation belts (colline, montane; see section 5.6.2).

5.6.2 Plant Communities

Climatic climax and edaphic climax plant communities may respond differently to climate change. Climatic climax communities respond by searching for a novel equilibrium with the available flora (e.g., Graham and Grimm 1990; Tallis 1991). This is considered to have been the case for the changes in vegetation in general since the last glaciation. For example, it has been shown for the beech-hemlock forest (*Fagus grandifolia* Ehrh.—*Tsuga canadensis* (L.) Carrière) in the Great Lakes region of eastern North America that the ranges of the two species have been fully coincident only during the past 500 years, whereas they have overlapped since around 6,000 years BP (Graham and Grimm 1990; Moore 1990).

A climatic community may persist in places with suitable edaphic conditions and so withstand the new climate as an extrazonal, edaphic climax (Walter 1984, 1985). For example, the pioneer alluvial pinewoods with Scots pine (*Pinus sylvestris* L.), buckthorn (*Hippophae rhamnoides* L.) and juniper (*Juniperus communis* L.) are presently edaphic plant communities, but were climatic climax at the Alleröd period (Pott 1993). The absence of competing, better-adapted species can even result in the persistence of the vegetation, even vegetation that does not correspond to the climax, given that the species can endure the new conditions physiologically or adapt genetically. The climatic climax of the thermocolline belt in the Insubrian climate at the Alps' southern border corresponds to forests with laurophyllous species. Because this climax vegetation could not recolonize the area from their refugia during the Holocene, the belt is now occupied by oak woodlands with chestnut (Gianoni, Carraro, and Klötzli 1988; see also Klötzli 1988).

For edaphic climaxes, plant communities can sustain a climatic change providing their limiting factors are not modified ("buffering"; Jonasson 1993). However, their range may change in relation to the positive or negative synergy of the climate change on such limiting factors. Thus, we can recognize a persistence (Pimm 1984) of the edaphic plant communities at three levels: persistence in time (several thousand years), persistence in space (several thousand kilometers), and persistence in altitude (several hundred meters). The examples in table 5.2, taken from the vegetation classes of Europe, particularly of the Alps, illustrate these three types of persistence during the Holocene. Cliffs and rock cavities offer examples illustrating the persistence of vegetation in time. For instance, carbonate rock cavities with dripping water in the northwestern Mediterranean area (mountains of Spain, Maritime Alps, Apennines) are colonized by maidenhair fern communities (*Adiantum capillus-veneris* L.) with several ancient endemic species of butter-

Table 5.2 Persistence of vegetation

	Time persistence	Spatial persistence	Altitudinal persistence
Asplenietea trichomanis[a]	×[1,2,3]	×	×
Montio-Cardaminetea[b]	×[4]	×	×[4]
Scheuchzerio-Caricetea fuscae[c]	×[5]	×	×
Isoëto-Nanojuncetea[d]	×	×[6]	
Adiantetea[e]	×[7]	×[7]	
Salicetea herbaceae[f]	×	×[1,8]	
Elyno-Seslerietea[g]	×[3]	×	
Thlaspietea rotundifolii[h]	×[1,3]	(×)	
Koelerio-Corynephoretea	×	(×)	
Caricetea curvulae[i]	(×)	(×)	
Festuco-Brometea[j]	×		
Oxytropido-Elynetea[k]	×		
Potametea[l]		×	
Phragmiti-Magnocaricetea[l]		×	
Oxycocco-Sphagnetea[m]		×	
Loiseleurio-Vaccinietea[n]		×[7]	
Vaccinio-Piceetea[o]		×[7]	

Note: ( ) partial persistence.

[a] cliffs; [b] springs; [c] swamps; [d] temporarily wet, bare habitats; [e] calcareous rock cavities with dripping water; [f] snowbeds; [g] cryophilous alpine swards: [h] screes; [i] some acidophilous alpine swards; [j] some dry grasslands; [k] some calcicolous alpine swards; [l] aquatic habitats; [m] peat bogs; [n] subalpine and alpine heaths; [o] boreo-montane forests. [1] Braun-Blanquet 1948; [2] Rechinger 1965; [3] Pawlowski 1970; [4] Zechmeister and Mucina 1994; [5] Braun-Blanquet 1967; [6] Grabherr and Kojima 1993; [7] Deil 1989, 1994; [8] Braun-Blanquet 1964.

worts (*Pinguicula* ser. *Longifoliae*) since the Miocene (Deil 1989, 1994). Cliffs of the southern Alps also offer examples of vegetation persistence in time, especially plant communities on limestone in the Maritime Alps with their ancient Tertiary relict species of the genera *Saxifraga* L. and *Moehringia* L. (Rioux and Quézel 1949).

New plant communities are likely to develop and partially replace the present ones, most likely of an intermediate composition compared to present communities. However, provided that there is no immigration of new species, they will still belong to the higher phytosociological classification units (alliances, orders, classes) known for the European Alps, because of their similarity to present species composition, and because of the limits for rapid dispersion of new invaders, particularly in the alpine belt. However, climate change may favor cultivated exotic species' invasion of natural plant communities. For instance, in the oak-chestnut woodlands of the thermocolline belt under the Insubrian climate at the southern border of the Alps, a whole array of cultivated, exotic laurophyllous species are invading the understory in the warmest places, where they now successfully reproduce ("laurophyllisation"; (Gianoni, Carraro, and Klötzli 1988; Klötzli et al. 1996).

In the most favorable sites, they are already part of the tree layer (Walther 1996; Carraro et al. in press). A plausible explanation for this expansion is the unprecedented sere of mild, nearly frostless winters which have occurred for several years.

5.6.3 Landscape

The natural landscape is constantly changing with time, independent of climatic variations. Changes in the landscape may be either slow and progressive or rapid and abrupt. The landscape can change slowly and inconspicuously toward an equilibrium with climatic conditions, as in the case of the beech-hemlock forest of eastern North America discussed above, or it can change rapidly, as in the case of natural catastrophes (e.g., volcanic eruptions, rock falls, floods, windstorms, fires, or climatic anomalies such as long droughts; e.g., Stine 1994; Street-Perrott 1994).

The cultural landscape (*Kulturlandschaft*) is changing very rapidly through human activities. Human impact is often more significant than other factors. The ecosystems and landscapes that respond to climate change may be very different than those found today (Di Castri 1992).

Landscape may respond very noticeably and differentially to climate change as it integrates all ecological and historical factors. Several examples during the Holocene illustrate a differential response of the vegetation, either lagging or expanding very rapidly within a landscape.

As an example of differential response within the same region, Küster (1990) showed, for the Auerberg Mont (1055 m a.s.l.) in the foothills of the northern Alps in southern Bavaria (Germany), significant differences in the development of past vegetation among three sites separated by only three kilometers with no physical barrier between them. Pollen profiles indicate that Norway spruce (*Picea abies* (L.) Karsten) arrived as much as 700 years later at the western site compared to the southern and the eastern sites. Also, the local extension of the species differed significantly among the sites. Around 7,000 years BP, the southern site supported less than 10 percent *Picea*, whereas pollen profiles for the western and the eastern site suggested 24 percent and 30 percent, respectively. These kinds of differences among the sites also occurred later during the expansion of European silver fir (*Abies alba* Miller) and beech (*Fagus sylvatica* L.).

The change in vegetation after the Wisconsin glaciation in the Grand Canyon (Arizona) is another example of differential response to general climate. There, changes in vegetation lagged changes in climate by 1,000–3,000 years (Cole 1985; Lewin 1985).

An example of a rapid expansion over a larger area is the expansion of Norway spruce (*Picea abies* (L.) Karsten) in the Scandes Mountains in Sweden. There, the presence of spruce has been recently confirmed more than 5,000 years prior to the date assumed using inferences from pollen data (Kullman 1995, 1996b). Spruce appears to have expanded its range very early after deglaciation to specific microhabitats up to some 1,000 km away from the nearest source area. According to Kullman (1996b), this demonstrates a climate-plant equilibrium prevailing throughout the Holocene.

5.6.4 Assessments

5.6.4.1 Impact of Global Change on Bryophytes Although bryophytes possess mechanisms (poikilohydry) allowing them to withstand drought, their broad altitudinal distribution is nevertheless related to general climate. Therefore, climate change might threaten the survival of stenoicious species restricted to a specialized habitat. For example, species living in the coldest habitats might disappear, like the bryophyte community *Dermatocarpetum rivularis* from seasonal high altitude, cold springs of melting water of permafrost block screes, with *Hydrogrimmia mollis* (B., S. & G.) Loeske, the moss species characteristic of this habitat, which has hardly ever been found with sporophytes in Europe (see Geissler 1976). Another example might be the coprophilous *Voitia nivalis* Hornsch. growing on chamois (*Rupicapra rupicapra* L.) excrements in *Carex curvula* All. swards between 2,500 and 2,700 meters a.s.l. in the eastern Alps. Generally speaking, species with a wider ecological amplitude than stenoicious species should not be threatened, especially if they show a high genetic variability and phenotypic plasticity, although fragmentation of their populations might occur.

Increasing atmospheric CO_2 concentration and nitrogen emissions, temperature, and humidity in a projected climate change would stimulate bryophyte growth (Sveinbjörnsson and Oechel 1992). Jauhiainen, Vasande, and Silvola (1994) showed through laboratory experiments with *Sphagnum fuscum* (Schimp.) Klinggr. that elevated CO_2 increase reduces length increment but has no effect on biomass production, and that supraoptimal nitrogen supply limits growth (see also Lee, Baxter, and Emes 1990). Nitrogen then becomes available to the higher plants, thereby changing the competitive relationships between mire species. Thus, although both productivity and the frequency of sexual reproduction might increase under predicted climate change, abundance might be reduced because of competition with more successful higher plants (Herben 1994). For the special habitat of northern peat lands, Gignac and Vitt (1994) predicted a decrease in bryophyte cover as a consequence of elevated evapotranspiration with global warming.

Wet acidic depositions would mainly affect neutrophilous taxa, with less effect on acidophilous species, which have natural resistance to low pH, and on calcicolous species, which have a naturally higher buffer capacity (Farmer, Bates, and Bell 1992). Many rare alpine bryophyte species belong to this latter ecological group. However, below pH 3.0, growth and reproduction decrease significantly, even with acidophilous species (Raeymakers and Glime 1986).

5.6.4.2 Broad-Scale Impact on Vascular Plants Because of the different distribution patterns of orophytes and endemics, many aspects are involved in assessing how climate change might affect their respective distributions that relate to other important factors instrumental in determining their distribution (such as history, topography, climate, and physiology).

According to Scharfetter (1938), glaciation was more destructive than the warmest interglacial periods. However, the warmest interglacial periods enabled forests to climb higher toward the summits of low mountains (1,800–2,300 m), thereby reducing many orophyte populations. This would be the case in global warming for many isolated endemics and orophytes living presently in refugia, such as tops of low mountains, mainly in the eastern Alps, because they would have almost no possibility to migrate higher (in the present nival belt), either because they could not move there rapidly enough, or because the nival zone is already absent (Grabherr, Gottfried, and Pauli 1994; Grabherr et al. 1995; Gottfried, Pauli, and Grabherr 1994). In addition to competition and changes of habitat conditions, one of the most important factors for orophytes might be their potential to acclimate their respiration at night (dark respiration) to a higher temperature (see Larigauderie and Körner 1995). The present altitudinal range, population size, conservation status (endangered/threatened or not), ecology (cool, wet or dry, warm habitats), and genetic and phenotypic diversity are parameters to be taken into consideration when assessing the general response of both a species and a particular population. However, a linear response to a temperature increase would be very unlikely. An increase of 1–2 K would still likely be in the range of tolerance of most alpine and nival species, but a greater increase (3–4 K) might not be (Theurillat 1995) (see also sections 5.6.4.4 and 5.6.4.5).

Endemics and orophytes with extant distributions are not expected to disappear in the climate change predicted. Likewise, species having a great potential for adaptative responses through genetic diversity, phenotypic plasticity, high abundance, or significant dispersal capacities are at the least risk of extinction (Holt 1990). However, the European Alps do not constitute a uniform orobiome (Walter 1984, 1985), and climate change might not have the same impact everywhere. Ranges of species showing a disjunction (north-south, east-west) or fragmented distribution might become even more fragmented, with regional disappearances, if they could not persist or adapt. Many plant populations interconnected today along a continuous alpine zone could become separated into isolated populations on the tops of some mountains (habitat fragmentation).

Plants from cold habitats, and from mesophilous habitats to some extent, would have to migrate upward and northward to find habitats with suitable conditions, unless they could persist locally because of favorable edaphic conditions. Isolated arctic, stenoicious, relict species that are pioneers in wet habitats might disappear, since these habitats are very limited and the implantation of artificial lakes for hydroelectric plants has already destroyed many. On the other hand, an increase in temperature should not affect endemics and orophytes inhabiting rock fissures in the montane and subalpine zones of the southern Alps because they are already adapted to extreme conditions, particularly if they grow on limestone. This flora appears to have survived abrupt and rapid warming (7 K) during the glacial-interglacial period (Zahn 1994).

5.6.4.3 Responses of Forests For the climatic climax or zonal vegetation, a quantitative change directly proportional to global warming could be expected, as Brzeziecki, Kienast, and Wildi (1995) showed for the forests of Switzerland. In proposed climate scenarios, warming is expected to be greater in the northern part of the Alps, and precipitation greater in the southern part. Because an increase in precipitation should mitigate the effects of the temperature increase, changes in the vegetation are less likely to occur under the humid Insubrian climate (e.g., Brzeziecki, Kienast, and Wildi 1995). For a 1–1.4 K increase in temperature, 30–55 percent of the forested pixels of Switzerland show a change of their classification types (phytosociological suballiances), according to a Geographic Information System–assisted sensitivity assessment (Kienast, Brzeziecki, and Wildi 1995, 1996). Classification changes are predicted for 55–89 percent of the forested pixels for an increase of 2–2.8 K. Analysis of the adaptation potential for the dominating tree species with a diameter at breast height (DBH) of at least 12 cm shows an increase of poorly adapted pixels from 25–30 percent for today's situation to 35–60 percent for a 2–2.8 K increase. This situation is reduced to 8–15 percent for the 2–2.8 K scenario when the analysis includes trees with a DBH of less than 12 cm.

However, forests' responses to climate change, and in particular tree species' responses, cannot be assessed based only on static modeling, without taking into account the dynamic aspect of transient stages. But even with dynamic models (see chapter 6), not every aspect can be considered, such as chilling temperatures, and the effect of late frosts, or the adaptation potential of tree species through their high genetic diversity, regional variability, and the maintenance of that genetic diversity. For instance, populations of Norway spruce (*Picea abies* (L.) Karsten) in northern Italy show a lower genetic variability than those in Switzerland and south Germany (mean of 1.8 alleles versus 2.4–2.6 per locus; 16.2 percent heterozygosity versus 22.2–25.2) (Müller-Starck 1994).

5.6.4.4 Responses of the Subalpine-Alpine Ecocline One widespread hypothesis (e.g., Ozenda and Borel 1991, 1994) is that global warming would shift vegetation belts upward in a more or less regular pattern. For example, the subalpine belt would shift upward into the area presently occupied by the alpine belt, which itself would shift into the present nival belt (figure 5.7). In contrast, Halpin (1994a, 1994b) hypothesized that a global, linear, upward shift in vegetation would not take place. Instead, he proposed that the vegetation zones' size and composition would change dramatically, though not in a regularly ordered pattern. Nevertheless, the difference

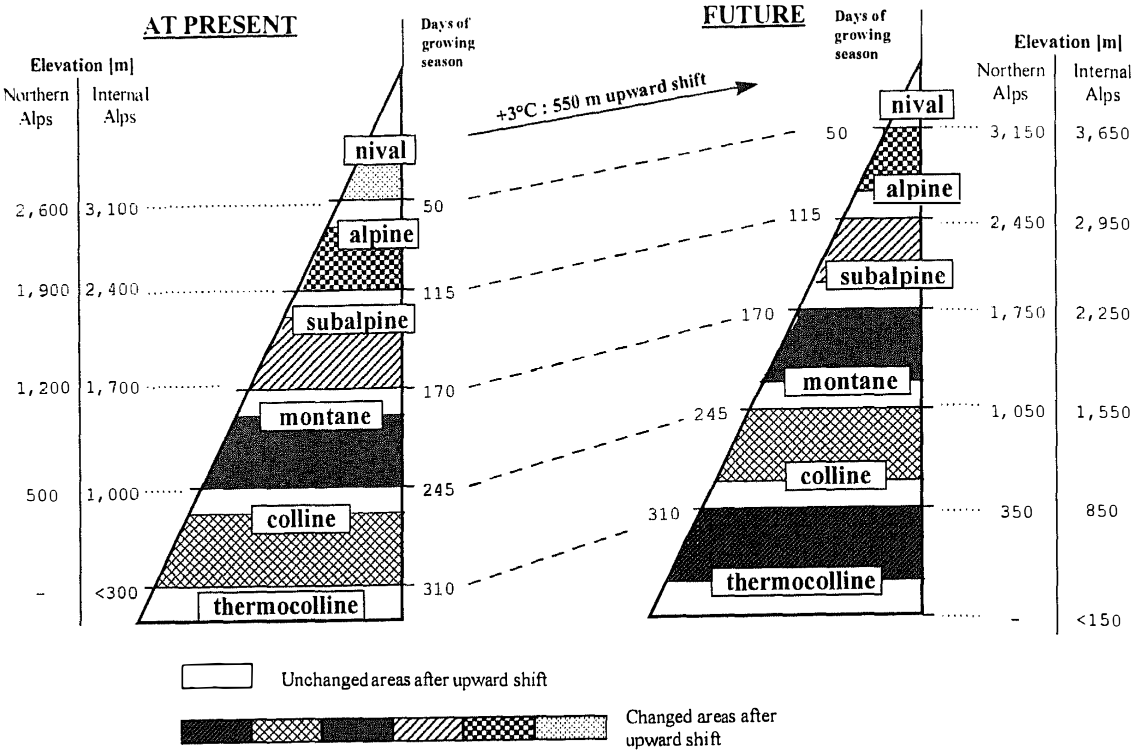


Figure 5.7 Linear upward shift of vegetation belts for a 3°C warming. It is predicted that more than 75 percent of each of the present belts would be occupied by the vegetation belt currently below; that is, less than 25 percent would stay unchanged. Elevations are given for the upper limits of each vegetation belt at present and for the future.

between these two viewpoints seems mainly conceptual (bioclimatic zone vs. ecoclimatic zone). In reality, the potential climatic climax is the same in both cases. Although the hypothesis of an upward shift of the present vegetation is tenable at a broad scale, the impact of climatic change will have to be appreciated at finer, regional, ecological scales. Therefore, regional climate scenarios are essential.

At the tree line, changes in vegetation would be complex. There, extreme events, edaphic and topographic factors already prevail, as in the alpine vegetation belt (see sections 5.4.2.3 and 5.4.3). Harsh topoclimates influence the establishment and growth of trees (e.g., Tranquillini 1979; Slatyer and Noble 1992; Holtmeier 1994). For phanerophytes, the *kampfzone* represents a temperature-related threshold whose inertia compensates for positive and negative variations in climate, preventing a linear variation of the forest limit (figure 5.8). For the tree line to expand upslope, even where it was artificially lowered by man, would require a more favorable climate for at least 100 years (Holtmeier 1994). Photogrammetric observations in Glacier National Park in northwest Montana during the last twenty to seventy years confirm this hypothesis, because tree lines under natural conditions have not yet moved, despite a 0.5 K warming during this century (Butler et al. 1994). Principally from palynological and macrofossil investigations, it was deter-

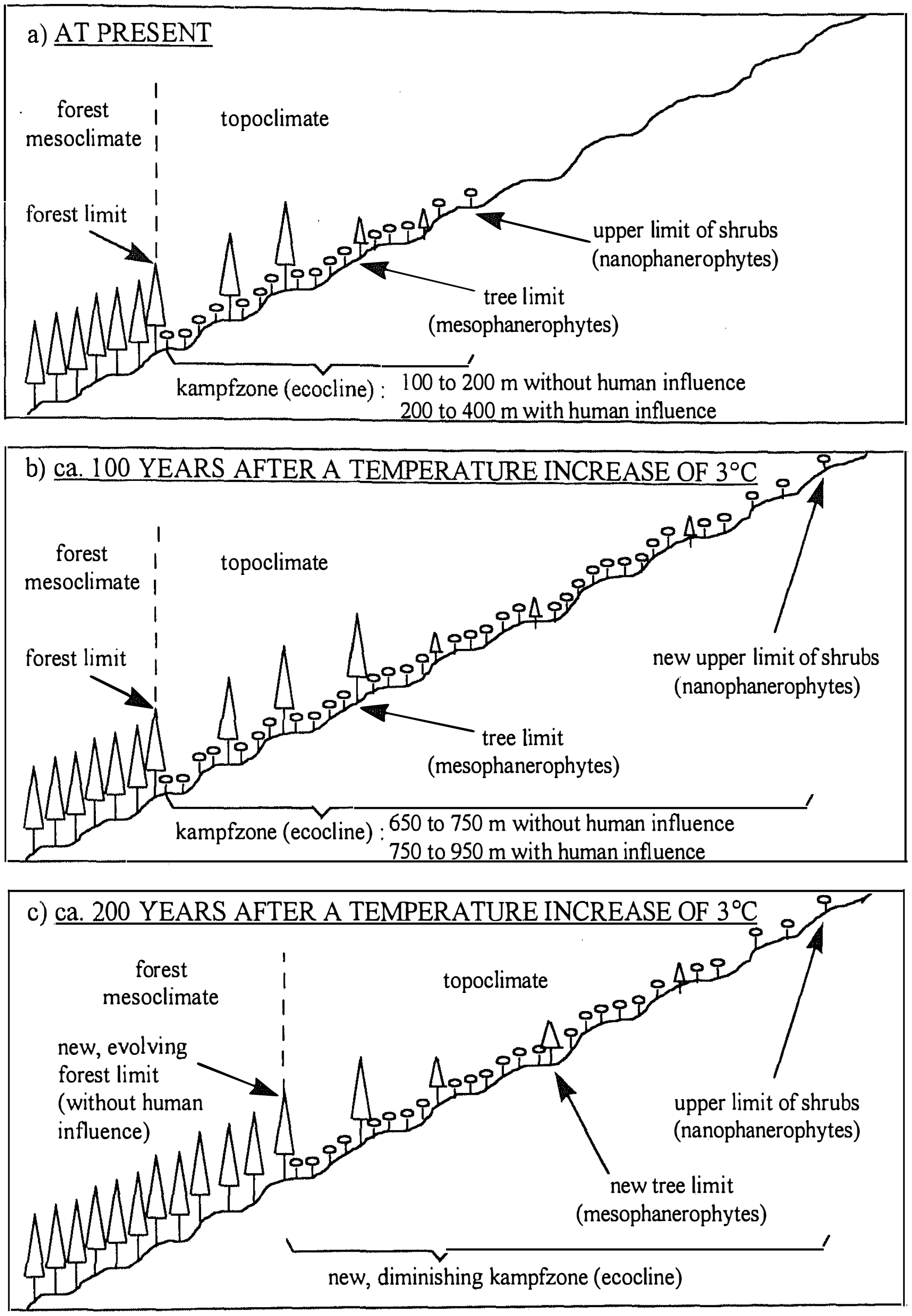


Figure 5.8 The subalpine-alpine ecocline (a) at present and its predicted evolution after a 3 K warming (b) for 100 years and (c) for 200 years.

mined that the forest limit did not extend upward more than 100–300 meters during the warmest periods of the Boreal and Atlantic periods of the Holocene (e.g., Burga 1988, 1993, 1995; Bortenschlager 1993; Lang 1993). Based on the general agreement that the mean annual temperature was 2–4 K greater than today during these periods, the forest limit would have been expected to extend from 350 to more than 700 meters higher for the 0.55 K/ 100 meter gradient, reaching the high alpine belt, in obvious nonconformity with palynological observations. Interestingly enough, however, these elevations match recent pedoanthracological observations (i.e., of soil charcoal) (Carcaillet, Barbero, and Talon 1996; Talon 1997). The apparent contradiction between the two methods could be elucidated by taking into consideration that charcoal of trees from the alpine belt is very likely that of *krummholz* (nano- and microphanerophyte) plants, which rarely or never produce pollen under the conditions of the alpine belt, explaining to some extent their absence in alpine pollen profiles.

Therefore, we can put forward the hypothesis that on one hand, an increase in mean annual temperature of 1–2 K might not shift the present forest limit upward by much more than 100–200 meters. Yet the tree line and the subalpine-alpine ecocline in general might show a greater and quicker response than the forest limit, with low trees occupying favorable places in the low alpine belt. On the other hand, it is inconceivable that the inertia of the temperature-related threshold would withstand a 3–4 K increase, equal to the temperature amplitude of an entire vegetation belt. With such an increase, the *kampfzone* would very likely invade the alpine belt, with a later shift in the forest limit into the low alpine. Indeed, heaths (chamaephytes) and to a lesser extent shrubs (nanophanerophytes) would likely react faster than forest ecosystems to a warming, invading alpine meadows within a few decades. Hence, the subalpine-alpine ecocline might extend upward with expansion of heaths following a warming, whereas the upslope expansion of forest would likely be much slower (panel (b) of figure 5.8). If a temperature increase of more than 2 K persisted for several centuries, forests could develop at higher elevations than at any time since the last glaciation. For a 1–2 K increase, human use might play a substantial role either in slowing down the upward shift of the subalpine vegetation through grazing or accelerating it through the abandonment of agricultural practices and afforestation.

Given the predicted climatic scenarios, those plants most apt to colonize the *kampfzone* and the low alpine zone would be those that combine properties such as climatic optimum in the subalpine level, moderate insensitivity to the present pH of the soil, efficient use of nitrogen, ability to have a positive feedback on the soil, resistance to soil movements, and a strong competitive ability, both in the short term (*r* characteristics) and in the long term (*K* characteristics). In the northern Alps, green alder (*Alnus viridis* (Chaix) DC.) appears to be a suitable candidate, at least under a suboceanic climate. In the southwestern Alps and in the dry intra-alpine valleys, larch (*Larix decidua* Miller), a pioneer species, would very likely extend its distribution upward.

The situation of the subalpine-alpine ecocline would provide a wealth of possibilities for phytoindicators of climate change through (1) the modification of species and the dominant life forms in heaths, heath swards, and swards; (2) the balance between heaths and meadows; (3) the invasion of subalpine shrubs like green alder or prostrate mountain pine and trees like larch and arolla pine; (4) the persistence or disappearance of vegetation types; and (5) the positive or negative effects of soils, orography, and geology. However, the movement of the tree line itself, and even more of the timberline, would be unlikely to be used to monitor the effects of climatic change because of the slow rate of upward spread and possible downward movements through extreme events (Slatyer and Noble 1992).

5.6.4.5 Responses of the Alpine Vegetation Because it occurs at the top of high mountains, alpine vegetation would potentially be the most endangered by climatic change, even if a nival belt lay above the alpine belt. Indeed, edaphic factors (relief, aspect, substrate, soils, periglacial processes) would play a key role in the new distribution patterns of alpine vegetation in the present nival belt. Increasing steepness at the upper alpine and nival belt (slope greater than 40°; see figure 5.4) would totally modify the present ratio in the cover of plant communities. Very likely, the present middle and high alpine plant communities on slopes less than 40° (for example, snow beds with *Salix herbacea* L., alpine swards with *Carex curvula* All.) would shrink and even disappear in some places. However, partial persistence would be likely, at least at higher elevations and cooler orientations where cryogenic processes and permafrost would limit the altitudinal shift of more thermophilic species. Steep slopes and active, unstable screes (particularly of carbonate rocks) would react much more slowly. Vegetation colonization might happen extremely slowly, as shown by observations on permanent plots on machine-graded ski runs (Delarze 1994). Nevertheless, we should not forget that tree species occupied the alpine belt at very high elevations prior to the neolithic period, according to pedoanthracological research (Carcaillet, Barbero, and Talon 1996; Talon 1997).

As for the subalpine-alpine ecocline, we can put forward the hypothesis that on the one hand, an increase in mean annual temperature of 1–2 K might affect only the lower alpine belt. On the other hand, a 3–4 K increase, which equals the temperature amplitude of an entire vegetation belt, would be likely to change the vegetation of the present alpine belt substantially. Today's alpine belt might show, after warming, a mosaic of subalpine elements (isolated arolla pine, fragments heaths and swards) in the warmest and most stable places and alpine elements in the coldest and least stable ones (open cryophilous swards with *Elyna myosuroides* (Villars) Fritsch, *Juncus trifidus* L., *Festuca halleri* All., *Festuca quadriflora* Honck., *Carex firma* Host on ridges and ledges, cushion plant communities with *Silene exscapa* All., *S. acaulis* (L.) Jacq., *Minuartia sedoides* (L.) Hiern, *Saxifraga bryoides* L. on superficial mineral soil with solifluction). The present high alpine vegetation would shift into the nival belt, where it already exists, but its extension might depend more strongly on edaphic factors and less on the general climate.

To illustrate the possible evolution of the upper subalpine and alpine vegetation in the near future according to a mean plausible climatic scenario, table 5.3 provides an assessment for the two regions investigated in the Valais in the Ecocline project.

Table 5.3 Predicted evolution under environmental changes of the plant communities of the subalpine-alpine ecocline in Belalp and Val d'Arpette at the end of next century

Vegetation units	Belalp Present	Belalp Predicted	Val d'Arpette Present	Val d'Arpette Predicted
Subalpine *Picea abies* forest	–	?	+++	>
Subalpine *Pinus uncinata* forest	–	–	+++	>
Thermophilous *Pinus cembra* forest	–	–	+++	>
Mesophilous *Pinus cembra* forest	–	–	++	<
Prostrated *Pinus uncinata* scrub	–	–	+++	>
Alnus viridis scrub	++	≫	+	= / <
Subalpine mesophilous *Rhododendron ferrugineum* heaths	+++	<	+	<
Subalpine meso-thermophilous *Rhododendron* and dwarf *Juniperus* heaths	++	≫	++	= / <
Subalpine meso-thermophilous *Calluna vulgaris* heath	+++	<	–	–
Thermophilous *Arctostaphylos uva-ursi* and dwarf *Juniperus* heaths	+	>	+++	> / =
Cryophilous *Empetrum hermaphroditum* and *Loiseleuria procumbens* low heaths	+++	<	+	<
Meso-thermophilous *Vaccinium* spp. and dwarf *Juniperus* heaths	–	≫	+++	>
Subalpine *Nardus stricta* swards	+++	≪	–	–
Subalpine-alpine *Carex sempervirens* and *Nardus stricta* swards	+++	< / =	++	< / =
Subalpine-alpine *Carex sempervirens* and *Festuca puccinellii* swards	++	< / =	+++	<
Mesophilous subalpine-alpine *Agrostis schraderana* meadows	+++	<	++	<
Subalpine thermophilous *Festuca varia s.l.* swards	+	>	++	=
Subalpine mesophilous *Calamagrostis villosa* meadows	–	>	++	=
Alpine *Festuca varia s.l.* (heaths-) swards	–	–	+++	=
Alpine *Festuca halleri* swards	++	<	+	=
Alpine *Carex curvula* swards	+++	<	–	–
Alpine *Elyna myosuroides* swards	++	= / <	–	–
Alpine *Salix herbacea* snow beds	++	<	–	–
Eriophorum angustifolium neutral swamps	++	= / <	–	–
Trichophorum cespitosum neutral swamps	+++	= / <	+	<
Neutral swamps with *Carex* spp.	+++	=	–	–
Neutral swamps with *Carex nigra*	++	=	–	–
Molinia caerulea wet meadows	–	–	+	<
Springs sensu lato	++	=	+	<
Rock fissures	+	=	+++	=
Screes	++	=	+++	=

Note: Predictions are based on the following environmental changes: increase of mean annual air temperature of 3 K, increase of precipitation by 20%, increase of atmospheric CO_2 concentration to 700 $\mu g \cdot l^{-1}$, nitrogen deposition of 5–30 $kg \cdot ha^{-1} \cdot year$, ongoing acidification, and no change in human use. Present cover of plant communities: –: absent; +: 1–100 m^2; ++: 100 m^2–1ha; +++: > 1ha. Predicted evolution: >: increase; ≫: strong increase; <: decrease; ≪: strong decrease; =: no change; ?: uncertain. Both sites located on siliceous rocks. The Belalp site (3 km^2, east oriented) is larger than the Val d'Arpette site (2 km^2, south oriented).

5.6.5 Assessments of the Response of the Subalpine-Alpine Soils

Climate change might have direct and indirect effects on subalpine and alpine soil ecosystems. The most important effects would concern the evolution of permafrost, the processes of material transfer, changes in the organic matter, and changes in nitrogen supplies. Johnson (1993) discussed several issues about the potential impact of climate change on the carbon cycle.

5.6.5.1 Differences between Carbonate and Noncarbonate Soils Climate change would have different effects on carbonate and noncarbonate soils. Because limestone soils have large chemical buffering capacity (Duchaufour 1983), their internal processes are less sensitive to changes than those of acid soils. Carbonate soils are characterized by an iron deficiency, large phosphate and HCO_3^- supplies, and the presence of nitrates instead of ammonium (e.g., Gigon 1971, 1983, 1987).

The weak physicochemical resistance of acid soils (except for the most evolved podzols) rapidly leads to changes in the soil's internal functioning. For example, the clay-humus complex may break up, acidity may increase, or aluminium may dissolve at toxic levels because of its solubility at low pH. Breymeyer and Uba (1989) arrived at similar conclusions by observing the decomposition of litter, which appeared to be faster on granitic soils.

5.6.5.2 Changes in Permafrost Cryosoils are closely associated with the distribution of permafrost. These soils have a permanently frozen layer at a certain depth below ground level and reduced biological activity. They can be practically bare of humus in the most extreme conditions where vegetation has hardly taken root, or they can show signs of organomineral evolution (humus-containing cryosoils). Study of the two types of surface, including colonization by vegetation and the evolution of organic residues, yields useful information about changes in permafrost. This pedological approach is a useful aid to studying permafrost, the thawing of which could be a major and rapid consequence of global warming. Depending on its type and thickness, the thaw of a permafrost body might take decades to centuries after an increase in the mean annual air temperature (Häberli 1994, 1995; Keller 1994).

5.6.5.3 Changes in the Processes of Material Transfer Soil supports numerous upward and downward movements of material. In an alpine climate, downward movement generally dominates upward because of a positive balance of precipitation over evapotranspiration. However, certain mesoclimates may be exceptions to this rule: the southern Alps, influenced by the Mediterranean climate with a dry summer season, and the inner Alpine valleys, with a continental tendency up to fairly high altitudes (e.g., at Zermatt, Valais). Thus, scenarios for material transfer under climate change must take mesoclimate into account.

The balance between precipitation and evapotranspiration determines the intensities of the three main downward transport mechanisms: *leaching* of dissolved ions, *flushing* of clay and *cheluviation* of organometallics. Any scenario under climate change must therefore take into account the distribution of precipitation over the year of the observed changes, especially in the spring (plants begin to grow, snow melts, podzols develop further) and in summer (maximum temperatures, maximum productivity).

In a more general context, Post et al. (1982) suggested that the pool of organic matter increases with precipitation, decreases with temperature (at constant precipitation), and increases with the ratio of precipitation over evapotranspiration. Johnson (1993) experimentally studied the effect of temperature increase's effect on the release of organic acids in podzolized subalpine soils. Their main conclusions: "Warming will likely lead to a decrease in organic acid leaching and to an increase in carbonic and/or nitric acid leaching, depending on soil nitrogen status ... Thus, a significant increase in soil temperature in cold-region soils may well lead to a shift from organic to carbonic acid dominance, with attendant changes in soil solution pH (increase) and iron and aluminium transport by cheluviation (decrease)." (See also Johnson et al. 1977, 359).

Leaching of basic cations could also be affected. Dambrine (1985) demonstrated the utility of the gravity flow fraction of the major elements in the soil solution for detecting short-term processes, and Keller (1991) investigated the case of heavy metals. Although these results appear to be clear-cut as regards temperature, they say nothing about the combined effects of changes in precipitation, evapotranspiration, and temperature. It is well known in ecology that the single-factor behavior of a process can be quite different from its multifactorial behavior.

5.6.5.4 Changes in Organic Matter How organic carbon in the soil would change as a result of climate change is unclear. Although experiments suggest that soil carbon would increase with rising temperature (Van Cleve, Oechel, and Hom 1990; Anon 1992; Gifford 1994), global models provide contrary patterns (Olson 1963; Melillo, Aber, and Muratore 1982). Studies on local mountainsides indicate that it is premature to draw conclusions because of the intervention of other ecological factors (e.g., links between organic matter and clays) and because of the diversity of organic matter in the soil. For example, Johnson (1993, 357) stated, "Thus it would seem unlikely that soil organic matter will follow the same idealised decay curves as fresh litter does."

Besides the stocks of organic matter, another aspect of soil organic matter that climate change could modify is its rate of decomposition, which is itself linked to the vegetation (Tinker and Ineson 1990). Higher temperatures would increase animal and microflora activity, which might enhance decomposition rates of organic matter in the subalpine and alpine soils. However, the quality of organic matter and litter prevails in the processes of decomposition, in particular, nitrogen content and the relative concentration of lignin and acid-soluble carbohydrates (Hobbie 1996). Thus, other effects might result from climate change.

For instance, subalpine ericaceous heaths might be able to colonize alpine meadows as the mean temperature increases. The quality of the litter might change with this change in flora. The more resistant, acidifying residues of the heath plants might dominate the more easily decomposable debris of the herbaceous meadow plants. Woody structures and thick cuticles in the litter are more resistant to physical degradation, and their chemical decomposition releases products like phenolic acids, which form complexes with metals, or like tannins, which are toxic to bacteria. A multiple effect could then result: increase in the carbon stock in the holorganic layers, decrease in biological activity, and increase in chelates.

Another important aspect to be taken into account is the increase of atmospheric concentration of CO_2, which could enhance primary productivity and thereby modify the carbon/nitrogen (C/N) ratio and, consequently, the chemical quality of litter (e.g. Bazzaz 1990; Woodward, Thompson, and McKee 1991; Coûteaux et al. 1991; Anderson 1992; Lambers 1993; Körner et al. 1996). Qualitatively, the litter and its rate of decomposition might change without any change in the flora's composition. However, not all species would follow this principle, as shown by the in situ quality of litter obtained under high CO_2 in temperate and tropical environments, which "was not significantly different from that produced in similar communities maintained at current ambient CO_2" (Hirschel, Körner, and Arnone 1997, 387). Although there was an effective small decrease in litter quality of the alpine sedge *Carex curvula* All. in an experiment of CO_2 enrichment conducted in an alpine sward in the Swiss Alps, Hirschel, Körner, and Arnone (1997) conclude that the decomposition rate might remain the same over the long-term.

Tracking changes in soil organic matter is important for understanding soil-vegetation dynamics and the carbon budget, but in mathematical ecosystem models organic matter is still too often regarded as merely a simple, temporary stock of carbon. To be plausible, any explanation of how the carbon stock evolves in the soil would have to include some detailed understanding of the dynamics of organic material, and in particular of the role that nitrogen content plays in the litter and of the conditions for releasing complexing acids (see section 5.6.5.5). Presently, no standard method exists for physicochemical analysis of the organic material, and so it is difficult to compare results from different studies (Johnson 1993).

5.6.5.5 Changes in Nitrogen Supply Global warming might enhance decomposition rates of soil organic matter, with consequent changes in the nitrogen cycle, an increase in nitrogen mineralization, lowering of the C/N ratio, and change of pH. Global warming might also affect the nitrogen content in subalpine soils by modifying the form of nitrogen in the spring. With low temperatures, mineral nitrogen is essentially in the ammonium form (NH_4^+). Given a 2–4 K increase of soil temperature, it would be transformed into nitrate (NO_3^-) (Pornon and Doche 1994).

An increase in nitrogen content of soils would have direct consequences for vegetation. In oligotrophic ecosystems like subalpine and alpine ones, slow-growing plants with low nitrogen requirements, low productivity, and low nutrients cannot use additional nutrients (e.g., Chapin and Shaver 1989; Steubing 1993) but faster-growing alpine plants can (Schäppi and Körner 1996). As a result of increased productivity and a more rapid turnover of soil nutrients, oligotrophic plant communities might disappear (Berendse 1993; Vitousek 1994). On the other hand, nitrogen availability to plants could decrease if an increase of carbohydrates released by nonmycorrhizal plants stimulated the abundance and activity of soil microorganisms (Díaz et al. 1993; Bazzaz 1996). A negative feedback loop could also operate through modification of the organic matter's quality, which would then benefit the oligotrophic vegetation. For a typical alpine meadow with *Carex curvula* All., Körner et al. (1996) showed that with elevated CO_2, only small amounts of additional nonstructural carbohydrates accumulate, both in above and underground parts. Thus, they suggested that a part of the additional net assimilation may be sequestered in the soil as a faster turnover of carbohydrates in roots or root exudation.

A change in the form of nitrogen available to plants, that is, a modification of the nitrate/ammonium ratio, might also have important ecological consequences. Pornon and Doche (1994, 1995a) observed that the alpenrose (*Rhododendron ferrugineum* L.) performed better for growth and germination where the nitrate/ammonium ratio was nearer to 0 than to 1. Troelstra, Wagenaar, and Smant (1995a, 1995b) demonstrated that heathland species adapted to ammonium-based nutrition can grow with nitrate as a source of nitrogen, but that more carbon is then allocated to root growth, changing the shoot/root ratio. However, transformation of ammonium into nitrates through nitrification is an acidifying process, with the leaching of basic cations and mobilization of aluminium. At the subalpine-alpine belts, where precipitation exceeds evapotranspiration, a permanent acidification can be expected. Under an oligotrophic vegetation, nitrates produced may also be leached if none of the species present can absorb nitrate selectively over ammonium, as may be the case under a closed heath. Then, a negative feedback loop could operate, leading to nutrient depletion.

Predicting changes in soil nitrogen is a complex question that cannot be dissociated from those of soil organic carbon (e.g., Körner 1989; Körner and Arnone 1992; Bowler and Press 1993; van de Geijn and van Veen 1993; Gifford 1994; Coûteaux, Bottner, and Berg 1995; Bazzaz 1996). Both positive and negative feedback mechanisms can occur in this relationship and affect the C/N ratio. Coûteaux, Bottner, and Berg (1995) concluded that increased atmospheric concentrations of CO_2 could decrease the nitrogen content of litter, and Körner et al. (1996) have confirmed this for some forbs in an alpine meadow. In contrast, Gifford (1994) suggested that the nitrogen cycle might track the carbon cycle in the long term through biological nitrogen fixation and, therefore, the nitrogen concentration of soils might increase. In addition to potential changes in nitrogen supply because of warming, nitrogen supply in subalpine and alpine soils is already increasing through atmospheric deposition by 5–30 kg/ha per year (Körner 1989).

5.6.6 Summary

- In highly structured vegetation, synusiae of the understory are unlikely to react directly to climate change but rather only indirectly to a change in their microhabitat conditions.
- Present climatic climax plant communities are likely to persist in climate change as edaphic climaxes.
- Present edaphic climaxes are likely to persist temporally and spatially in climate change according to their buffering capacities, that is, so far as their limiting factors are not changed.
- Natural landscape is likely to change at a differential rate, according to its component elements (lagging vs. rapid change).
- The cultural landscape that will undergo climate change may be very different from today's.
- The response of species, plant communities and landscape to a temperature increase is not likely to be linear, and there may be an inertia of 1–2 K.
- A temperature increase of 3–4 K would very likely have a profound effect at every level of complexity, since it equals the temperature amplitude of an entire vegetation belt.
- Fragmentation, diminution of populations, and selective extinctions of high alpine and arctic stenoicious relict plant populations of bryophytes and vascular plants are likely over the entire Alps if the temperature increases by 3–4 K.
- Alpine endemics restricted to tops of low mountains (i.e., those lacking nival belts, mainly in the eastern Alps) are likely to be severely endangered of disappearance/extinction if the temperature increases by 3–4 K.
- Phenotypic plasticity and genetic adaptation might buffer the effect of climatic change in some cases for vascular plants, and perhaps more frequently for bryophytes.
- Changes in forest types might occur in 30–55 percent of the forested area for an increase of 1–1.4 K, and in up to 55–89 percent for a 2–2.8 K increase, according to static modeling of Swiss forests (Kienast, Brzeziecki, and Wildi 1995, 1996).
- Adaptation of forests and tree species to climate change cannot be suitably established without taking into account the typically high genetic diversity of tree populations and the maintainance of that diversity.

- For an increase of 1–2 K in the mean annual temperature, the present upper subalpine forest limit is not likely to shift upward much more than 100–200 meters, because of its temperature-related inertia, but the *kampfzone* might move into the low alpine belt in favorable places.
- For an increase of 3–4 K in the mean annual temperature, the *kampfzone* would be very likely to invade the alpine belt, with an upward shift of the forest limit into the low alpine belt.
- With an increase of 3–4 K in the mean annual temperature, subalpine elements would be likely to invade the entire alpine vegetation belt, and new plant communities would be likely to replace in part the present communities.
- For an increase of 1–2 K in the mean annual temperature, human use might slow down the subalpine vegetation's upward shift, in particular that of heaths, shrubs, and trees, through an intensification of pasturing. In contrast, humans could also accelerate the shift through abandoning agricultural activities and afforestion of the upper subalpine belt.
- The upward shift of the present alpine vegetation into the nival belt, where it exists, might depend more on edaphic factors than on climatic ones because of the upper alpine and nival belts increasing steepness. Therefore, it is likely that present alpine plant communities on gentle slopes would disappear.
- Carbonate soils would likely be less prone to react to climate change than noncarbonate soils, thus acting nonsynergistically on vegetation change.
- Processes in soils operate at different rates, and many happen on the timescale of one year or tens of years. The accepted idea that soils evolve on a scale of centuries or millenia must be abandoned in considerations of climate change.
- Organic matter in soils is the key factor that would be affected, directly or indirectly, qualitatively and quantitatively, by climate change, but its evolution cannot be dissociated from that of soil nitrogen content.
- Nitrogen content, form, and cycle would be affected, and cannot be dissociated from changes in organic matter, as, for example, an increase in humification.

5.7 CONCLUSION

The plant and soil ecosystems of the European Alps are important for many biological, socioeconomic and cultural reasons. Because of their great ecological diversification, the Alps offer numerous habitats, which explain their high biodiversity.

On the basis of the information presented in this chapter, it appears that mountain ecosystems and soils would present a contradictory response to predict climate change, apparently being simultaneously characterized by sensitivity and resistance to it. Many uncertainties remain as to climate change's possible effects on subalpine and alpine ecosystems and soils in the

Alps, and it seems impossible to propose an ecosystem evolution valid for the entire Alpine chain simply because of the diverse mesoclimates, with all possible gradations between oceanic, continental, and Mediterranean influences. For this reason, and because of the interdependence of ecological and biological processes, their multifactorial, nonlinear effects, and the uncertainties about climate changes themselves, it is impossible to predict reliably soil and vegetation ecosystems' response to climate change at the regional level. Only general assessments can be made, such as those summarized in section 5.6.6.

Vegetation's apparently contradictary response to climate change comes from differential reactions, both temporally and spatially, of climatic and edaphic plant communities and ecosystems, because the climatic ecosystems are inclined to react, whereas the edaphic ones are not. This phenomenon grows in importance as ecological diversity increases. Biological inertia may also act synergistically with the edaphic factors, dependent on the ecosystem structure and the strategy of the species as well as their physiological and genetic characteristics.

As far as the biota is concerned, high mountains seem able to counterbalance the impact of climatic change to a certain extent. Indeed, mountains offer options for potential adjustment to the climatic requirement of the biota mainly through the possibility of altitudinal migration or shifting from more south-facing slopes to more north-facing ones. Thus, high mountains act as sanctuaries for preserving biodiversity; the presence of very old species in many mountain systems bears witness to this. However, such counterbalancing has limits. Glaciation did breach this effect, but certainly as much through mechanical destruction and the physical barriers of glaciers as through the very cold climate itself. With warming, no such destruction and obstructions would occur. Nevertheless, we do not know to what extent the Alps' protective capacities could stand a rapid increase in temperature. We are inclined to agree with some authors (e.g., Körner 1995) that an increase of 1–2 K would not affect the diversity of the Alpine chain very much. Paleoecological data showing the small variation (about 100–300 m) in the tree line during the Holocene period support this viewpoint. Within this temperature range, changes in the flora would occur on the ecological level (micro- and macrohabitats), and these would have limited implications on the phytogeographical level. An increase of temperature greater than 3 K and lasting for centuries would have serious implications on both the ecological and phytogeographical levels, because such an increase would be on the order of or greater than the temperature range of a vegetation belt (3.8 K).

To understand and assess the impact of climate change on plant distributions in high mountain areas and to produce models, we must consider the differential response between climatic and edaphic ecosystems, along with biological characteristics, from the structure of ecosystems to genetics, within the paradigm of the individual reaction of species, for which the following principles can be proposed:

1. Proceed regionally, to work as much as possible under a uniform mesoclimate.

2. Determine the ecological inertia of the main ecosystems and soils with respect to climate, in particular relative to edaphic factors.

3. Evaluate the biological inertia of ecosystems with respect to climate, in particular relative to their structural complexity, and of species relative to their phenotypic plasticity and their genetic diversity.

4. Conceive studies at related spatial scales, from population to landscape and vice versa (strategic cyclical scaling; Root and Schneider 1995), and on a temporal basis, to avoid pseudopredictability (Gosz 1991, 1992),

5. Combine present data and palaeodata, field experiments, modeling, and monitoring, along with regional climate models.

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GLOSSARY

Definitions are mostly taken or adapted from: Allaby, M. 1985. *The Oxford Dictionary of Natural History*. Oxford: Oxford University Press. Art, H. W. 1993. The *Dictionary of Ecology and Environmental Science*. New York: Henry Holt & Co. Foth, H. D. 1990. *Fundamentals of Soil Science*. New York: John Wiley & Sons.

Acclimation: Response of a plant to a change in its environment through modification of its physiological mechanisms to support the new conditions.

A-horizon: See *horizon*.

allele: Common shortening of the term "allelomorph." One of the several forms of a gene arising by mutation, hence differing in DNA sequence, and occupying the same relative position (locus) on homologous chromosomes.

allele frequency: The commonness of an allele in a population.

allogamy: Mating system consisting of cross-fertilization among different, individuals belonging to the same species that is, in plants, fertilization of a flower with pollen produced by another individual.

allozyme: Common shortening of the term "alloenzyme." One of the isozymes coded for by different alleles at the same locus.

alpine: In the phytogeographical sense, the zone in high mountains above the tree line and below the snow line. By this meaning, the term "alpine" does not necessarily apply to the Alps. See also vegetation belt.

alpine belt: See *vegetation belt.*

alpine zone: See *vegetation belt.*

ammonium: The ion NH_4^+.

antheridium (plural **antheridia**): Male sex organ or gametangium, within which male gametes (spermatozoids) are formed in algae, fungi, bryophytes, and ferns. In bryophytes, it is a multicellular globose to broadly cylindric, stalked structure.

apomixis: Asexual reproduction in plants without fertilization or meiosis, consisting of the development of an individual from an unfertilized egg (reproductive cell) or a somatic cell (any other nonreproductive cells).

archegonium (plural **archegonia**): Female sex organ or gametangium, containing the single egg cell in algae, fungi, bryophytes and ferns. In bryophytes, it is a multicellular, flask-shaped structure consisting of a stalk, a swollen base or venter, and a slender neck.

Arcto-Tertiary: Term indicating the subtropical flora occupying the Northern Hemisphere during the Tertiary, from which orophytes originated in the high mountains of the Northern Hemisphere.

asexual reproduction: Reproduction without the sexual processes of gametes (sex cells), for example, apomixis.

autogamy: Mating system consisting of the self-fertilization of an individual, that is, in plants, fertilization of a flower with its own pollen. Also extended in the genetic sense to fertilization of a flower with the pollen produced by other flowers of the same individual.

azonal vegetation: Vegetation that is independent of the climate (as opposed to zonal vegetation, that is, orobiomes and zonobiomes). For example, the vegetation of cliffs, screes, and wet places is azonal.

belt: See *vegetation belt.*

biogeochemical turnover: The movement of chemical elements from organism (biological part) to physical environment to organism in a more or less circular pathway. The form and the quantity of elements varies through the cycle.

biomass: The total weight of the living components in an ecosystem at any moment, usually expressed as dry weight per unit area.

biome: Biological subdivision of the earth's surface that reflects the ecological and physiognomic character of the vegetation. Biomes are the largest geographical biotic communities.

orobiome: Biome resulting from the altitudinal succession of particular vegetation belts in high mountains because of the regular diminution of temperature with increasing elevation.

pedobiome: Biome resulting from particular edaphic (soil) conditions instead of climatic ones.

zonobiome: Biome resulting from a climatic region. On a broad level, zonobiomes are arranged latitudinally, for example, tropical rainforest biome, desert biome, temperate biome, tundra biome.

biosphere: The part of the earth's environment in which living organisms are found.

BP: See *horizon.*

BPh: See *horizon.*

Bps: See *horizon.*

bryophyte: A division of plants, that includes the mosses, liverworts, and hornworts. They are nonvascular, green plants whose gametophytic generation is conspicuous and dominant and whose sporophytic generation is ephemeral.

buffer capacity: A measure of the ability of a buffer to neutralize. Loosely, the ability of a solution to absorb acids or bases without changing its pH.

C/N ratio: The ratio of the mass of organic carbon to the mass of organic nitrogen in soil or in biomass.

canopy: Usually, the upper level of woody communities where tree branches and leaves are most dense and the distinctive microenvironment which they form. The term may be applied to any terrestrial plant community in which a distinctive habitat is formed in the upper, denser regions of the taller plants.

carbohydrate: A class of organic molecules produced by plants through photosynthesis, including sugars and starches, such as glucose and cellulose.

carbon balance: The physiological ratio in plants between the production of carbohydrates and their use as a source of energy through catabolism. A negative carbon balance leads to the death of the plant once all reserves have been used, since energy demand exceeds energy production.

carbonic acid: The molecule H_2CO_3.

catabolism: The part of cellular metabolism encompassing the reactions that yield energy through the degradation of food molecules.

cation: Ion carrying a positive electrical charge.
basic cations: Ions that can neutralize acids, such as Ca^{++}, Mg^{++}, K^+, Na^+.

chamaephyte: A plant in which surviving organs (perennating buds) lie very close (less than 50 cm) to the ground. (One life form of Raunkier s classification system.)

chelates: Organo-metallic molecules that form a ring structure secured by multiple chemical bonds.

cheluviation: The removal of organo-metallic chelates from the soil, for example, from the upper layers during podzolization.

clay: (a) A soil component consisting of particles smaller than 0.002 millimeters in equivalent diameter.
(b) an aluminium silicate mineral having a layered structure (phyllosilicate) and the ability to take up and lose water readily, such as kaolinite and vermiculite.

climax community: The final stage of a plant succession, in which vegetation reaches a state of equilibrium with the environment. The region's climate and soil largely determine its nature.
climatic climax: The final stage of plant succession that climate mainly determines.
edaphic climax: The final stage of plant succession that edaphic (soil) processes mainly control.

cline: Gradual change in gene (allele) frequencies or character states within a species across its geographic distribution.

clonal plant: A plant that, through vegetative growth, forms more or less extensive patches constituted of modular parts without actual detachment. When separated, each modular part can grow independently and propagate the plant.

colline belt: See *vegetation belt.*

colluvial: Adjective from *colluvium.* A general term applied to deposits on a slope or at the foot of a slope or cliff that were moved there chiefly by gravity.

complexing acids: The organic acids that have the property of forming a chelate that can bind metallic cations such as iron or aluminium.

continentality: A measure of how a place's remotness from the oceans and oceanic air affects its climate.

coprophilous: Growing on or in dung.

crenic acids: Small organic acids, precursors of the fulvic acids.

cryogenic: In soils, processes produced by freeze-and-thaw cycles.

cryophilous: Preferring to grow at low temperatures.

cryosoil: Soil characterized by a temporarily or perennially frozen soil horizon (permafrost).

cryoturbation: General term for the disturbance of ground due to freezing and thawing, such as upward movement of the ground surface or individual particles due to the formation of ice in the soil.

cryptopodzol: See *podzol.*

cuticule: (a) Thin, waxy, protective layer covering the surface of the leaves and stems of plants. (b) The outer layer of arthropods (e.g., insects) formed by proteins and chitin.

Devonian: A period of the Paleozoic era (the first era of "obvious" life) that began 410 million years ago and lasted approximately 65 million years.

dioecious: Possessing male and female reproductive organs on separate, unisexual, individual plants.

diploid: An organism with two chromosome sets in each cell (excluding the reproductive cells), one from each parent.

DNA (deoxyribonucleic acid): A complex organic molecule found in all animals and plants cells that contains the genetic information passed from one generation to the next.

ecocline: Gradual change in community composition or ecosystem type along a major environmental gradient.

ecophysiology: The study of the physiology of organisms in relation to their environment.

ecosystem: A functioning unit of nature that combines communities of living organisms and the environmental parameters with which they interact.

ecotone: Narrow and fairly sharply defined transition zone between two or more different communities.

ecotype: A locally adapted genetic variant within a species. Ecotypes retain their physiological and morphological differences when transplanted to a single location.

ecotypic differentiation: Different selection pressures of different environments result in the development of different ecotypes within a single species.

edaphic: Of or influenced by the soil.

edaphic climax: See *climax*

endemic: Indigenous to and restricted to a particular geographic region.

subendemic: An organism extending slightly outside a particular geographic region to which it is mainly restricted.

enzyme: The proteins of the cell that catalyze chemical reactions (see also *allozyme, isozyme*).

Eocene: Tertiary epoch that began approximately 55 million years ago and ended 17 million years later, during which mammals underwent much expansion.

eutrophication: Process of nutrient enrichment, especially of nitrogen and phosporus in aquatic ecosystems, and by extension in all ecosystems. Human activity greatly speeds up this otherwise slow process (over geological time). Contrast with *oligotrophic.*

evapotranspiration: Term for water loss from a given area during a specified period of time by evaporation from the soil surface and transpiration from plants combined.

extrazonal vegetation: Vegetation found outside the range where it is zonal (i.e., determined by climate) because edaphic factors compensate for the difference in climate. The vegetation which normally occurs in a dry, warm climate is an extrazonal vegetation when it is found in a wet, temperate climate.

flora: All the plant species that make up the vegetation of a given area.

flushing: The removal of clay minerals from the soil.

formation: In vegetation description and analysis, a classificatory unit that implies a distinctive physiognomy rather than a distinctive species composition.

fulvic acids: The yellow mixture of complex organic molecules that remains in alkaline solution of organic matter after acidification removes humic acid.

functional type: Grouping of species according to some of their functional traits (e.g., legumes fixing atmospheric nitrogen through bacteria in their root nodules). Functional types allow a comparison among ecosystems differing in their species composition.

gametophyte: The haploid phase (the phase with one set of chromosomes) of a plant during which gametes are produced by mitosis.

gelifluction: The downslope movement of water-saturated layers of soil or rock debris over a frozen ground. Gelifluction may occur on slopes of even as little as 1°.

gene flow: The movement of genes within a population and from one population to another by the dispersal of pollen, seeds, or individuals.

genetic drift: Random fluctuations in gene frequencies occurring in an isolated population from generation to generation. Genetic drift results from chance combinations of different characteristics and is independent of the forces of selection. Although drift occurs in all populations, its effects are most marked in very small isolated populations, in which it gives rise to the random fixation of alternative alleles.

genetic marker: A marker at the genetic level (such as a specific enzyme).

genetic polymorphism: See *polymorphism.*

genotype: The genetic composition, latent or expressed, of an organism, as opposed to its phenotype; often, the particular combination of alleles at one locus or at a set of loci.

geophyte: A land plant that survives unfavorable periods by means of underground food storage organs, such as bulbs, tubers, and rhizomes. Buds arise from these to produce new aerial shoots when favorable growth conditions return. (One life form of Raunkier's classification system.)

habitat: Living place of an organism or community, characterized by its physical or biotic properties.

microhabitat: The portion of a more general habitat actually frequented by a specific organism, group of organisms within a community, or small, specialized plant community, and often characterized by a distinct microclimate.

holorganic: Strongly dominated by organic material (e.g., top soil layers like O-horizon).

homeohydry: Stage of plants that are able to regulate their rate of water loss. Homeohydric plants (like ferns or flowering plants) are opposed to poikilohydric plants.

horizon: In pedology, a relatively uniform soil layer that lies, at any depth in the soil profile, parallel, or nearly so, with the soil surface, and that is differentiated from genetically related horizons above and below by contrasts in physical, chemical, and biological properties or characteristics.

A-horizon: Organo-mineral horizon formed at the surface and characterized by an accumulation of humified organic matter intimately mixed with the mineral fraction.

BP: A soil horizon in which chelates carried from the overlaying layers has been precipitated from solution (**BPh**—with humus accumulation; **BPs**—with iron and aluminium accumulation).

O-horizon: The litter layer with its subhorizons of decomposition (fragmentation, fermentation, humification).

humic acids: A dark mixture of complex organic substances that can be extracted from soil by various alkaline agents and is precipitated by acidification to pH 1 or 2.

humification: Development of humus from dead organic material. Also, the process whereby the carbonic molecules of organic residues are transformed and converted to humic substances through biochemical and/or chemical processes.

humine: The most humified part of organic matter, very resistant to alteration.

humus: An organic soil material so thoroughly decayed that the identity of the biologic source cannot be recognized, that is, all of the organic compounds in soil exclusive of undecayed plant and animal tissues, their partial decomposition products, and the soil biomass. Resistant to further alteration.

intraspecific: Occurring among individuals within a species.

isozyme: Common shortening of the term "Isoenzyme." Each form of an enzyme that catalyzes a given chemical reaction.

kampfzone (German word): Transition zone between the subalpine and the alpine belts of stunted and often prostrate trees (designated as Krummholz) found between the upper limit of tall, erect trees growing in forest densities (the timber line) and the extreme upper limit of tree growth (the tree line); that is, the limit of the microphanerophytic life form.

kinetic: Describes in particular the speed at which enzymes catalyze chemical reactions.

krummholz zone (German word): See *kampfzone.*

layer (in soils): See *horizon.*

leaching: The removal of materials (especially cations and anions) in solution from the soil by the action of percolating liquid.

life form: An organism's structure, form, habits, and life history. In plants, especially, characteristic life forms, in particular morphological features, are associated with different environments. This observation has formed the basis of life form schemes for the classification of vegetation, such as Raunkier's system. (See, e.g., *chamaephyte, geophyte, phanerophyte, therophyte.*)

lignin: Complex aromatic substance, resulting from the polymerization of phenyl propanoid subunits, present in many plant cell walls, especially the wood of vascular plants, not yet detected in bryophytes. Its function appears to be to cement and anchor cellulose fibers and to stiffen the cell wall.

liverwort (hepatic): Common name for plants of the division Hepatophyta (bryophytes).

locus (plural loci): Specific place on a chromosome where a given gene is located. At each locus there is one gene; if that gene can take several forms (alleles), only one will be present at a given locus. Homologous chromosomes contain identical sets of loci in the same linear order.

loess: Unconsolidated material transported and deposited by wind, consisting of predominantly silt-sized particles (0.002–0.05 millimeters) and showing little or no stratification.

meiosis: The form of cell division in which the number of chromosomes is reduced by half, occuring in reproductive cells of sexually reproducing organisms. Meiosis involves two consecutive cell divisions with only one replication of the chromosome set, thereby producing four sexual cells (gametes) characterized by one-half the parental genetic information.

mesoclimate: A local variation in climate found only in a restricted area, such as a small valley.

metabolism: All the chemical and physical activities that sustain an organism. Metabolism involves the breakdown of organic compounds to create energy (catabolism) that is used to create complex compounds (anabolism) such as proteins from simpler compounds. Plant metabolism involves the creation of organic compounds through photosynthesis as well as their use to create energy.

microclimate: A very small-scale variation from the overall climate pattern, usually caused by local physical conditions such as topography (topoclimate) or the structure of a plant community (e.g., the microclimate at the ground level, at the canopy, etc.). Microclimates are related to microhabitats.

microhabitat:: See *habitat.*

microphanerophyte: See *phanerophyte.*

mineralization: The breakdown of organic matter into its inorganic chemical components as a result of faunal and microbial activity in soils.

Miocene: Tertiary epoch that began approximately 24 million years ago and ended 5 million years ago.

mitochondria: Specialized, capsule-shaped or threadlike functional structures (organelles) in the cytoplasm of cells that contain genetic material and many enzymes. Mitochondria are the site of processes (primary reaction of respiration) that provide energy for cell metabolism. They are also involved in the synthesis of proteins.

montane belt: See *vegetation belt.*

moss: Common name for a plant belonging to the division of bryophytes.

mutation: (a) Process by which a gene or a chromosome set undergoes a structural, inheritable change. (b) Gene or chromosome set that has undergone a structural change at random. The majority of mutations are changes within individual genes (e.g., of the DNA sequence at some point of the chromosome), but some are gross structural changes of chromosomes or changes in the number of chromosomes.

mycorrhizae: Literally "fungus root." The association, usually symbiotic, of specific fungi with the roots or other structures of higher plants. The fungal mycelia help the plant absorb minerals and in return absorb energy compounds the plant produces.

nanophanerophyte: See *phanerophyte*.

nitrate: The ion NO_3^-. Nitrates are important as concentrated sources of nitrogen. They are very water soluble and easily leached from the soil.

nitric acid: HNO_3, a very corrosive strong acid.

nitrification: Biological oxidation of ammonium to nitrite and nitrate, or a biologically induced increase in the oxidation state of nitrogen. The various stages of nitrification are carried out by a group of bacteria collectively called nitrobacteria or nitrifying bacteria.

nival belt: See *vegetation belt.*

nival zone: See *vegetation belt.*

norm of reaction: The relation between phenotype and environment (see also *phenotypic plasticity*).

O-horizon: See *horizon.*

oceanicity: Maritime influences' effects on a climate.
  peroceanic: Showing a high oceanicity.

oligotrophic: Of low nutrient content, especially with regard to nitrogen, and therefore with low productivity. Contrast with *eutrophic.*

organic acids: Acids composed of organic molecules and the functional group –COOH.

orobiome: See *biome.*

orophyte (also *oreophyte*): Plant growing at high altitudes (usually from the subalpine belt) and showing specialized adaptations to cold conditions.

pedobiome: See *biome.*

pedoanthracology: The study of charcoal in soils.

pedosphere: The part of the biosphere that contains the soil layer.

periglacial: A term referring to an environment in close proximity to a glacier, more generally applied to any environment in which freeze-and-thaw cycles are dominant surface processes.

peroceanic: See *oceanic.*

pH: A measure of the relative concentration of hydrogen ions in a solution. It is calculated as the negative logarithm to the base ten of the hydrogen ion concentration in moles per liter. The lower the pH, the more acidic is the medium; the higher the pH, the more alkaline.

phanerophyte: A woody plant (tree or shrub) in which surviving organs (perennating buds) are located more than 50 cm above the soil level. (One life form of Raunkier's classification system.) Phanerophytes may be subdivided further according to their height as nano- (less than 2 m), micro- (2–8 m), meso- (8–30 m), and megaphanerophytes (more than 30 m). Another subdivision distinguishes between evergreen and deciduous.

microphanerophyte: Young tree or shrub 2–8 meters in height.

nanophanerophyte: Young tree or shrub 0.5–2 meters in height.

phenolic acids: The phenols with an acidic functional group –COOH.

phenology: The study of the relationship between climate and periodic natural phenomena such as bud bursting or flowering of plants.

phenophase: A distinguishable phase in the life cycle such as flowering or bud burst that is used in phenological studies.

phenotype: The observable manifestation of a specific genotype; those properties of an organism produced by the genotype in conjunction with the environment that are observable. Organisms with the same genotype may have different phenotypes because of the effects of the environment and of the gene interaction.

phenotypic plasticity: Variation in the phenotypic expression of a given genotype; a measure of the amount of variation in the observable aspects of a quantitative genetic character among individuals.

photosynthesis: The series of chemical reactions by which plant cells transform light energy into chemical energy by producing simple sugars (or other energy compounds) and oxygen from carbon dioxide (CO_2) and water.

phytocoenose: A plant community or the vegetative components of a biotic community (biocoenose).

phytogeography: The study of plant distribution throughout the world, with a focus on how environmental factors have influenced evolution and distribution.

phytosociology: The branch of plant ecology that studies the description and classification of plant communities based primarily on floristic rather than life form or other considerations, and the interrelations among the populations of various plant species. Also called "plant sociology."

plant community: A group of plants living together in the same area, usually interacting or depending on each other for existence.

Pleistocene: The first epoch of the Quaternary subera of geologic time. The Pleistocene lasted from approximately 2 to 0.1 million years ago.

podzol: A mineral soil type formed at an advanced stage of leaching by podzolization and identified by an eluviated and bleached horizon and an iron-colored BP horizon (spodic horizon). Also called "spodosol."

cryptopodzol: A soil type lacking the visual characteristics of a podzol but in which podzolization nevertheless occurs.

podzolization: One of the major processes of soil evolution consisting of the process of removal of iron and aluminium, humus, and clay minerals, with a very strong acidification, from the surface of soil horizons by cheluviation.

poikilohydry: Stage of plants that are not able to regulate their rate of water loss and therefore contain roughly the same amount of moisture as their immediate environment. Poikilohydric plants (like bryophytes or lichens) are resistant to prolonged drought periods.

polygenic character: A trait whose variation is determined by several genes.

polymorphism: The existence of phenotypic variation in a population, whether or not genetically based.

genetic polymorphism: The existence of genetically based variation in a population.

polyploid: An individual having more than two sets of homologous chromosomes, such as a tetraploid, which contains four sets of homologous chromosomes.

polysaccharide: A biological polymer made up of many sugar molecules. Polysaccharides are complex carbohydrates including starch and cellulose. They can be broken down into their simple sugar components and used by organisms as a source of energy.

pseudovicariance: See *vicariance.*

ranker: A poorly evolved soil on acidic rocks, with an A-horizon directly laying on the bedrock.

recombination: The process occurring at meiosis through which offspring can display new genetic combination of the DNA producing different gene associations than either parents, resulting in new combinations of traits.

reduction: The opposite of oxidation; a chemical reaction in which a compound undergoes a decrease in oxidation state by gaining electrons, for example the reduction from Fe^{3+} to Fe^{2+}. Reduction of one compound is always accompanied by oxidation of another compound.

relict: Applied to organisms that have survived while other related ones have become extinct.

relict community: Community that formerly had a much wider distribution but that now occurs only very locally. Such contraction can be caused by various factors, including climatic change.

runoff: The portion of precipitation that flows (freely) over the soil surface into streams.

sexual reproduction: Reproduction involving the fusion of gametes (sex cells).

solifluction: The gradual downslope movement of soil saturated with water.

specific heat: The quantity of heat in calories required to raise the temperature of one gram of a substance by 1°C.

spodic: A term applied to a soil horizon characterized by illuvial accumulations of amorphous materials composed of aluminium and of organic carbon with or without iron. A spodic horizon is the diagnostic feature of a podzol (or spodosol).

sporophyte: The spore-producing diploid generation in the life cycle of plants. In higher plants, the sporophyte is the dominant generation, forming the conspicuous plant. In lower plants such as bryophytes, the gametophyte is the dominant and conspicuous generation, and the sporophyte remains attached to the gametophyte and is partially dependent on it.

stenoicious: Applied to an organism that can live only in a restricted range of habitats.

subendemic: See *endemic.*

subalpine belt: See *vegetation belt.*

synusia (plural **synusiae**): A functional unit within a distinct layer of a plant community composed of plants of similar life forms, phenology, and ecological requirements.

tannins: A group of acidic, aromatic compounds occurring widely in plants, such as oak bark or tea leaves, very resistant during the decay of the organic matter. Tannins are toxic substances with astringent properties whose principal function appears to be to render plant tissues unpalatable to herbivores.

Tertiary: Period in the earth's history that began 65 million years ago and ended some 2 million years ago, followed by the Pleistocene. During the Tertiary, mountains such as the European Alps, Andes, and Rockies were formed, especially during the last 40 million years of the epoch. Most of the orophytes separated from the surrounding flora of the warm lowlands in the late Tertiary (Pliocene).

texture: In pedology, the relative proportions of sand, silt, and clay in the fine earth of a soil sample, which give a distinctive feel to the soil when handled and which are defined by classes of soil texture.

thermocolline belt: See *vegetation belt.*

therophyte: A plant that completes its life cycle rapidly during periods when conditions are favorable and survives unfavorable conditions (cold, heat) as a seed; it is thus an annual or ephemeral plant. (One life form of Raunkier's classification system.)

tiller: In grasses and sedges, a lateral shoot arising at ground level.

timberline: (also **forest line**, **forest limit**, ***Waldgrenze***): Line that marks the altitudinal limit of trees that grow erect and tall (more than 8 m; mesophanerophytes) and form a forest.

topoclimate: See *microclimate*.

toponymy: The study of place names.

tree line: (Also **tree limit**, ***Baumgrenze***) A line marking the limit of a zone of stunted tree growth (2–8 m; microphanerophytes), as is often found above the elevations at which trees grow uniformly erect and form a forest (timberline).

vascular plants: A division of plants that have vascular tissues, that is, conducting tissues through which water and nutrients are transported. The division comprises the ferns and fernlike plants (pteridophytes), the conifers and conifer-like plants (gymnosperms), and the flowering plants (angiosperms).

vegetation belt: Altitudinal section of a mountain characterized by a specific climate determining the growing period and vegetation. A vegetation belt forms a bioclimatic zone. In the European Alps, a vegetation belt has an altitudinal extension of approximately 700 meters, corresponding to a temperature range of 3.8 K, and a variation in growing period that ranges across 65 days.

thermocolline belt: The lowest vegetation belt in the temperate regions, characterized by a growing season of more than 310 days and zonal hop-hornbeam forests.

colline belt: The vegetation belt in the temperate regions occurring above the thermocolline belt, characterized by a growing season of 245 to 310 days and oak and hornbeam forests, suitable for the cultivation of vine, corn, and chestnut.

montane belt: The vegetation belt in the temperate regions occurring above the colline belt, characterized by a growing season of 180 to 245 days and beech, silver fir, and scots pine forests, suitable for the culture of cereals.

subalpine belt: The vegetation belt in the temperate regions, occurring above the montane belt, characterized by a growing season of 115 to 180 days and coniferous forests, suitable for the mowing of meadows. The subalpine belt is the upper forest belt.

alpine belt: The vegetation belt in the temperate regions occurring above the subalpine belt, characterized by a growing season of 50 to 115 days and low heaths and swards, suitable only for pasturing.

nival belt: The highest vegetation belt in the temperate regions, occurring above the alpine belt, characterized by a growing season of less than 50 days, with snow remaining on flat ground throughout the summer and only a loose, sparse vegetation of vascular plants.

vegetation complex: A particular, spatial association of plant communities, often mosaic-like, that is related to a specific combination of topographical and edaphic factors and that forms a relatively homogenous part of the landscape.

vicariance: In general, the replacement of a species inhabiting a territory by one or several neighboring species in other areas (geographical vicariance). The replacement according to ecological conditions (e.g., siliceous soils and calcareous soils) is called the ecological vicariance.

false vicariance: Applies to two unrelated species having the same level of ploidy (as opposed to true vicariance).

pseudovicariance: Applies to a species where two different stages of polyploidy (e.g., diploid and tetraploid) show continuous and complementary areas of distribution.

true vicariance: Applies to two species having the same level of ploidy that differentiated from a common ancestor (as opposed to false vicariance).

zonal vegetation: Vegetation determined by the general climate in orobiomes and zonobiomes.

zonobiome: See *biome*.

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