5 Vegetation at the Upper Timberline

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5.1 Introduction

The upper timberline is one of the most fascinating vegetation boundaries in the Alps (Reisigl and Keller 1989) and in the mountain ecosystems of the world in general. Depending on the environmental conditions such as climate (oceanic External Alps vs. continental Inner Alps) or geology (limestone vs. silicate), different woody species may occur at the upper timberline in the European Alps. The boreal conifers *Picea abies, Larix decidua, Pinus cembra, Pinus uncinata,* and *Pinus mugo* are highly frost resistant (resistance down to –70 °C, Sakai and Larcher 1987; see also Chap. 10), thus they are the most widespread alpine timberline species. Other conifers such as *Abies alba, Pinus sylvestris* and deciduous trees such as *Fagus sylvatica* and *Acer pseudoplatanus* with lower frost resistance can reach the timberline only in the oceanically influenced External Alps where milder winter climate predominates. Among the shrubs few deciduous species reach the high-altitudinal coniferous forests: *Sorbus aucuparia, Sorbus chamaemespilus, Lonicera coerulea.* In addition, *Betula pendula* and *Populus tremula* occur as pioneer species up to the limit of the forests. The shrub *Alnus alnobetula* (syn. *A. viridis)* pre-dominates the azonal vegetation on slopes along running water or in avalanche paths, or forms secondary communities on abandoned moist pastures at the timberline.

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5.2 Growth forms at the timberline

The forests close to the timberline have a lower canopy density and the trees grow to a smaller height. A considerable change of the growth form is significant with increasing altitude (see Chap. 1). Conifers show already in the high-montane belt a typical columnar form with acute crowns. Steep slopes, snow pressure and wind are responsible for stem deformations causing sabre (bow) or harp forms, flags, scrubs or knee forms (Schönenberger 1981; Holtmeier 2003). Most tree species spread their branches down to the ground (e.g. *Fagus sylvatica*, Fanta 1981). Timber atolls (= tree groups, Tranquillini 1979) formed by *Picea abies* or *Larix decidua* are characteristic for the timberline ecotone. According to Kuoch and Amiet (1970) such atolls are a special form of vegetative propagation by layering. On branches covered by litter and humus adventitious roots are formed and the distal part of the branches becomes an erect tree.

5.3 Plant communities at the timberline

A natural timberline can be observed only in very few places of the Alps (Mayer 1974; Tranquillini 1979; Ellenberg 1996). *Pinus cembra*, for instance, is able to build a closed forest up to the limit of tree growth, forming a sharp timberline (Tranquillini 1979). In general, however, due to anthropogenic impacts a scattered timberline with a broad transition zone ("*Kampfzone*"; cf. Chap. 1) can be found above the closed forest, forming a mosaic of forest-, dwarf shrub heath- and grassland patches. Palynological records confirm the anthropogenic impact for thousands of years (Bortenschlager 1993). Burning of high-altitude forests has been recorded already since the neolithic period (Patzelt et al. 1997) and then - more enhanced - since the bronze-age (Neuwinger 1970; Patzelt et al. 1997, see also Chap. 3).

Due to massive impacts and clearings during the middle age, the timberline was lowered by 200-400 m (Friedel 1967; Breitenmoser 1998). Today, several anthropo-zoogenic communities extend on the potential forest sites at the timberline (communities of the classes Loiseleurio-Vaccinietea, Molinio-Arrhenatheretea, Caricetea curvulae, Seslerietea variae) forming a mosaic of forest relicts with open grassland patches and dwarf shrubs. Recently, land abandonment and changes in agroforestry have caused a significant change below and at the timberline zone, thus the area of forests has been increasing during the last decades and extending on formerly deforested sites (Brändli 2000; Bätzing 2003). However, the secondary suc-

cession towards a forest seems to depend highly on the type of the anthropo-zoogenic community. In the Swiss National Park for instance, succession models predict 515 to 630 years for tall-herb communities to be replaced by pine forests (Schütz et al. 2000). In general, forest regeneration seems to fail on areas where a forest would be highly desired for protection against avalanches, land slides and erosion (Bätzing 2003).

In the following the most important plant communities at the timberline will be described.

5.3.1 Spruce forests (*Picea abies* communities)

Among the forest communities occurring up to the timberline the so-called "subalpine" spruce forests are the most widespread ones. They are less dense compared to montane spruce forests and the trees are typically columnar with acute crown forms. At the timberline *Picea* is generally intermingled with *Pinus uncinata* (W-Alps) or *Pinus mugo* (E-Alps), both species colonizing the shallow rocky sites (Ozenda 1988).

Subalpine spruce forests are widely distributed in the Inner and Intermediate Alps, occurring at 1600 - 1900 m a.s.l.. In the External Alps they occur up to 1800 m a.s.l. In the northern External Alps subalpine *Picea abies* forests are common from Dauphiné to the eastern end of the Alps. In the southern External Alps they become increasingly rare in the W, e.g. in Switzerland (Ott et al. 1997). In the SW-Alps *Picea abies* is largely missing.

More or less similar subalpine spruce forest types were described in the E-and W-Alps (Wallnöfer 1993a; Ott et al. 1997; Ewald 1999). Subalpine spruce forests on silicate (Homogyno-Piceetum, Larici-Piceetum) are widespread, e.g. in the central chains of the E-Alps, in the Swiss National Park, Tarentaise, Alps de Savoie and relictic also in the French S-Alps (Mayer 1986). *Pinus cembra* and *Larix decidua* can be present in the tree layer. The understorey is rich in mosses, dwarf shrubs (*Vaccinium myrtillus*) and grasses (*Calamagrostis villosa*).

On moist, nutrient-rich soils in shadowy locations spruce forests with tall forbs (Adenostylo alliariae-Piceetum) are characteristically developed in the subalpine belt. They occur both in the E- and W-Alps (Ellenberg and Klötzli 1972; Zukrigl 1973; Frey 1995).

On substrates rich in carbonate a distinct species-rich type can be found (Adenostylo glabrae-Piceetum, Calamagrostio variae-Piceetum, Wallnöfer 1993a; Ott et al. 1997). *Larix decidua* occurs regularly in the tree layer, occasionally also *Acer pseudoplatanus* and *Abies alba*. In the Julic Alps

the understorey of this forest type is enriched by illyric elements (Mayer 1986).

On dry, shallow limestone and dolomite slopes an open spruce forest type with *Acer pseudoplatanus, Sorbus aria* and *S. aucuparia* is typical for the Northern Calcareous Alps (Carici albae-Piceetum, Wallnöfer 1993a) and in the Swiss Alps (Polygalo chamaebuxi-Piceetum, Ott et al. 1997).

5.3.2 Fir forests (*Abies alba* communities)

In general the main distribution of *Abies alba* lies in the montane belt of the External and Intermediate Alps, while it occurs only sporadically in subalpine forests. An exception are subalpine fir forests in the southern W-Alps where *Picea abies* is rare or absent (Mercantour, Argentera, Liguric Alps, Alps of Ticino). The community called Rhododendro ferruginei-Abietetum can be found on north-facing slopes on siliceous bedrock at 1550 - 1900 m a.s.l. (Kuoch 1954; Barbero et al. 1970; Ott et al. 1997). It is characterized by a high frequency of *Larix decidua* in the tree layer and by *Rhododendron ferrugineum* in the understorey. The Rhododendro-Abietetum is often situated in close contact with subalpine larch forests (Kuoch and Amiet 1970).

5.3.3 Larch-Swiss stone pine forests (*Larix decidua-Pinus cembra* communities)

In the Inner Alps and partly also in the Intermediate Alps a Larici-Pinetum cembrae forms an upper subalpine forest belt between subalpine spruce forests and the timberline. In addition in some parts of the northern External Alps spatially limited *Pinus cembra* forests exist (Ott et al. 1997; Walentowski et al. 2004). In the French W-Alps (Dauphiné) the Larici-Pinetum cembrae reaches 2500 m a.s.l., in the Swiss Alps 2400 m, in the central chains of the E-Alps 2300 m, in eastern chains 2000 m a.s.l. In protected niches *Pinus cembra* is able to grow also up to 2700 m a.s.l. (Monviso-area, Italy, Hofmann 1970).

The most widespread larch-Swiss stone pine community is the Larici-Pinetum cembrae on siliceous soils. Larch may be completely absent, whereas spruce may occur sporadically. The understorey is rather similar to that of subalpine spruce forest on silicate: either rich in mosses and grasses (*Avenella flexuosa, Calamagrostis villosa, Luzula* spp.) or dominated by dwarf shrubs (*Vaccinium* spp., *Juniperus communis* ssp. *alpina*). Anthropo-zoogenically influenced forests show openings and they are dominated by *Rhododendron ferrugineum* or *Calamagrostis villosa.*

On south-facing rocky slopes on silicate in the W-Alps a xerophilous type of the Larici-Pinetum cembrae with *Juniperus communis* ssp. *alpina, Cotoneaster integerrimus* and *Arctostaphylos uva-ursi* was described (Cotoneastro-Pinetum cembrae; Béguin and Theurillat 1982; Ozenda 1988).

On calcareous bedrock (e.g. Calcareous Alps of Salzburg, Dolomites) another type of the Larici-Pinetum cembrae with high frequency of larch can be found (Mayer 1974; Oberdorfer 1992). *Sorbus chamaemespilus* and *Lonicera coerulea* form the shrub layer. All the three *Rhododendron* species (*Rh. hirsutum, Rh. ferrugineum, Rh. intermedium*) may be present. Also tall forbs (eventually on moist slopes even *Alnus alnobetula*) or *Pinus mugo, Rhodothamnus chamaecistus* may appear.

A xerophilous type on carbonate with *Erica carnea* and *Sesleria albicans* in the understorey was described in the Italian Alps (Odasso 2002) and in the Swiss Alps (Frehner et al. 2005).

5.3.4 Larch forests (*Larix decidua* communities)

Larix decidua is frequently encountered in various subalpine forest communities, such as the Larici-Pinetum cembrae (Mayer 1962). It often occurs as a pioneer species. Beyond the distribution area of *Pinus cembra* pure larch forests are predominating in the subalpine belt of the SW-Alps (Barbero et al. 1970; Ozenda 1988). A frequent though partly anthropogenic community is the Junipero-Laricetum. It is an open forest on sunny and dry siliceous slopes with *Juniperus communis* ssp. *alpina, Vaccinium myrtillus, Calamagrostis villosa* in the understorey (Frehner et al. 2005).

In other parts of the Alps less extensive larch communities mostly on rocky substrate or on bolder were described. In the NE- and SE-Alps on limestone and dolomite larch forests dominated by *Rhododendron hirsutum* and/or *Rhodothamnus chamaecistus* were recorded (Zukrigl 1973).

On shallow south-exposed slopes on silicate the Junipero sabinae-Laricetum occurs in the Austrian Inner Alps (with *Juniperus sabina, J. communis* ssp. *alpina, Calamagrostis varia*; Wallnöfer 1993b).

A subalpine Adenostylo alliariae-Laricetum rich in tall forbs can be found in the Inner Alps of Switzerland (Ott et al. 1997).

5.3.5 *Pinus uncinata* forests

In the W-Alps *Pinus uncinata* forests substitute the subalpine *Picea abies* communities and the Larici-Pinetum cembrae on extremely shallow soils on calcareous and dolomitic sites, less frequently on silicate. The distribution

area of *Pinus uncinata* extends from the Sea Alps to the Fernpass and Ofenpass, respectively. It is a low-demanding species regarding the supply of nutrients and water (Kuoch and Schweingruber 1975). *Pinus uncinata* forests can be found both in the external mountain ranges and in the inner mountain chains (Schweingruber 1972; Ozenda 1988; Frey 1995). In the Swiss National Park (Graubünden) *Pinus uncinata* forests are covering large areas (Braun-Blanquet et al. 1954). In part they can be considered as a pioneer stage after clearings (Mayer 1974).

Frequently, *Pinus uncinata* can be found in close contact with subalpine spruce forest forming an environmental catena from shallow nutrient-poor soils to well developed soils where spruce predominates. Similar to the *Pinus mugo* scrubs, the description of the communities results according to the dominance of different dwarf shrubs – *Erica carnea*, *Rhododendron hirsutum* and *Rh. ferrugineum*, *Juniperus communis* ssp. *alpina* and *Arctostaphylos uva-ursi* (for instance Erico carneae-Pinetum uncinatae, Mayer 1986). Badly-growing spruce and larch can be mixed in. In the Swiss National Park, *Pinus uncinata* is intermingled with *Pinus sylvestris* ssp. *engadinensis*.

5.3.6 Prostrate pine scrub (*Pinus mugo* communities)

The main distribution area of *Pinus mugo* lies in the E-Alps. There, in the External Alps, the Intermediate Alps and on extreme sites of the Inner Alps it covers wide areas between 1800 and 2200 m a.s.l. (Wagner 1985). In avalanche paths and on boulder scree the species can reach down to the montane belt. In the W-Alps *Pinus mugo* occurs extremely rarely (Barbero et al. 1970; Ozenda 1988).

High floristic similarities to the *Pinus uncinata* communities can be observed (Mayer 1974; Wallnöfer 1993c). From shadowy, steep slopes on limestone or dolomite a Rhodothamno-Rhododendretum hirsuti was described with *Pinus mugo*, *Rhodothamnus chamaecistus*, *Rhododendron hirsutum*, *Sorbus chamaemespilus* and *Dryas octopetala*. The Erico carneae-Pinetum prostratae characterizes south-exposed scree areas. In this community species of the alpine grasslands are already present in the understorey together with the dwarf shrubs *Daphne striata* and *Juniperus communis* ssp. *alpina*.

On silicate stands mainly of the Inner and Intermediate Alps species-poor *Pinus mugo* communities appear on shallow rocky sites or on bolder scree. Here, *Rhododendron ferrugineum*, *Vaccinium* spp. and *Juniperus communis* ssp. *alpina* are the typical companion species.

5.3.7 Sycamore-beech forest (*Acer pseudoplatanus-Fagus sylvatica* communities)

Upper montane and subalpine sycamore-beech forests occur mainly in oceanic mountain chains characterised by high precipitation, thus in the northern and southern External Alps with main distribution in the NW-Alps (Kuoch 1954; Ott et al. 1997) and in Swiss Jura (Moor 1952). The community was described as Aceri-Fagetum and Saxifrago rotundifoliae-Fagetum (Willner 2002). Typical sites are steep slopes, furrows and boulder scree. Apart from *Acer pseudoplatanus* and *Fagus sylvatica,* also *Ulmus glabra, Picea abies* and rarely also *Abies alba* occur in the tree layer. According to the high air humidity of these stands the stems are covered abundantly by lichens (Reisigl and Keller 1989). On steep slopes snow pressure provokes a pronounced sabre (bow) form of the stems. Contorted and stunted growth can also be observed on sites near the timberline (Fanta 1981). *Sorbus aucuparia, Lonicera alpigena, L. nigra, Ribes alpinum, Rosa pendulina* are found in the shrub layer. In the S-Alps, for instance on the Monte Baldo, *Laburnum alpinum* and *L. anagyroides* are characteristic shrub species. Tall forbs dominate in the species-rich understorey.

5.3.8 Green alder and willow scrub

Due to the higher precipitations in the External and Intermediate Alps *Alnus alnobetula* (syn. *A. viridis*) is able to colonize moist stands in steep avalanche paths, along running water and small brooks at the timberline ecotone. In steep furrows *Alnus alnobetula* descends to the montane belt. The community Alnetum viridis is generally located on deep, moist and nutrient-rich soils (Oberdorfer 1978; Karner and Mucina 1993). These conditions are favourable for an abundant tall forb occurrence.

Along the streams tall willow communities may be developed nearly up to the timberline ecotone (*Salix pentandra, S. myrsinifolia, S. appendiculata*). Willow scrubs with low height extend from the timberline ecotone up to the lower alpine belt especially on north-exposed bolder scree slopes (*Salix waldsteiniana, S. caesia, S. foetida)* or on moraines (*Salix glaucosericea, S. helvetica, S. hastata, S. breviserrata,* Grabherr and Mucina 1993).

5.3.9 Dwarf shrub heath

On siliceous soils dwarf shrub heaths form a close mosaic with the remnant forest at the timberline ecotone (Schweingruber 1972). They belong

to the class Loiseleurio-Vaccinietea (Grabherr 1993a). The small scale distribution of the dwarf shrub species depends on snow cover during winter and wind exposure, respectively. *Rhododendron ferrugineum* occupies the depression sites, *Vaccinium myrtillus, V. vitis-idaea, Arctostaphylos uva-ursi, Juniperus communis* ssp. *alpina* grow on more exposed slopes, *Vaccinium gaultherioides, Empetrum hermaphroditum* towards the windswept sites and on the extremely exposed stands a lichen heath with *Loiseleuria procumbens* (Creeping Azalea wind heath or chamois heath carpet, Ellenberg 1988) predominates.

5.3.10 Substitutional communities due to human landuse at the timberline

For hundreds of years the timberline ecotone has been influenced by human activities and regular landuse maintained more or less treeless zones. Extended species-rich substitutional communities can be found, i.e. dwarf shrub heaths with 30-40 vascular plant species or subalpine meadows and pastures showing up to 60 species (Ozenda and Borel 2003). Communities of the class Loiseleurio-Vaccinietea are among the most obvious ones. As secondary invaders after abandonment of the traditional landuse since the 1950s, these communities expanded also onto the meadows and pastures in the timberline ecotone. Especially the *Rhododendron ferrugineum*-heath spreaded all over the siliceous Inner Alps and indicates areas which have been forest in former times (Lüdi 1921). Dry slopes with high amounts of sunshine are secondarily colonized by a Junipero-Arctostaphyletum with *Calluna vulgaris, Juniperus communis* ssp. *alpina, Vaccinium* spp. and *Arctostaphylos uva-ursi* (Braun-Blanquet et al. 1954; Grabherr 1993a).

The main grassland communities in the potential forest area are those dominated by *Nardus stricta* (for instance the Sieversio-Nardetum strictae; Peppler-Lisbach and Petersen 2001). In the *Nardus stricta* grasslands elements from different communities co-dominate (i.e. species typical for Vaccinio-Piceetea, Mulgedio-Aconitetea, Molinio-Arrhenatheretea, Caricion curvulae). Vegetation mosaics of grassland patches, dwarf shrub heaths and forest patches or single trees are characteristic for most timberline sites in the Alps. Species of the alpine belt may be already present. Numerous grassland communities (mainly dominated by *Festuca* spp.) have been described from the transition zone between timberline and alpine belt (Grabherr 1993b). One of the most frequently occurring farmed grassland types in the timberline ecotone is the Crepido-Festucetum commutatae (Ellmauer and Mucina 1993). It can be found as herb-rich pasture

or extensively mown hay meadow and is characterized by a mixture of lowland, montane and alpine grassland species.

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