What determines the timberline?

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Both the northern (latitudinal) and the upper (altitudinal) timberlines are phytogeographic transitions between the forested boreal vegetation zone and treeless areas. These two timberlines, which intermingle in northern Fennoscandia, are mainly controlled by the cold climate, although other natural and anthropogenic factors are of noticeable importance at least locally. The roles of the various controlling factors are discussed in this article. The timberline and tree line in northern Finland are usually formed by the mountain birch (*Betula pubescens* ssp. *tortuosa*), which extends further than the Scots pine (*Pinus sylvestris*) or the Norway spruce (*Picea abies*). The northern coniferous timberline in Finland follows approximately an isoline that represents an effective temperature sum of 600 degree days. Hazardous events also regulate the growth and occurrence of trees in addition to average conditions. Trees growing at the timberline have adapted themselves in many ways to the prevailing harsh circumstances. Pollen research and megafossil analyses (such as tree ring studies) show that the timberline has moved and its tree species composition has changed, primarily due to climatic fluctuations. This is one clear indication that the timberline is a dynamic 'combat zone'.

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Introduction

The boreal vegetation zone, characterised by coniferous forests, comprises almost the whole of Finland. Often named the *taiga*, especially by Russian scientists, this zone is bordered in the far north by the treeless arctic vegetation zone, the *tundra*, and the phytogeographic transition between these two main zones is called the *timberline region*. The position of the timberline is mainly controlled by the cold climate, although many other natural and anthropogenic factors are of noticeable importance, at least locally. The timberline region is a visually attractive and ecologically important ecotone. This article considers the factors determining the location and nature of the timberline, especially in northern Finland.

Timberline terminology

The terms related to the timberline are numerous and rather ambiguous (Hustich 1966, 1979; Heikkinen 1984b; Heikkinen et al. 1995). According to Hustich (1966), the timberline region consists of a series of forest and tree lines, which range from closed forest to the treeless area (Fig. 1). The southernmost, or lowest, definable line is the *economic forest line*. Forest fellings should not be extended beyond this line, because natural regrowth will be uncertain. The *physiognomic forest line*, where the forest clearly thins out so that 'the squirrel is unable to jump from tree to tree', is most generally regarded as the timberline. This line is also called the *biological forest line* (or *empirical*, *phytosociological*, or *vegetative forest line*), because up to this line the forest regenerates naturally. The propagation of trees may be slow and random, however, because seed years are infrequent. The physiognomic forest line is often drawn along the line where the canopy coverage is about 30 percent. Above and north of this line the trees become smaller and grow in groups or individually. This belt is bounded by the *tree line*, the extreme boundary where trees are still arboreal in size and shape. Finally, one arrives at the *tree-species line*.

There are nevertheless stumps or logs of dead

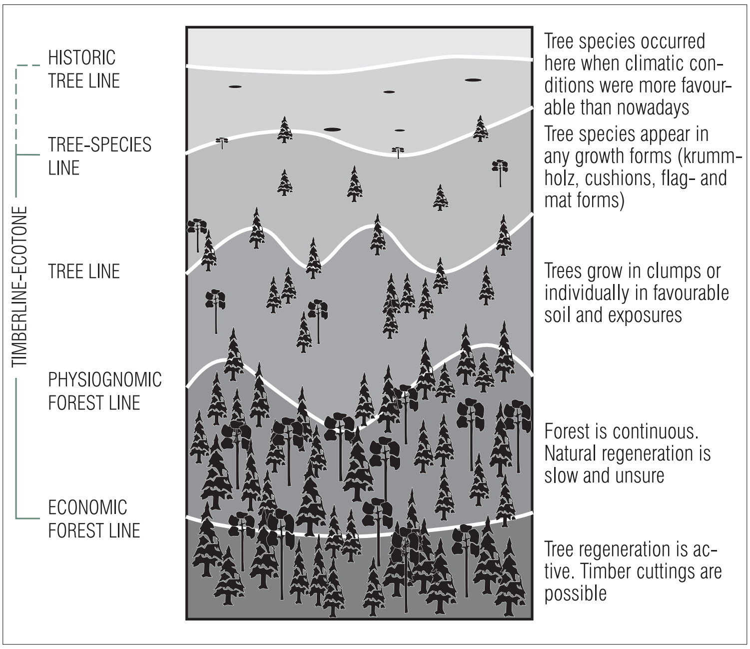

Fig. 1. The timberline region. The idea and concepts according to Hustich (1966).

trees to be found in lakes and mires located beyond and above these forest and tree lines, proving that climatic conditions were once more favourable than they are today. In many cases, human action has also devastated the marginal forests (Hustich 1966; Mattsson 1995). The outermost remnants of dead trees indicate the location of the *historical tree line*.

The timberline in northern Finland can be latitudinal or altitudinal in character. As the altitude increases, the temperature declines at an average lapse rate of 0.65 degrees centigrade (ºC) per hundred metres. The horizontal distance over which a similar cooling takes place is about one hundred kilometres.

When climatic conditions attributable to latitude primarily determine the position of a timberline, it is called *northern* or *arctic timberline*. Beyond it stretches the treeless *tundra*. The cooling of the climate in a vertical direction determines the timberline on the fells, so it is often referred to as the *upper* or *alpine timberline*. The area above the tree line is called the *open fell summit* (*paljakka* in Finnish). In northern Fennoscandia, for instance, the latitudinal and altitudinal – and also oceanic and continental – features vary in many ways, making the characterisation of timberlines problematic (Moen 1999).

The northern and upper timberlines resemble each other in many respects, although the rhythm and intensity of solar radiation and illumination may differ widely. This is evident when conditions at the northern timberline are compared with those affecting the upper timberline at middle latitudes, not to mention lower latitudes. At places on the northern timberline, where the topographic features are not variable, the vegetation cover is fairly homogeneous, but at the upper timberline the relief plays a major role. This results in unequal exposure to solar radiation and wind, so that growth conditions vary over short distances, giving rise to a vegetation mosaic (e.g., Heikkinen 1984b; Autio 1995).

The tree-species composition of the northern timberline in Eurasia differs markedly from that in North America: the bush-like juniper (*Juniperus communis*) is the only tree species common to both continents (Hustich 1966; Troll 1973). In spite of this, however, so many climatic parameters and indicators follow the northern timberline relatively well (Tuhkanen 1980, 1984) that almost the same external factors apparently control the tree species occurring on both continents.

The timberline and tree line in northern Finland are usually formed by the mountain birch (*Betula pubescens* ssp. *tortuosa*), which extends further than either the Scots pine (*Pinus sylvestris*) or the Norway spruce (*Picea abies*). The most northerly birches are not always proper trees, however, but are often low-growing, stunted, and ramified (Holtmeier 1985).

Regulating factors

Trees growing at the timberline struggle for existence and to propagate themselves in spite of the severe conditions. This is why the timberline region is often referred to as a 'combat zone' (Heikkinen et al. 1995: 8). The width of this zone may only be a few tens or hundreds of metres at a mountainous upper timberline, but on Canadian and Siberian lowlands it can be hundreds of kilometres wide.

Efforts are being made to find out which climatic factor is strongest in regulating the location of the timberline – in other words, which factor is the most critical to the vital functions of trees. So far no clear answer has been found. It was discovered long ago that the timberline more or less follows the 10 ºC isotherm for the warmest month of the year (Supan 1884; Köppen 1919). Temperature sums and lengths of various thermal seasons have also frequently been used to characterise tree lines (Tuhkanen 1980, 1984, 1993). The position of the timberline seems to relate relatively well to climatic parameters, such as the length of the growing season, the effective temperature sum, the duration of the frost-free season, potential evapotranspiration, precipitation during the growing season, the amounts of light and nutrients, carbon dioxide deficiency, and relative humidity (Hare 1954; Hustich 1958; Tuhkanen 1980, 1984). The values for radiation parameters, such as annual global net radiation and net radiation during the growing season (Ritchie 1960), are associated with the position of the boreal and arctic vegetation zones, and the location of the timberline has also been explained in terms of airmass climatology (Bryson 1966). The position of the arctic front in summer closely coincides with the northern timberline in Eurasia and Canada (Mitchell 1973; Tuhkanen 1993), while in Finnish Lapland the northern forest and tree lines are seen to be associated with effective temperature sums (Fig. 2).

Many local features may also cause deviations from the potential climatic timberline and tree

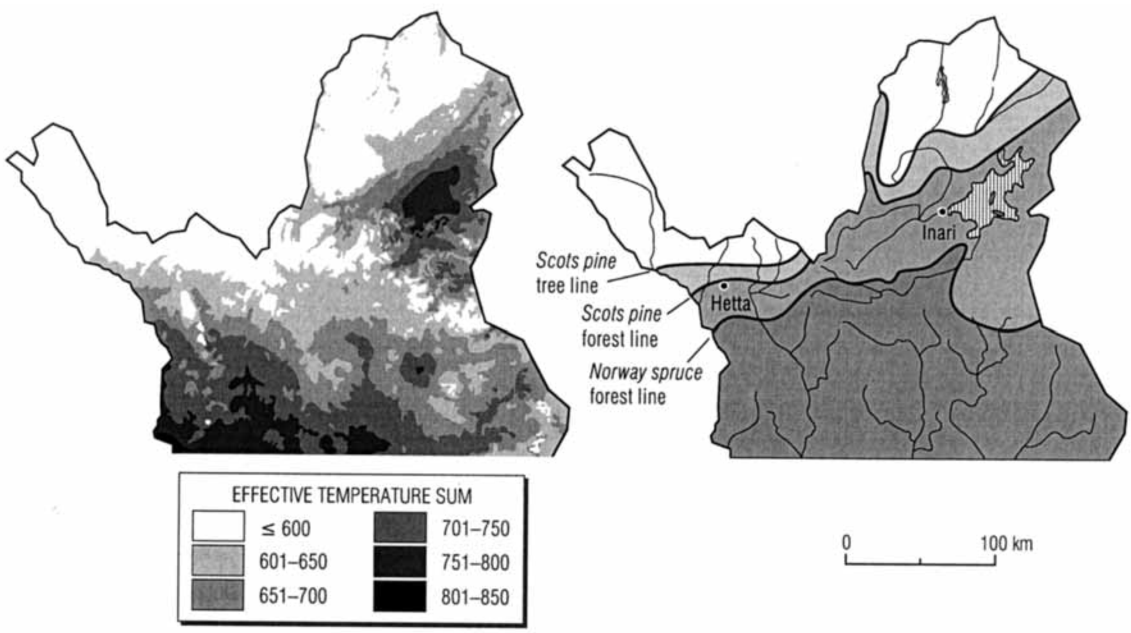

Fig. 2. The thermal factors have a significant impact on the location of the timberline in Finland, as elsewhere: comparison of the locations of certain forest and tree lines with calculated temperature sums in the normal period 1961–1990 (Ritari & Nivala 1993; Tasanen & Veijola 1994).

line. The influence of topographic features, soil conditions, or paludification, for instance, may force the timberline and tree line southwards or to lower altitudes (Eronen 1979; Tasanen & Veijola 1994; Autio 1995; Veijola 1998). Although trees growing under extreme conditions have adapted themselves to drastic environmental changes in addition to average climatic conditions, random, hazardous events may also regulate their occurrence and growth (Hustich 1983).

The wind may chop trees down or desiccate their foliage, or abrasion by ice and snow particles carried in the wind may destroy those parts of a tree that protrude from the snow, whereas the branches growing below the snow surface will be protected in winter (Holtmeier 1981, 1985). Particularly spruces benefit from this, to the extent that their lower branches may touch the ground, take root, and grow into cloned individuals (Fig. 3).

Fig. 3. Severe conditions in the timberline region can affect the shape of trees. Trees grow branches and needles more readily, or exclusively, on the leeside. Abrasion by ice crystals carried in the wind is strongest just above the snow cover. (Photo: Olavi Heikkinen, 08/91).

Low air temperatures sometimes cause growth disturbances. Night frosts occur most frequently in valley bottoms, into which the heavy, cold air drains on calm nights (Jalkanen & Närhi 1993). Temperature inversion often occurs in such places during the growing season, causing serious damage to the trees or even their death (Tikkanen & Heikkilä 1991). *Cold air lakes* may hinder reforestation in depressions even in southern Finland (Rajakorpi 1985).

As the snow cover protects trees from frost desiccation and abrasion, the remotest trees are often found growing in valleys, where the soil is also more favourable than on steep, rocky, and often frost-shattered slopes (Wardle 1980; Kullman 1981). Heavy loads of snow, rime, and ice accumulating on trees can break their crowns and branches in early winter, particularly on elevated terrain (Fig. 4), causing the timberline on many fells to remain further south than it would be on purely climatic grounds (Norokorpi & Kärkkäinen 1985; Norokorpi 1994).

There are several biological factors, such as plant diseases and animals, that threaten trees in marginal areas. Insects can sometimes cause damage over large areas. By way of example, the larvae of a geometrid, *Epirrita autumnata*, destroyed thousands of square kilometres of birch woods in Lapland in 1965–1966 (Kallio & Lehtonen 1973), and the area still has not recovered from the damage. Parts of the affected area are likely to turn into tundra-like vegetation under the present climatic conditions (Haapasaari 1988) and reindeer grazing.

The timberline is not always natural, as human activities have affected it for centuries, shifting it southwards and to lower altitudes. Fires, grazing, and air pollution have also destroyed or strained forests in timberline regions (Sirén 1961; Hämet-Ahti 1963; Hustich 1966; Mattsson 1995). A timberline that results from this human influence can be called an *anthropogenic timberline*.

A dynamic timberline

Trees at the timberline have various means of adaptation and self-defence against cold, wind, and snow. The tops of spruces in the north are pointed, which reduces the snow load on the crown (Fig. 5). Trees growing at the timberline are usu-

Fig. 4. Trees struggle for survival in the timberline region. The photograph is taken on the Aakenustunturi fell in 1994, when the crown snow-load caused severe damage to the trees. (Photo: Jyrki Autio, 03/94).

ally smaller than elsewhere. The spruce, birch, and juniper, in particular, which grow as trees in sheltered forests, may be bush-like, cushion-shaped, or even mattress-shaped on the upper fell slopes (Holtmeier 1981). Pine, on the other hand, does not vary much in shape.

Some tree species, such as spruce and birch, sometimes propagate only vegetatively under severe conditions. This is necessary when the climate is so harsh that the trees are unable to produce seeds capable of germination during the summer months. The Scots pine, however, is not able to regenerate vegetatively. Its northern limit is thus located in areas where the trees still receive enough warmth to produce viable seeds (Henttonen et al. 1986).

As to the vital functions of trees at the northern timberline, they have in many ways adapted themselves to a short, light summer and a long, cold winter. Growth begins quickly at the beginning of the growing season, and the trees have a lower optimum temperature than those in the south, so that they can utilise all the light they receive for twenty-four hours in the day. Furthermore, the needles of conifers reach a greater age in the north than in the south (Jalkanen 1993). The physical and biochemical adaptability of the cells enables them to become inured to the cold in winter.

Pollen research (Hyvärinen 1993) and megafossil analyses, such as tree ring studies (e.g., Eronen 1979), show that the timberline has moved and its tree-species composition has altered as a result of climatic fluctuations. The birch was the pioneer tree species in Finnish Lapland, spreading to the area soon after the deglaciation, which took place about 10,000–8,800 years ago. Pine forests later replaced the birch woods, at least on the lowlands. The pine forests of Lapland were at their thickest and most extensive about 7,500–4,000 years ago (see Eronen et al. 1991; Veijola 1998), when the climate was on average warmer than nowadays. The limits of both pine and birch have retreated since then. The spruce, which remains behind the birch and pine in Finnish Lapland and grows at lower altitudes, spread to Finland from the east, reaching its northern limit some 2,500 years ago (Moen 1999).

The timberline, which is controlled by many factors, is primarily dependent on climatic conditions and tends to advance during favourable climatic periods that last for some decades or centuries (e.g., Heikkinen 1984a). When the climate began to warm up after the Little Ice Age (around 1500–1800 AD), saplings of various tree species appeared beyond the timberline in many places in Fennoscandia (Hustich 1958). In some cases these pioneers died without ever becoming full-grown.

An unfavourable climatic period of a few decades or centuries may not necessarily force the timberline to retreat, although it may prevent the

Fig. 5. Example of the adaptation of trees to a natural hazard. The narrow, pointed spire prevents the drifting snow from forming a damaging snow load in the crown. (Photo: Olavi Heikkinen, 03/90)

trees from regenerating. If cold periods continue for long, the timberline is bound to recede (Kullman 1993) or be reduced to a chain of isolated relicts, as has happened in Canada, for instance (Nichols 1976; Payette & Gagnon 1979).

Human activity is apparently accelerating the global greenhouse effect. It may therefore be assumed that temperatures are rising and the vegetation period is being prolonged, especially at high latitudes. The quantity of carbon dioxide, a significant greenhouse gas, in the atmosphere has been on the increase since the nineteenth century. This has probably stimulated photosynthesis in trees and enhanced their growth. It has already been suggested that tree growth has accelerated recently, especially at high elevations, due to the increased atmospheric carbon dioxide content (e.g., Cooper et al. 1986), but not all researchers share this view unreservedly. Changes in the growth rate of trees and shifting of the timberline may not, however, be directly related to each other (McCarroll et al. 1999).

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