

Christian Körner

A re-assessment of high elevation treeline positions and their explanation

Received: 3 October 1997 / Accepted: 14 April 1998

Abstract In this review I first compile data for the worldwide position of climate-driven alpine treelines. Causes for treeline formation are then discussed with a global perspective. Available evidence suggests a combination of a general thermal boundary for tree growth, with regionally variable “modulatory” forces, including the presence of certain taxa. Much of the explanatory evidence found in the literature relates to these modulatory aspects at regional scales, whereas no good explanations emerged for the more fundamental global pattern related to temperature per se, on which this review is focused. I hypothesize that the life form “tree” is limited at treeline altitudes by the potential investment, rather than production, of assimilates (growth as such, rather than photosynthesis or the carbon balance, being limited). In shoots coupled to a cold atmosphere, meristem activity is suggested to be limited for much of the time, especially at night. By reducing soil heat flux during the growing season the forest canopy negatively affects root zone temperature. The lower threshold temperature for tissue growth and development appears to be higher than 3°C and lower than 10°C, possibly in the 5.5–7.5°C range, most commonly associated with seasonal means of air temperature at treeline positions. The physiological and developmental mechanisms responsible have yet to be analyzed. Root zone temperature, though largely unknown, is likely to be most critical.

Key words Climate · Developmental biology · Forest · High altitude · Timberline

Introduction

Treelines, wherever they occur, at thermal, drought, waterlogging, nutritional or salt stress gradients, repre-

sent an abrupt transition in life form dominance; they are lines beyond which massive single stems and tall crowns either cannot be developed, become unaffordable, or are disadvantageous. Depending on the dominant environmental driver, the structural and physiological causes for such life-form transitions will differ. The high-altitude forest boundary, here termed “alpine treeline” for consistency with older terminology, is possibly the best known and most studied of all distribution boundaries of trees, but still awaits a conclusive functional explanation that applies across the non-arid mountains of the world. In this contribution I will first illustrate the global patterns of alpine treeline position and their relationship to climate, and will then discuss approaches towards their mechanistic interpretation. Situations where treelines are significantly lower than the climate-driven boundary (e.g. because of human land use, including fire) are excluded from this analysis as far as possible, but will be discussed briefly. Unlike previous attempts, this review does not account for regional peculiarities and the fine-tuning of any particular alpine treeline, but adopts a rather coarse and global perspective, with functional explanations of treeline elevation not expected to match the actual treeline position any better than ± 100 m in elevation (i.e. the full range of reported postglacial treeline oscillations at local scales; cf. Rochefort et al. 1994).

Conventions

For practical reasons, a “tree” in the current context is defined as an upright woody plant with a dominant above-ground stem that reaches a height of at least 3 m, independently of whether reproduction occurs or not. This height ensures that such a tree would have its crown closely coupled to prevailing atmospheric conditions and protrude from deep snow where snow occurs. The definition of a “line” is more subtle, because, as formulated so elegantly by Armand (1992), “any natural boundary is in reality a transition zone, which has its own two

Ch. Körner
Botanisches Institut, Universität Basel, Schönbeinstrasse 6,
CH-4056 Basel,
e-mail: koerner@ubaclu.unibas.ch

boundaries. They are, in turn, also transition zones with their own boundaries, and so on endlessly. So localization of a natural border is in principle inexact and therefore determined by convention". Most people would intuitively agree about the position of the forest boundary when it is viewed from an airplane at great distance, but would strongly disagree when faced with the local situation on the ground.

What are useful conventions? There are several in use. The upper "limit" of the closed forest has been called the "timberline", but "closure" rarely ends abruptly, nor does it always require logs of "timber" size to establish a forest. A commoner situation is a gradual decline of tree size and opening of the canopy. The upper limit of the occurrence of tree *species*, i.e. the uppermost outposts of individuals in the "kampfzone" is another approach, but this "tree species limit" may conflict with the definition of tree given above or put too much weight on peculiar microhabitat conditions (in the case of isolated tree outposts). The "treeline" (or "forestline") takes a middle position (preferred here) and roughly marks a line connecting the highest patches of forest within a given slope or series of slopes of similar exposure. This definition corresponds to the one used by Brockmann-Jerosch (1919) and Däniker (1923) in their classical monographs on treeline biology of the Alps, and it is the definition used by Hermes (1955) in his global survey. Since timberline and treeline are coupled boundaries the fundamental mechanisms causing their general position should be similar. While forestline would terminologically be more adequate, I retain treeline because this term is in wide use and has become selfexplanatory.

The term "subalpine" is avoided here intentionally, to avoid what Löve (1970) has described as follows: "one can only sadly state that utter confusion reigns, and it is almost necessary to know where, geographically, and to which "school" the discussant belongs in order to make sense out of chaos and misunderstanding". A logical definition would be the transition zone ("ecocline") between the upper limit of the closed montane forest (the timberline?), and the tree species line (i.e. the beginning of the treeless alpine zone), but not everybody might agree on that. Subalpine parkland is another plausible term for this transition zone (Rocheport et al. 1994). In central Europe closed forests, several hundreds of meters below the treeline, are often termed subalpine, which would correspond to what is called upper montane forest in other parts of the world.

Current altitudinal positions of climatic treelines

A large number of authors have described the worldwide positions of treelines (for instance Troll 1973; Wardle 1974; Franz 1979; Baumgartner 1980; Arno 1984). Historical trends have recently been reviewed by Rocheport et al. (1994). For tropical and subtropical mountains reviews have been published by Ohsawa (1990), Miehe

and Miehe (1994) and Leuschner (1996). However, the most extensive quantitative analysis so far is that of Hermes (1955) who published his results in a local geographical report and in German, which may be why it has not received the attention it deserves. The following discussion leans heavily on the large data set of Hermes, which also includes snowline elevations. The snowline provides a purely physics-driven reference (Troll 1961), a thermal boundary which connects points above which the ground remains snow-covered for most of the year and precipitation falls as snow (approximately the elevation of the 0°C isotherm of the warmest month).

After carefully checking the large data set of Hermes (1955) I decided to eliminate four treeline and five snowline entries either because they were unrealistic when compared to other entries from the same region or because they referred to extremely windy and maritime climates (Scotland, 56°N, and coastal Norway, 62°N) with depressed treeline altitudes. However, the inclusion of these few points would not have changed the conclusion. The peculiarity of such "island treelines" will be discussed in a separate paragraph. Only a few numbers needed to be corrected based on my own observations, and four treeline altitudes, for the Sierra Nevada and White Mountains of California, the Rocky Mountains of Colorado and the Sangre de Cristo Mountains of New Mexico were added, because this region of the world was missing in Hermes' analysis. Finally the data set was completed by 26 numbers for treeline altitudes from Wardle (1974, again disregarding the special group of small oceanic islands). The resultant 120 data pairs for treeline and snowline plus 30 individual treeline numbers (i.e. a total of 150 treeline entries) were used for the polynomial regression analysis shown in Fig. 1.

In considering Fig. 1, one has to account for two points. First, Hermes, in his terminology, listed data for timberline and not treeline (see discussion under conventions). However, from reading his definition, it seems that he used criteria closer to treeline as defined above (he speaks of "groups of trees of 3 to 5 m high"), but it is possible that for some regions his mean altitudes rank

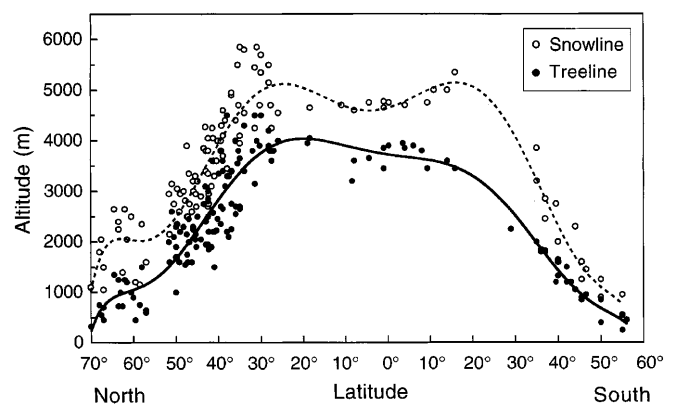


Fig. 1 The latitudinal position of treeline and snowline taken from a worldwide survey by Hermes (1955), supplemented by data from various other sources

somewhere between timberline and treeline, i.e. may be 50–100 m lower than treeline as defined here. Second, *Hermes* (except for Alaska) did not differentiate humid and cooler coastal slopes (commonly with lower limits) from drier and warmer inland slopes (with higher limits), causing a great deal of the altitudinal scatter at each latitude seen in Fig. 1.

A linear regression of the treeline altitude/latitude relationship in the northern hemisphere between 70° and 45°N yields a change in treeline altitude of 75 m per degree of latitude. Over the whole temperate-subtropical transition (50–30°N) the slope is 130 m per degree of latitude. The lower slope at higher latitudes agrees with the analysis of Malyshev (1993), who found a range between 70 m and 90 m for various transects in northern Asia. Adopting a worldwide perspective these patterns suggest that:

1. There is no strict correlation between the altitude of the alpine treeline and latitude, even if one takes account of the thermal equator being 6–7° north of the geographical equator. There is a steep, almost linear increase of treeline altitude in the temperate zone with the maximum altitude reached in the subtropics at 32° northern and 20° southern latitude. Over a range of 50° across the equator treeline position does not change significantly with latitude. The highest treeline elevations are not found at the equator, but in the northern subtropics.
2. The variation around the latitude-specific mean is small in the southern hemisphere (e.g. the north-to-south cordilleras of South America, the mountains of Indonesia and New Zealand), and is large in the northern hemisphere where the bulk of mountain masses is situated in continental areas. For instance, at 40°N treeline elevations vary between 2100 and 3700 m altitude. In the Alps alone, at 47°N, the range is 1600–2300 m over short distances. Climatic factors not closely related to latitude must have a strong influence on treeline formation.
3. The above biological trends run parallel to physical trends represented by the snowline. The snowline, just like the treeline, does not vary significantly over the same 50° span of lower latitudes. The combination of these two data sets suggests a common physical driver for snowline and treeline across the globe.

Treeline-climate relationships

Any discussion of vegetation-climate relationships suffers from three fundamental problems, namely (1) auto-correlation between different climate factors, (2) averaging procedures, and (3) from the uncertainty of whether present or past climates are reflected in the current patterns. After considering these problems, I will discuss two questions: does the worldwide distribution of treelines follow a common thermal boundary and if so, which? What explains the intrazonal variation and the pan tropical plateauing of treelines?

Auto-correlation

At the same altitude, lower latitude is associated with higher mean temperatures, lower seasonal amplitudes of temperature, longer duration of the growing period, larger diurnal amplitudes of temperatures, higher solar angles and peak radiation, often decreasing cloudiness and precipitation/evaporation ratios. In the case of the alpine treeline all these components of the climate are important, even if one of them, as for instance a particular mean temperature, shows a good correlation with treeline position.

Means are generally problematic

This will be discussed below in more detail, but often this is the only information available. It is not helpful for an understanding of the treeline phenomenon to state that “everything matters”, that all climatic factors must be considered, climatic means cannot be used, and so on, instead of carefully analyzing what is available. Existing data should allow us to rank the importance of environmental factors and pinpoint the key ones to a first approximation, even if some other determinants may also sometimes be important. It is also critical to make a distinction between gradual climatic influences (e.g. decreasing carbon gain, slower growth) and threshold effects (e.g. freezing damage, interruption of cell division).

Past rather than current climates may have determined treelines

Because of the long life span of many treeline-forming tree species and the resilience of established forest communities to environmental changes, substantial temporal separation between climate and treeline position is to be anticipated. Ives (1978) states: “to relate natural timberlines in Colorado to climatic parameters of the twentieth century will have an air of unreality in face of the trees’ ability to persist through perhaps several thousand years”. The Methuselahs of treeline trees Ives refers to are quite rare, but one to a few hundred years of climatic carry-over stored in today’s treelines is plausible. However, from what is known today, treelines have fluctuated during the past 10 000 years much less (< 200 m) than might have been expected from historical climatic change, and current treelines are only a little depressed (< 100 m in the temperate zone) compared to the post-glacial maximum (e.g. Zúgrig 1975; Bortenschlager 1977, 1993; Wijmstra 1978; Scuderi 1987; Ives and Hansen-Bristow 1983; Schweingruber 1987; Rochefort et al. 1994; Graumlich and Brubaker 1995). Similar observations have been made in the Arctic (Scott et al. 1987b). Also in the Andes, available evidence from pollen in lake sediments suggests that the treeline was never more than 200 m higher than today (Lauer 1988).

The above aspects constrain local explanations of treelines, but on a global scale, they will only increase

the noise around an overall relatedness to climatic drivers (which we seek here) and, perhaps, introduce some systematic “error” (lags) with respect to global climate trends. One additional difficulty is that climate data and treeline positions are hardly ever published together, and climate recording stations are commonly not where natural treelines are. Adequate data for solar radiation are non-existent for treelines of most parts of the world. Fortunately temperatures of tree crowns near treeline are relatively close to air temperatures (Caldwell 1970; Grace 1977; Goldstein et al. 1994; James et al. 1994), and soil temperatures also tend to be closer to mean air temperatures under trees than under treeless vegetation, which experiences radiative warming (Wini-gar 1981; Körner et al. 1986; Miede and Miede 1994). Though usually better coupled to the atmosphere than low stature vegetation Grace (1988), dense tree canopies at treeline, may still warm up by 1–2 K compared to air temperature (e.g. annual mean for the Alps of +1.8 K reported by Gross 1989; +2 K for July in the Rocky Mountains of Wyoming by Hadley and Smith 1987), and larger mean deviations have been reported for bright periods (Gross 1989; Goldstein et al. 1994). Short term maxima of leaf to air temperature differences under clear sky conditions may exceed ± 5 K (Tranquillini 1963; Smith and Carter 1988; Gross 1989; negative deviations during the night). However, this is not specific to treelines but is true everywhere, and James et al. (1994) concluded that thermal coupling of conifer shoots with ambient air is in fact higher at high altitude.

Air temperature of the warmest month

Since the 19th century alpine treelines have repeatedly been stated to coincide with a mean air temperature of the warmest month of about 10°C (for references see Brockmann-Jerosch 1919; Daubenmire 1954; Holtmeier 1974; Grace 1977). From the data I have extracted from various sources and plotted in Fig. 2 (uppermost line) it seems this is a temperate-zone perspective on the world. For instance, the treeline on Mt. Wilhelm in New Guinea at 3850 m (5°S) lies at a mean air temperature of only 5.6°C (there is only a 0.3 K “seasonal” variation). Similarly low mean temperatures apply to climatic treelines in the afro-alpine and tropical-andean climate (Miede and Miede 1994; climate data from Rundel 1994). According to Wardle (1971, his Table 1) the treeline in the Craigieburn Range in New Zealand (1300 m, 43°S) matches the 11.6°C isotherm for the warmest month, i.e. twice the value for New Guinea. In the Scottish Cairngorms (58°N) *Pinus sylvestris* grows up to 600 m altitude with a July mean of $c. 11.4^{\circ}\text{C}$ (Grace 1977). Ohsawa (1990) lists numbers for Hokkaido which suggest a warmest month mean for the 1600 m treeline of 12.4°C , similar to the 13°C reported by Takahashi (1944) for the birch treeline at 2350 m in the Hida Mountains. In the central, more “continental” part of the Alps, the mean air temperature of the

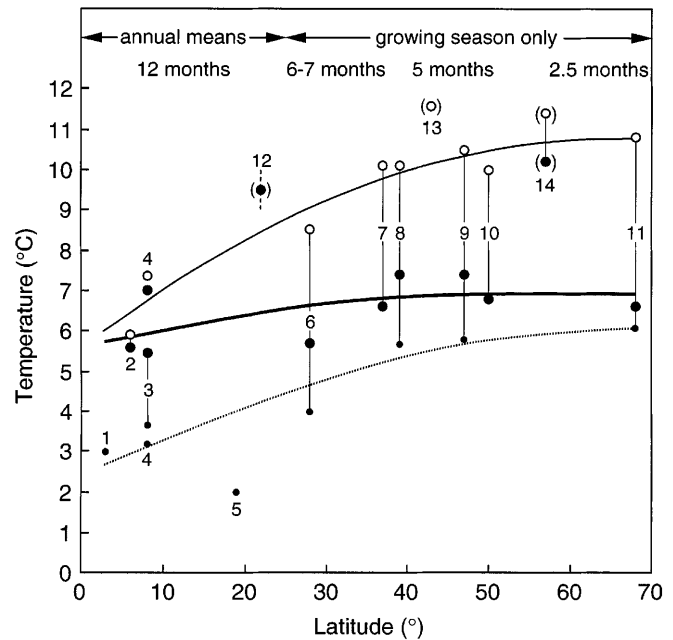


Fig. 2 Temperatures at alpine treelines for various latitudes (sites for which the seasonal course of temperature was available). *Upper line*: mean air temperature of the warmest month. *Middle line*: mean air temperature for the growing season, for sites north of 28° latitude calculated by averaging monthly means for May, June, July, August and September. *Lowest line*: seasonal mean air temperatures for extremely high altitude patches of forest (“forest outposts”). Data points for one mountain area are connected by vertical lines. Where interpolations were necessary, the regional seasonal adiabatic lapse rate was used (between 0.45 and 0.6 K/ 100 m). Treeline sites and altitude (extreme): 0 East-slope Ecuador, 3800 m; 1 Kilimanjaro (3950 m); 2 Mt. Wilhelm, New Guinea 3850 m (4100 m); 3 Bale Mountains, Ethiopia 4000 m (4100 m, only rough estimates of temperature); 4 Venezuelan Andes 3300 m (4200 m); 5 *Polylepis* record, N. Chile (4900 m); 6 Khumbu Himal (Everest region) 4200 m (4420 m, both altitudes for sunny slopes, 200 m less on shade slopes, hence the arrow); 7 White Mountains, California 3600 m; 8 Rocky Mountains front range, Colorado 3550 m (3900 m); 9 Tyrolean central Alps, 2100 m (upper point) and mean for three additional treeline locations between 1800 and 2100 in the Swiss Alps (2500 m); 10 Rocky Mountains, Alberta 2400 m; 11 Northern Scandes, Abisko, N. Sweden 650 m (750 m). Island mountains not considered in the lines fitted to the data: 12 Maua Kea, Hawaii 3000 m; 13 Craigieburn Range, New Zealand 1300 m; 14 Cairngorms, Scotland 600 m. Data for the coastal Mt. Rainier near Seattle range were halfway between the island and mainland data, but were omitted for clarity. Compiled from data by Arno (1984); Aulitzky (1961); Goldstein et al. (1994); Grace (1977); Hermes (1955); Hnatiuk et al. (1976); Lauer (1988); Lauscher (1976/1977); Miede (1989); Miede and Miede (1994); Rundel (1974); Sonesson and Hoogesteger (1983); Troll (1973); Wardle (1971, 1974).

warmest month measured right at the treeline at 2100 m (47°N) for 6 consecutive years is 9.5°C (Aulitzky 1961), close to Daubenmire’s figures for the Rocky Mountains. Finally a subarctic example: the upper limit of the birch forest (not its *krummholz*-form) at $c. 680$ m altitude in Northern Sweden (68°N) coincides with a mean air temperature of the warmest month of 10.5°C . The mean for the arctic treeline in Siberia is 11.2°C (Malyshev 1993).

The “warmest month” rule systematically overestimates the actual temperatures during the growing sea-

son. Since growth tends to be much more sensitive to temperature than photosynthesis (Körner and Larcher 1988; Körner and Peláez Menéndez-Riedl 1989; see also below) and because most of the expansion growth outside the tropics and subtropics occurs early in the season when temperatures are still low, this temperature is also of limited physiological relevance. Accordingly, the very detailed analysis of the latitudinal variation of the upper treeline in northern Asia by Malyshev (1993) showed that temperatures exceeding 0 or 5°C are clearly more effective overall than temperatures exceeding 10°C. Ellenberg (1963) had already suggested counting the days with means of air temperature above 5°C, and he found that 100 days fitted treeline positions in the Alps much better than warmest month means. Various other authors have found measures of treeline temperature to correlate better with treeline position when temperatures below +5°C are ignored (e.g. sums of monthly mean temperatures above 5°C; Ohsawa 1990). Aulitzky (1961) reported that -5 cm soil temperature exceeds 5°C for 128 days at the treeline of the central Alps in Tirol, but climatic data permitting such an analysis are hard to obtain for other regions.

Temperatures for whole growing seasons

Only a few treeline temperatures for whole growing seasons were found, and they show a much smaller discrepancy between treeline temperatures across latitudes (lower thick line in Fig. 2). While warmest-month temperatures on average differ by *c.* 5 K between temperate and tropical treelines, seasonal means differ by only 1 K. With more detailed information on diurnal courses of temperature variation it may turn out that this remaining difference is due to the greater weight of nighttime temperatures in the calculation of means for the tropical treelines compared to high latitudes where nights are shorter during the growing period than in the tropics. Since most plant temperature responses are non-linear, means composed of diurnally fairly constant temperatures, as in the case of arctic-alpine treelines, compared with numerically identical means, resulting from a wide diurnal amplitude, as in the tropics, differ in their biological meaning. If metabolic processes such as mitochondrial respiration with their exponential temperature response are related to the treeline phenomenon (see Dahl 1986), one would indeed expect higher arithmetic mean temperatures for treelines at higher latitudes. This discussion illustrates the difficulties in using means when biological processes are being considered. A careful latitudinal comparison of treeline climates based on the frequency distribution of hourly means of temperatures or temperature sums could clarify the situation.

Treelines on oceanic islands and forest outposts

These do not fit the overall pattern. The first tend to occur at much higher mean air temperatures, whereas

the latter can occur at much lower mean air temperatures. The season means for the Cairngorms in Scotland and for Mauna Kea in Hawaii are at least 3 K above those of the mainland mountains, which must be related to the maritime climate (Wardle 1974; Leuschner 1996). A missing “*Massenerhebungseffekt*” (Barry 1992) cannot be stressed here, because we are considering actual temperatures and not altitudes, although effective organ temperatures may differ from air temperatures. Higher wind speeds (tighter atmospheric coupling, Grace 1977) and greater cloudiness may be one explanation; the use of means of a fairly buffered island climate compared to means of oscillating climates (see above) is another one.

Forest patches at elevations above what is commonly believed to be the “proper” climatic treeline are more difficult to explain (lowest line in Fig. 2). They do occur in all parts of the world. For instance, in the Swiss Alps near Zermatt groups of “proper” *Pinus cembra* trees can be found on rocky outcrops as high as 2500 m, 200–300 m above the treeline. Holtmeier and Broll (1992) describe tree islands *c.* 400 m above the treeline in the Rocky Mountains. Miehe (1989) reports 20-cm-diameter, 3.5-m-tall *Juniperus recurva* trees for the Mt. Everest region at 4420 m altitude, several hundred meters above the line of more continuous tree occurrence in the Central Himalayas. According to Troll (1973) groups of conifer trees reach 4600 m altitude in eastern Tibet, and *Polylepis tomentella* trees are found in northern Chile at altitudes between 4800 and 4900 m (Hermes 1955; Troll 1973). In Venezuela *Polylepis sericea* stands are found up to 4200 m, i.e. 900 m above the “official” treeline (Goldstein et al. 1994), and form impressive forests at 4100 m.

The global approach of Miehe and Miehe (1994) to an understanding of the “outpost problem” appears to support the hypothesis of Ellenberg (1958) that some of these forest outposts are remnants in an otherwise deforested landscape due to centuries or millennia of human land use by grazing and fire, i.e. not the result of particularly sheltered, warm habitats. Goldstein et al. (1994) report an analysis of 256 *Polylepis* stands in Venezuela by H. Arnal in which no preference of slope orientation to the sun was found, which contradicts a widespread supposition. Beaman (1962) also found no exposure effect (north versus south) on treeline elevation in Mexico. In the case of the *Polylepis* stands, but also in *Pinus cembra* in the Alps and *P. hartwegii* on the Mexican volcanoes (personal observation) the “shelter hypothesis” and the “remnant hypothesis” may find a common denominator in the ground structure: the block fields on which high altitude forest patches are commonly found prevent fire from spreading because of a lack of a continuous cover of fuel (dry grass). As grazing land these block fields are not very useful, but for seedlings they may provide some shelter. Once established, these forest islands may create an interior climate which is buffered against climatic extremes (cf. Slatyer and Noble 1992), but again, concrete microclimatological data are still missing. Depending on whether one

favors the “fossil” or the “shelter” hypothesis, the treeline reflecting today’s climate, particularly in the subtropics and tropics, might or might not be a few hundred meters higher than we actually see it (the lowest line in Fig. 2). Assuming a “true” treeline position at the current position of remnants would, however, only be justified in the case of outpost forests, and should not be based on the occurrence of isolated trees.

The tropical plateauing of treeline altitudes

It is not conclusively resolved why treelines are highest in the northern subtropics and are found at lower altitudes in the humid equatorial tropics. Increasing precipitation and cloudiness tend to reduce treeline elevation. Ohsawa et al. (1985) concluded that the “summer heat” of higher latitudes is missing in the equatorial tropics and that the longer “season” is not an adequate substitute for lower growth temperatures. Since these same factors also cause snowline elevation to decrease, there appears to be a common climatological reason for the parallel plateauing of the treeline and snowline curves in Fig. 1. The best evidence for the positive effects of relatively low moisture supply on treelines are altitudinal records in eastern Tibet and northern Chile where trees are found growing not too far from 5000 m altitude under rather dry conditions, compared to the prevailing treeline altitudes in the humid tropics at or substantially below 4000 m. Whether reduced solar radiation for photosynthesis or reduced temperatures due to enhanced cloudiness and less convective warming are the key is again uncertain. Personally I favour temperature, because there is no convincing evidence that carbon assimilation per se is the most limiting component of tree growth at high altitudes (as will be discussed below).

Summary of climate-treeline relationships

The warmest-month model is inadequate to predict treelines worldwide. Growing season means (or, perhaps, some even better descriptions of integrated bio-temperature) are more closely correlated with treeline altitudes across latitudes and range between 5.5 and 7.5°C, which comes close to the 7°C mean for soil temperatures considered by Walter and Medina (1969), Walter (1973) and others to coincide with treelines (cf. Miede and Miede 1994). Winiger (1981) arrived at a 8–9°C range, but his selection of tropical mountains includes several for which treeline depression by factors other than climate has been described (e.g. East African volcanoes, Kinabalu in Borneo). Data compiled by Kitayama (1992) suggest a mean of 7°C for Kinabalu. A seasonal mean of 6–7°C is reported by Ohsawa (1990) for south and east Asia. However, if the uppermost forest islands are considered to indicate the natural climatic treeline, then the critical temperatures for tropical

and subtropical treelines would be 2.5–5°C (but true onsite temperatures are missing) which is less than for such outposts at higher latitudes (5.5–6°C).

In view of the relatively close cross-latitude relationship between the bulk of the current treeline altitudes and seasonal mean temperatures (independent of the range of local annual temperature extremes!) a direct thermal rather than any other explanation of treeline altitude is the most plausible (Troll 1961). This was also the conclusion of Brockmann-Jerosch (1919) from his very detailed analysis of the climatic relationships of treelines across the Swiss Alps. Physiological reasons for the 5.5–7.5°C threshold temperature across a wide spectrum of plant species, belonging to rather different phylogenetic groups, need to be found.

Accounting for the latitudinal bias of means as discussed in this section, this rather limited data set provides no substance for assuming that season length plays a particular role in determining the worldwide transition from the high altitude forest to the alpine life zone. Only long-term micro-meteorological studies, such as those available for a few temperate zone mountains, will allow us to substantiate the temperature relationships of the treelines of the world. It seems that phytogeographic, and partly also physiological, knowledge has developed much farther than our knowledge of the actual life conditions at the treeline ecotones.

Attempts at a functional explanation of treeline

The following five groups of – partly interrelated – mechanisms may dictate the climate driven transition from forests to the alpine life zone (for references see the following paragraphs).

1. The *stress* hypothesis: repeated damage by frost, frost desiccation or phototoxic effects after frost impair tree growth.
2. The *disturbance* hypothesis: mechanical damage by wind, ice blasting, snow break and avalanches or herbivory and fungal pathogens (often associated with snow cover) may remove similar or more biomass or meristems as can be replaced by growth and development below certain temperatures (see 4 and 5).
3. The *reproduction* hypothesis: pollination, pollen tube growth, seed development, seed dispersal, germination and seedling establishment may be limited and prevent tree recruitment at higher altitudes.
4. The *carbon balance* hypothesis: either carbon uptake or the balance between uptake and loss are insufficient to support maintenance and minimum growth of trees.
5. The *growth limitation* hypothesis: synthetic processes which lead from sugars and amino acids to the complex plant body may not match the minimum rates required for growth and tissue renewal, independently of the supply of raw materials (e.g. photoassimilates).

Alone or in combination type 4 and 5 mechanisms may lead to insufficient *tissue maturation* when the growing season is short and may, in seasonal climates, sensitize plants to type 1 and 2 damage or prohibit reproduction.

This suite of explanations of the treeline phenomenon has largely emerged from observations in certain temperate-zone mountains (Alps, Rocky Mountains). The question then is, what controls alpine treelines worldwide between 70°N and 55°S latitude, including all climatic zones, with and without seasons, and across such different *phylogenetic groups* as for instance Pinaceae, Podocarpaceae, Fagaceae, Rosaceae and Ericaceae? Which of the explanations developed for temperate-zone conifers would lose power, and which would gain, if one adopts a global perspective?

Whatever the common, basic mechanism that leads to the abandonment of massive tree-stems and tall, closed canopies at a certain altitude, it cannot be associated with *seasonality*, because treelines are also formed in non-seasonal climates, and, as has been shown above, at surprisingly similar temperature regimes. In the following I will discuss the potential causes of treeline formation listed here with a global perspective.

Damage by frost and winter desiccation

Frost damage may contribute to treeline formation. However, in climates with a thermal season the dangerous period is not the coldest part of the year, when the frost tolerance of treeline species generally exceeds environmental demand. Consequently, Brockmann-Jerosch (1919) found no correlation between annual absolute minima of air temperature and treeline position in the Alps, and considering the global distribution of treelines it is obvious that no such correlation exists at this largest scale either. Tranquillini (1979) and Larcher (1985) conclude that frost damage does not threaten survival of trees in the temperate zone treeline ecotone, but may contribute to distorted growth by partial injuries (cf. Däniker 1923). At tropical treelines freezing damage could theoretically occur during clear nights at any time of the year, but data from A. Sakai for New Guinea (in Sakai and Larcher 1987) and Larcher (1975) and Goldstein et al. (1994, p. 142) for Venezuela indicate that it is rather unlikely that frost damage plays a decisive role in treeline formation.

Winter desiccation is one of the most widely assumed causes for treeline formation. Damage to needles and branches can be caused by late winter water losses not being replaced because of frozen soil or stem bases (Michaelis 1934; Larcher 1963, 1985; Tranquillini 1979, 1982; Sowell et al. 1982; Sakai and Larcher 1987; Hadley and Smith 1990; and many others). The mention of “winter” makes it clear that this cannot be a cause for treeline formation in general (Troll 1961), but it may be a component contributing to the fine-tuning of treeline position in some temperate zone mountains. The problem with winter desiccation is that if damage occurs it will become

only visible much later, and a causal interpretation becomes problematic (Larcher 1963; Wardle 1981a). As suggested by Kerner (1869, p. 41) over a century ago summer pre-disposition correlates with the degree of winter desiccation, e.g. because of insufficient maturation of leaf cuticles or buds (Baig and Tranquillini 1980; Tranquillini and Platter 1983; Wardle 1981b). Direct damage to needle surfaces by winter conditions such as cuticle abrasion has also been suggested to contribute to excess moisture loss (Holtmeier 1974; Hadley and Smith 1983; see discussion by Grace 1989).

However, the phenomenon of winter desiccation at alpine treelines does not seem to be common even within the temperate zone. No indication or possibility of winter drought was seen by Sakai (1970) in *Pinus sylvestris* and *P. banksiana*, by Slatyer (1976) in *Eucalyptus pauciflora*, by Marchand and Chabot (1978) in *Abies balsamea* and *Picea mariana*, by McCracken et al. (1985) in *Nothofagus solandri*, and by Grace (1990) in *Pinus sylvestris*. Winter desiccation is mainly observed in young trees and diminishes with age and size of branches or trees (Larcher 1963; Marchand and Chabot 1978). Marchand (1991) went a step further and detached whole trees and could demonstrate by comparison with uncut controls that significant water supply from the root zone does occur in late winter. Hence, winter desiccation may be a problem for young trees above the treeline in some parts of the temperate zone (according to Tranquillini 1979, it sets the krummholz limit in the Alps), but cannot explain the worldwide alpine treeline phenomenon as such.

The published evidence for type 1 and 2 damage in young individuals above the treeline of certain temperate-zone regions is not questioned here, but in view of the global patterns illustrated above, and also the mechanistic explanations discussed below, one is forced to consider these limitations as regional or zonal, and “modulatory” acting on top of more fundamental limitations. Removing these typical temperate-zone, seasonality-related impacts would either not affect treeline position but allow a different, perhaps less abrupt transition from dense forest to shrubby tree growth, as often seen in the tropics, or facilitate a minimal advance of taller trees within the given range of the ecotone (LaMarche and Mooney 1972). Because treeline research was and still is largely a temperate-zone domain, the explanatory power of tropical treelines, which are evidently situated in similar thermal regimes compared to the growing period of seasonal climates, have largely been overlooked.

Tissue losses by disturbance

The issue of tissue losses due to mechanical damage, and snowcover-related browsing and snow mold, has been controversial, but such losses have rarely been considered critical for established trees rather than as modulating the chances of regrowth in the *Kampfzone* or

krumholz belt (Däniker 1923; Schröter 1926; Turner 1968; LaMarche and Mooney 1972; Holtmeier 1974; Frey 1977; Tranquillini 1979; Larcher 1985). Fire is a most significant modulating agent at some tropical, subtropical and temperate zone treelines (Lauer and Klaus 1975; DeBenedetti and Parsons 1979; Beck et al. 1986; Miede and Miede 1994; Rochefort et al. 1994; Ellenberg 1996), but is not a climatic determinant (in the strict sense).

Seedling establishment

It is not obvious why alpine plants, including many woody shrubs, should be able to establish seedlings, and trees should not (once viable seed is locally produced or brought in). Given the low frequency of successful seedling establishment events required to form a treeline forest (Stevens and Fox 1991), and the short distances to source trees, seed availability also does not appear to hold the answer (e.g. Griggs 1946), even though it has been shown that the reproductive success of trees diminishes with altitude (e.g. Wardle 1981b; Sveinbjörnsen et al. 1996) and that competition with low vegetation plays an important role (e.g. Franklin et al. 1971; Noble 1980; Wardle 1981b; Scott et al. 1987b; Young 1993; Hättenschwiler and Körner 1995). In fact seedlings, dwarfed trees or krumholz are quite abundant above the treeline in many parts of the world (though with a few exceptions, e.g. at fire-controlled treelines, e.g. Lauer and Klaus 1975), which itself illustrates that treeline formation cannot universally be associated with a lack of viable diaspores (e.g. Griggs 1946; Oswald 1963; Clausen 1965; Norton and Schönenberger 1984; Grace and Norton 1990; Marchand 1991). Accordingly, several authors have also reported successful attempts of planting tree seedlings above treeline (e.g. Wardle 1971; Schönenberger and Frey 1988; Ferrar et al. 1988). "Trees are continually invading higher ground beyond treeline and as regularly are being killed off" was the way Griggs (1946) characterized the situation he observed at the Kodiak Sitka spruce treeline, and Daly and Shankman (1985) concluded, "seedling establishment by conifers above tree limits is occurring on a more than occasional basis".

The question is, why do seedling populations above treeline not develop into a forest, but rather remain nested in the graminoid or shrubby ground cover or form crippled scrub? In many cases, particularly at higher latitudes, hypotheses 1 and 2 can add to the explanation of this phenomenon, but either hypothesis 4 or 5 (discussed below) is likely to gain significance as such saplings get taller, and one of these is likely to set the ultimate limit. No doubt, any advance of a treeline would require seedling survival above the current treeline elevation. However, observational evidence suggests that it is not the seedling life stage, but the subsequent emergence from the warmer boundary layer near the ground (or within a shrubby ground cover; see Grace

and Norton 1990, and the discussion by Stevens and Fox 1991) which is decisive for the establishment of a tree. Seedling establishment is quite responsive to short-term climatic changes, and recent advances of recruitment cohorts have been documented for northern Europe and western North America (reviews by Innes 1991; Rochefort et al. 1994; see also the discussion by LaMarche and Mooney 1972). Whether and how fast this will be followed by a proportional treeline advance remains to be seen.

The carbon balance

Half a century of leaf gas exchange studies in treeline trees has revealed no particular disadvantages compared to low altitudes except for the reduction of the length of the active period in extra-tropical areas. Many studies have illustrated the relative insensitivity of photosynthesis in treeline trees to temperature over the range of predominant daytime field temperatures during the growing season, because of thermal acclimation and the broad shape of the photosynthetic temperature response (e.g. Pisek and Winkler 1958, 1959; Slatyer and Ferrar 1977; Häslér 1982; Goldstein et al. 1994). Rada et al. (1996) report a highly positive carbon balance of high Andean *Polylepis* and conclude that the carbon assimilation machinery is well adapted to life near this tropical treeline. Substantial rates of photosynthesis have repeatedly been measured at 0°C, and a quarter to a half of maximum rates are reported for +5°C. Modest altitudinal reductions in photosynthetic capacity reported in the literature disappear in most cases when rates are expressed by unit leaf area rather than dry mass, because a dry mass basis reflects the well known altitudinal reduction of specific leaf area (greater fraction of cell wall material; for literature see Körner et al. 1986), rather than a reduction of metabolic activity of protoplasts.

Similarly, much of the divergence seen in the literature with respect to altitudinal trends in dark respiration disappears when actual tissue temperatures during relevant periods are considered (Pisek and Winkler 1958; for leaves only nighttime temperatures are relevant, because daytime losses are already accounted for by net photosynthesis). Comparisons of respiration rates of high- and low-altitude tissues measured at equal temperatures are ecologically rather meaningless. Schulze et al. (1967) illustrated that only 2–3 weeks (117 h at maximum rate) of photosynthesis during summer are required to cover the total respiratory loss (140 mg CO₂ g⁻¹ dry matter) of needles in winter at 3100 m altitude in *Pinus aristata*. Most recently Wieser (1997) demonstrated that respiratory losses during the three coldest months of the winter in *Pinus cembra* shoots can be covered by a single day's carbon gain in the growing season.

In the temperate zone, both the growing season moisture regime and the nutritional status of needles in treeline-trees are rather more favourable for photosynthesis than in trees at low elevation, an observation that

holds for most high altitude vegetation (Tranquillini 1979 pp. 52, 80; Körner and Mayr 1981; Körner and Cochrane 1985; Körner 1989). Comparative studies in the Alps by Benecke et al. (1981), in California (Mooney et al. 1964), Australia (Slatyer 1978) and New Zealand (Benecke and Havranek 1980) match the picture derived from Tranquillini's data. Taken together, the available shoot- and needle-based gas exchange data do not support the idea that insufficient photosynthetic activity during a given growing season, or excess respiratory losses, and thus a marginal annual shoot carbon balance, can explain the temperate-zone treeline.

On a whole-plant basis, carbon relations may still be burdened by tree-specific *carbon investments*. Obviously, the mean fraction of axial structures decreases stepwise from the life form tree to shrub and perennial forb – the latter representing the dominant life form at highest altitudes (Körner 1994). The altitudinal reduction of the stem fraction associated with this life form transition may be unrelated to a carbon balance problem and simply may reflect the reduction in plant size for whatever reason. In the “eternal” season of a humid tropical treeline climate the burden of a stem should be less important for the carbon balance and treeline could be expected to advance to comparatively higher altitudes (lower isotherms) if its position in the temperate zone were “depressed” by the carbon cost of a stem – a trend not detectable from available data.

Unfortunately dry matter allocation is extremely poorly documented for trees in general and treeline trees in particular, even though its significance may exceed that of leaf photosynthetic rates as a determinant of the carbon balance (Körner 1991, 1994). This reflects the human fascination with electronic machinery rather than spades, but lacks any scientific rationale. The scarce published information (see for instance Oswald 1963), together with some new data collected recently (M. Bernoulli and Ch. Körner, unpublished work), do not suggest a pronounced shift of dry matter compartmentation across the treeline ecotone (if any, there is an increasing trend in leaf mass per total tree mass with altitude). It is still unclear whether investments in fine roots increase with altitude in trees as they do in forbs, and exports to ectomycorrhiza and fine root turnover are unknown (both have been suggested to be particularly important for high-altitude forests; cf. Moser 1966; Wardle 1971; Vogt et al. 1984). In their analysis Stevens and Fox (1991) also emphasized the possibility of a root-based explanation of treeline, but they suggest that “central place foraging” in large, single stemmed individuals in an increasingly patchy and climatically hostile environment may cause a cost/benefit problem.

A conclusive picture of the carbon relations of treeline trees is not yet available. One way of solving this problem may be modeling the annual and long-term carbon balance, the greatest uncertainties of which are the proportions of dead and live tissue, tissue-specific respiration and the unknown below-ground sinks. As will be illustrated starting from leaf gas exchange data is

a rather hopeless approach, because CO₂ assimilation is unlikely to be the bottleneck for growth at the treeline, even though correlations may prove to have some predictive power (Scuderi et al. 1993). Currently available data from growth analysis (Tranquillini 1979) do not favour the carbon limitation hypothesis. While the balance between gains and losses may control distribution boundaries of trees along light or aridity gradients (Boysen-Jensen 1949) this does not seem to be the case at the alpine treeline, but the experimental test (for instance manipulating the carbon balance by in situ CO₂ enrichment) has not yet been done. Tranquillini (1979, p. 80) stated: “...one can safely conclude that neither the rapid decrease in tree height, nor the total elimination of woody plants is primarily due to inadequate dry matter production” (sensu carbon balance).

Growth and development: a hypothesis for treeline formation

A unifying theory for the alpine treeline must account for discrepancies such as the two- to three-fold (!) difference in the daily doses of quantum flux at treelines in the central Alps or subtropical Andes compared to the treeline in New Guinea, which is almost permanently enveloped in clouds (Körner et al. 1983). It must further account for variation in season length from 2.5 months in arctic-alpine birch treelines to 12 months in equatorial tropics, and for regions with heavy snow pack and none at all. Under all these life conditions we find treelines at seasonal mean air temperatures between 5.5 and 7.5°C. The thermal conditions at natural climatic treelines clearly need further investigation, but the consistency in available temperature data is too obvious to be dismissed as a meaningless correlate.

On the basis of what has been discussed, I hypothesize that there is a minimum temperature that permits sufficient production of new cells and the development and differentiation of functional tissue of higher plants, a limitation which is unrelated to the carbon balance. In the following I will present some evidence in favour of this growth limitation hypothesis, and show how it may be linked to the tree life form. The concept of a lower thermal threshold for tree growth in which carbon sinks rather than carbon sources control production is only a special case of a more general rule.

The reason why such growth limitations affect trees first, and shrubs and forbs only at much higher elevations, has to do with life-form-specific effects on microclimate. Shoot apical meristems of trees cannot benefit from radiant canopy warming during the day or stored warmth in the topsoil during the night, as subsoil leaf meristems of many alpine graminoids and rosette forbs or dwarf shrubs do (e.g. Körner and Cochrane 1983; Grace and Norton 1990), but experience convective cooling through tight atmospheric coupling (Grace 1988). Thereby tissue expansion may become blocked periodically, and trees “lose” a substantial fraction of

the season and most nights (even during otherwise warm periods) for structural growth.

In addition, trees – particularly when they form dense canopies – efficiently prevent soil heat flux and radiative warming of their own rooting zone. The tree life form has evolved as a means for light competition under warm soil conditions, a point made earlier by Slatyer and Noble (1992). Closed tree canopies at the treeline create cold soils, which impair root activity (e.g. Däniker 1923; Shanks 1956; Wardle 1968; Ballard 1972; Munn et al. 1978; Körner et al. 1986; Holtmeier and Broll 1992; Fig. 3), an aspect so far not seriously considered in discussion of the treeline. In Montana (2300 m) for instance, –50 cm soil temperatures were nearly 5 K lower under forest compared to adjacent grassland during summer (Munn et al. 1978). As a consequence, snow cover is often extended under high altitude forests as compared to adjacent treeless terrain (Alps, Tranquillini 1979, p. 55; Sierra Nevada of California, personal observations). In the central Alps the warmest-month mean of –10 cm soil temperature under grassland 300 m above the climatic treeline is between 13 and 14°C (unpublished data for 2 years; see also Gross 1989; Körner et al. 1986). Soil warming under low vegetation is also a likely reason why isolated trees can be found high above treeline.

This hypothesis, if valid, also provides a simple explanation for the abundance of non-structural carbohydrates and lipids as well as the high concentrations of leaf nitrogen in treeline trees and dwarf shrubs near treeline, because of a lack of “dilution by growth” (e.g. Tschager et al. 1982; Körner 1989), but this field definitely needs more research. The hypothesis centers around the assumption that the treeline is not caused by carbon shortage, but is created by sink inhibition as a result of low temperature. Dahl (1986) proposed that ATP supply (mitochondrial respiration) is the critical factor, but many other processes involved in tissue formation (e.g. protein synthesis) may be limited by low temperature. The fact that treelines occur at similar seasonal mean temperatures with partial pressures of CO₂ (not the mixing ratio) varying from 94% of values

occurring at sea level in subarctic-alpine treelines to only about 55% at the upper limit of tree growth in some subtropical mountains (a drop only partially balanced by enhanced diffusion; Körner et al. 1991) further underlines that carbon supply is unlikely to be decisive. Whole-tree CO₂-enrichment experiments at treeline would be an excellent way to test this rationale.

Evidence in support of the growth limitation hypothesis

I am not aware of any direct evidence for a threshold temperature for the production and differentiation of a critical mass of new cells in growing tree tissue. However, there is a bulk of information on growth responses to temperature in treeline trees and their seedlings, which stands in obvious contrast to any attempt to stress carbon acquisition as an explanation for the abrupt limitation of tree growth.

Tranquillini (1979) describes ten examples in which altitudinal variations of tree growth were studied from seedlings to mature trees in a number of different temperate mountain regions and both, in terms of short term (daily) rates as well as in terms of cumulative growth. In all cases dramatic reductions of growth rates (factors of 2–4) were found at altitudes close to treeline, often across gradients of only 200–300 m of altitude. Neither does solar radiation significantly change over such gradients in the temperate zone, nor does the 1–2 K temperature difference exert a significant change of photosynthesis, as is well documented in the relevant gas exchange literature. The change in season length may be 2–3 weeks, nothing compared to the differences seen along latitudinal gradients of treelines. In other words, there exists a tremendous discrepancy between altitudinal trends in growth and the potential for photosynthetic gas exchange.

More recent evidence of low temperature limitation of extension growth in treeline conifers was provided by Loris (1981), Grace (1989) and James et al. (1994). Loris monitored electronically the radial thickness of *Pinus cembra* for 2 full years in the Alps. From his time courses of “radial cambial growth” and temperature during the growing season it appears that radial increments ceased whenever temperatures fell below c. 5°C, a temperature permitting needles to assimilate at over 60% of the maximum for overcast and 25% of the maximum of bright weather conditions (Pisek and Winkler 1959). James et al. (1994) monitored shoot height extension of *P. sylvestris* over two seasons at the treeline in Scotland and found a low threshold meristem temperature between 5 and 6°C in native trees, and between 6.5 and 7.5°C in potted seedlings. Early season shoot extension growth is largely based on last season reserves and not dependent on concurrent photosynthesis. Summarizing results from seasonal stem growth analysis in the same species at the polar treeline by other authors, Grace (1989) expects no growth below 7°C. The above evidence is in line with dendro-ecological analysis

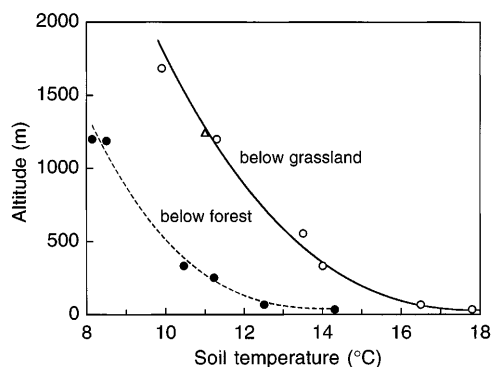


Fig. 3 The altitudinal variation of soil temperatures under grassland and closed forests of *Nothofagus menziesii* in mid summer in the southern Alps of New Zealand. From Körner et al. (1986)

which revealed close correlation between treering width and temperature at high altitudes (e.g. Schweingruber et al. 1979; Eckstein and Aniol 1981; Frenzel and Matisch 1981; Turner and Schönenberger 1981).

Cold soils severely constrain growth and activity of roots (cf. Tranquillini 1979 p. 37). Turner and Streule (1983, cited in Schönenberger and Frey 1988) observed roots at the treeline with root windows and found no root growth at soil temperatures below 3–5°C, with 5% of maximum rates only reached once soil temperatures exceeded 6°C (Fig. 4). Bilan (1967) showed for *Pinus taeda* the existence of root-growth threshold temperatures at mixed temperature regimes between 10/1.7 and 10/4.4°C (i.e. 24-h means between 6 and 7°C). **Low root temperatures also affect shoot functioning:** Havranek (1972) found a linear correlation between daily means of root zone temperature and in situ sums of daily photosynthesis in *Pinus cembra* between 0 and 7°C, but no such dependency at higher temperatures. **In situ root zone temperatures in adult trees also exert immediate, almost linear effects on stomatal conductance and photosynthesis** (once a low threshold between 1 and 4°C is exceeded) with no indication that this response is associated with cold soil induced needle water deficits (Carter et al. 1988; Day et al 1989; Körner et al. 1995). Scott et al. (1987a) found a linear correlation ($r = 0.95$) between cumulative root zone temperature and shoot elongation in subarctic *Picea glauca* experiencing atmospheric temperature and moisture conditions quite favourable for photosynthesis, again **indicating tight control of shoot activity by a below ground signal**. Hellmers et al. (1970) were able to block growth in potted *P. engelmannii* seedlings by exposing them to a daytime temperatures of 15, 19, 23, 27 or 35°C but a night temperature of only 3°C. At a 7°C night temperature significant growth (> 10% of optimum) occurred

only when daytime temperatures were between 19 and 23°C; at colder or warmer daytime temperatures the 7°C night treatment also reduced growth to negligible rates. *Betula* seedlings from the arctic-alpine treeline show no net growth or nutrient uptake at 5°C (Karlsson and Nordell 1996).

Altogether these experiments document the significance of a critical soil temperature under otherwise close to optimum photosynthetic conditions during the day. The existence of a critical temperature for tree growth has been a self-evident assumption in most of the growth analytical work at alpine treelines (e.g. Oswald 1963; Higgins and Spomer 1976; Ott 1978). Intrigued by the rapidity of the reduction of tree vigour near treeline Däniker (1923) was convinced that a minimal “quantity of warmth” is required for what he called “life activity”. **The most sensitive (critical) range of temperatures for direct effects on growth and development appears to be higher than 3 and lower than 10°C, perhaps in the 5.5–7.5°C range most commonly associated with treeline positions according to Fig. 2, but the physiological and developmental mechanisms responsible await to be clarified.**

Suggestions for future research

This sink-oriented hypothesis of treeline formation provides a much better explanation of the pronounced effects of small changes in temperature seen in tree rings of treeline trees (e.g. Mikola 1962; Schweingruber et al. 1988; Grace and Norton 1990). **There is no gas-exchange related basis to explain a doubling of ring width for a 2–3 K warmer season (or 300–500 m lower altitude) even taking account of some auto-correlation with sunshine hours. Frost, wind, winter drought and snow effects, or even fire may modify local treeline positions, but can not explain the overall global pattern.** In order to test the hypotheses and suggestions presented in this paper, four fields of research should receive particular attention in the future:

1. A comparative assessment of tissue temperature, shoot apical and root temperature in particular, in the high elevation treeline ecotones of the world.
2. A quantitative assessment of the carbon supply status of treeline trees by careful analysis of the seasonal abundance of mobile reserves, as compared to trees from lower elevations.
3. A conclusive test of the carbon balance hypothesis by examining the effect of atmospheric CO₂ enrichment. Such a test would not only greatly contribute to an understanding of the treeline phenomenon, but would help substantiating ongoing discussions of the possibility of treeline advances due to rising CO₂ concentrations alone (e.g. LaMarche et al. 1984; Innes 1991; Nicolussi et al. 1995).
4. A suite of manipulative experiments and field observations related to tissue formation in the critical

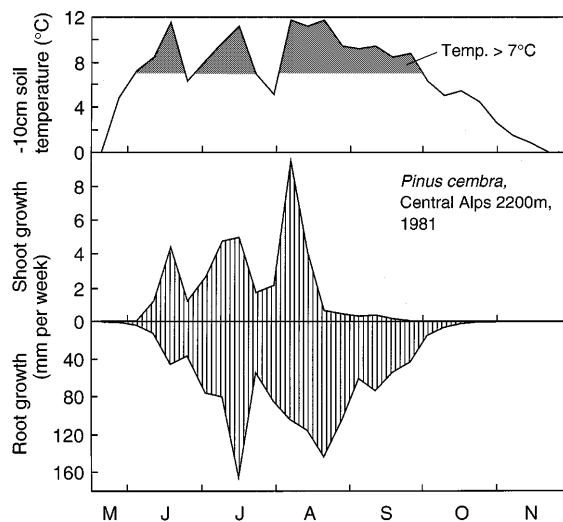


Fig. 4 In situ temperature dependence of root growth in *Pinus cembra* in the Swiss central Alps at 2200 m. From Turner and Streule (1983, cited in Schönenberger and Frey 1988)

range of temperatures (0–10°C), both above and below the ground.

Attempting a mechanistic understanding, Däniker (1923) studied tissue formation, cell size and cell wall properties by simple light microscopy, driven by the awareness that what we would call developmental cell biology has great explanatory potential for the alpine treeline phenomenon as a low temperature boundary for tissue growth per se. The cellular processes involved open a wide field of research in which molecular physiology and plant ecology need to become partners. The experimental and observational evidence available today, 75 years after Däniker's work, largely supports the view of the treeline as a thermal boundary for developmental, formative processes i.e. growth (see Dahl 1986). Trees, with their raised canopy stretching shoot apices into cold air and negatively affecting the temperature of their roots, co-determine their distributional limit at high altitudes by their inherent life form.

Acknowledgements This analysis emerged from planning and conducting project 31-45822.95 of the Swiss National Science Foundation. I gratefully acknowledge the hospitality of the Abisko Research Station of the Royal Swedish Academy of Sciences where most of this text was prepared during a sabbatical leave. S. Pelaez-Riedl helped with literature and diagrams. Fritz Schweingruber and two critical reviewers contributed a lot to the current shape of the text.

References

- Armand AD (1992) Sharp and gradual mountain timberlines as a result of species interaction. In: Hansen AJ, Castri F di (eds) Landscape boundaries. Consequences for biotic diversity and ecological flows (Ecological studies 92). Springer, Berlin Heidelberg New York, 360–378
- Arno SF (1984) Timberline. The Mountaineers, Seattle
- Aulitzky H (1961) Lufttemperatur und Luftfeuchtigkeit. Mitt Forstl Bundesversuchsanst Mariabrunn 59:105–125
- Baig MN, Tranquillini W (1980) The effects of wind and temperature on cuticular transpiration of *Picea abies* and *Pinus cembra* and their significance in desiccation damage at the alpine tree-line. *Oecologia* 47:252–256
- Ballard TM (1972) Subalpine soil temperature regimes in south-western British Columbia. *Arct Alp Res* 4:139–146
- Barry RG (1992) Mountain weather and climate, 2nd edn. Routledge, London
- Baumgartner A (1980) Mountain climates from a perspective of forest growth. In: Benecke U, Davis MR (eds) Mountain environments and subalpine tree growth. New Zealand Forest Service, Wellington, pp 27–40
- Beaman (1962) The timberline of Iztaccihuatl and Popocatepetl, Mexico. *Ecology* 43:377–385
- Beck E, Scheibe R, Schulze ED (1986) Recovery from fire: observations in the alpine vegetation of western Mt. Kilimanjaro (Tanzania). *Phytocoenologia* 14:55–77
- Benecke U, Havranek WM (1980) Gas-exchange of trees at altitudes up to timberline, Craigieburn Range, New Zealand. *NZ For Serv Tech Pap* 70:195–212
- Benecke U, Schulze ED, Matyssek R, Havranek WM (1981) Environmental control of CO₂-assimilation and leaf conductance in *Larix decidua* Mill. I. A comparison of contrasting natural environments. *Oecologia* 50:54–61
- Bilan MV (1967) Effect of low temperature on root elongation in loblolly pine seedlings. *International Union of Forest Research Organisations (Proc 14th Congress, Munich)* 4/23:74–82
- Bortenschlager S (1977) Ursachen und Ausmass postglazialer Waldgrenzschwankungen in den Ostalpen. In: Frenzel B (ed) Dendrochronologie und postglaziale Klimaschwankungen in Europa. Steiner, Wiesbaden, pp 260–266
- Bortenschlager S (1993) Das höchst gelegene Moor der Ostalpen "Moor am Rofenberg" 2760 m. (Dissertationes Botanicae) 196. Cramer, Berlin pp 329–334
- Boysen-Jensen P (1949) Causal plant geography. *Biol Medd* 21:1–19
- Brockmann-Jerosch H (1919) Baumgrenze und Klimacharakter. (Pflanzengeographische Kommission der Schweiz. Naturforschenden Gesellschaft, Beiträge zur geobotanischen Landesaufnahme 6). Rascher, Zürich
- Caldwell MM (1970) The wind regime at the surface of the vegetation layer above timberline in the Central Alps. *Centralbl Gesamte Forstwes* 87:65–74
- Carter GA, Smith WK, Hadley JL (1988) Stomatal conductance in three conifer species at different elevations during summer in Wyoming. *Can J For Res* 18:242–246
- Clausen J (1965) Population studies of alpine and subalpine races of conifers and willows in the California High Sierra Nevada. *Evolution* 19:56–68
- Dahl E (1986) Zonation in arctic and alpine tundra and fellfield ecobioses. In: Polunin N (ed) Ecosystem theory application. Wiley, London, pp 35–62
- Daly C, Shankman D (1985) Seedling establishment by conifers above tree limit on Niwot Ridge, Front Range, Colorado, USA. *Arct Alp Res* 17:389–400
- Däniker A (1923) Biologische Studien über Baum- und Waldgrenze, insbesondere über die klimatischen Ursachen und deren Zusammenhänge. *Vierteljahresschr Naturforsch Ges Zürich* 68:1–102
- Daubenmire R (1954) Alpine timberlines in the Americas and their interpretation. *Butler Univ Bot Stud* 2:119–136
- Day TA, DeLucia EH, Smith WK (1989) Influence of cold soil and snowcover on photosynthesis and leaf conductance in two Rocky Mountain conifers. *Oecologia* 80:546–552
- DeBenedetti SH, Parsons DJ (1979) Natural fire in subalpine meadows: a case description from the Sierra Nevada. *J For* 1979:477–479
- Eckstein D, Aniol RW (1981) Dendroclimatological reconstruction of the summer temperatures for an alpine region. *Mitt Forstl Bundesversuchsanst Wien* 142:391–399
- Ellenberg H (1958) Wald oder Steppe? Die natürliche Pflanzendecke der Anden Perus. *Umschau* 22:645–648
- Ellenberg H (1963) Vegetation Mitteleuropas mit den Alpen in kausaler, dynamischer und historischer Sicht. Eugen Ulmer, Stuttgart
- Ellenberg H (1996) Paramos und Punas der Hochanden Südamerikas, heute grossenteils als potentielle Wälder anerkannt. *Verh Ges Ökol* 25:17–23
- Ferrar PJ, Cochran PM, Slatyer RO (1988) Factors influencing germination and establishment of *Eucalyptus pauciflora* near the alpine tree line. *Tree Physiol* 4:27–43
- Franklin JF, Moir WH, Douglas GW, Wiberg C (1971) Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. *Arct and Alp Res* 3:215–224
- Franz H (1979) Hochgebirgsökologie. Ulmer, Stuttgart
- Frenzel B, Maisch I (1981) Klimatische Analyse der Jahrringbreiteschwankungen an der alpinen Waldgrenze. *Mitt Forstl Bundesversuchsanst Wien* 142:399–416
- Frey W (1977) Wechselseitige Beziehungen zwischen Schnee und Pflanze – eine Zusammenstellung anhand von Literatur. *Mitt Eidg Inst Schnee- Lawinenforsch* 34
- Goldstein G, Meinzer FC, Rada F (1994) Environmental biology of a tropical treeline species, *Polylepis sericea*. In: Rundel PW, Smith AP, Meinzer FC (eds) Tropical alpine environments. Cambridge University Press, Cambridge, pp 129–149
- Grace J (1977) Plant response to wind. Academic Press, London
- Grace J (1988) The functional significance of short stature in montane vegetation. In: Werger MJA, Van der Aart PJM, During HJ, Verhoeven JTA (eds) Plant form and vegetation structure. SPB Academic Publishers, The Hague, pp 201–209

- Grace PJ (1989) Tree lines. *Philos Trans R Soc Lond B* 324:233–245
- Grace J (1990) Cuticular water loss unlikely to explain tree-line in Scotland. *Oecologia* 84:64–68
- Grace J, Norton DA (1990) Climate and growth of *Pinus sylvestris* at its upper altitudinal limit in Scotland: evidence from tree growth-rings. *J Ecol* 78:601–610
- Graumlich LJ, Brubaker LB (1995) Long-term records of growth and distribution of conifers: integration of paleoecology. In: Smith WK, Hinckley TM (eds) *Ecophysiology of coniferous forests*. Academic Press, San Diego pp 37–62
- Griggs RF (1946) The timberlines of northern America and their interpretation. *Ecology* 27:275–289
- Gross M (1989) Untersuchungen an Fichten der alpinen Waldgrenze (Dissertationes Botanicae 139). Cramer, Berlin
- Hadley JL, Smith WK (1983) Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming, USA. *Arct Alp Res* 15:127–135
- Hadley JL, Smith WK (1987) Influence of krummholz mat microclimate on needle physiology and survival. *Oecologia* 73:82–90
- Hadley JL, Smith WK (1990) Influence of leaf surface wax and leaf area to water content ratio on cuticular transpiration in western conifers, USA. *Can J For Res* 20:1306–1311
- Häsler R (1982) Net photosynthesis and transpiration of *Pinus montana* on east and north facing slopes at alpine timberline. *Oecologia* 54:14–22
- Hättenschwiler S, Körner Ch (1995) Responses to recent climate warming of *Pinus sylvestris* and *Pinus cembra* within their montane transition zone in the Swiss Alps. *J Veg Sci* 6:357–368
- Havranek W (1972) Über die Bedeutung der Bodentemperatur für die Photosynthese und Transpiration junger Forstpflanzen und für die Stoffproduktion an der Waldgrenze. *Angew Bot* 46:101–116
- Hermes K (1955) Die Lage der oberen Waldgrenze in den Gebirgen der Erde und ihr Abstand zur Schneegrenze (Kölner geographische Arbeiten 5). Geographisches Institut, Universität Köln
- Hellmers H, Genthe MK, Ronco F (1970) Temperature affects growth and development of Engelmann spruce. *For Sci* 16:447–452
- Higgins PD, Spomer GG (1976) Soil temperature effects on root respiration and the ecology of alpine and subalpine plants. *Bot Gaz* 137:110–120
- Hnatiuk RJ, Smith JMB, McVean DN (1976) Mt Wilhelm Studies 2. The climate of Mt Wilhelm. Australian National University Press, Canberra
- Holtmeier FK (1974) Geoökologische Beobachtungen und Studien an der subarktischen und alpinen Waldgrenze in vergleichender Sicht. Franz Steiner, Wiesbaden
- Holtmeier FK, Broll G (1992) The influence of tree islands and microtopography on pedoecological conditions in the forest-alpine tundra ecotone on Niwot Ridge, Colorado Front Range, USA. *Arct Alp Res* 24:216–228
- Innes JL (1991) High-altitude and high-latitude tree growth in relation to past, present and future global change. *Holocene* 1:168–173
- Ives JD (1978) Remarks on the stability of timberline. In: Troll C, Lauer W (eds) *Geocological relations between the southern temperate zone and the tropical mountains*. Franz Steiner, Wiesbaden, pp 313–317
- Ives JD, Hansen-Bristow KJ (1983) Stability and instability of natural and modified upper timberline landscapes in the Colorado Rocky Mountains, USA. *Mountain Res Dev* 3:149–155
- James JC, Grace J, Hoad SP (1994) Growth and photosynthesis of *Pinus sylvestris* at its altitudinal limit in Scotland. *J Ecol* 82:297–306
- Karlsson PS, Nordell KO (1996) Effects of soil temperature on the nitrogen economy and growth of mountain birch seedlings near its presumed low temperature distribution limit. *Ecoscience* 3:183–189
- Kerner (1869) Die Abhängigkeit der Pflanzengestalt von Klima und Boden. (Festschrift 43. Jahresvers Deutscher Naturforscher und Aerzte 29–45). Wagner'sche Universitäts-Buchhandlung, Innsbruck
- Kitayama K (1992) An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* 102:149–171
- Körner Ch (1989) The nutritional status of plants from high altitudes. A worldwide comparison. *Oecologia* 81:379–391
- Körner Ch (1991) Some often overlooked plant characteristics as determinants of plant growth: a reconsideration. *Funct Ecol* 5:162–173
- Körner Ch (1994) Biomass fractionation in plants: a reconsideration of definitions based on plant functions. In: Roy J, Garnier E (eds) *A whole plant perspective on carbon-nitrogen interactions*. SPB Academic The Hague, pp 173–185
- Körner Ch, Cochran P (1983) Influence of plant physiognomy on leaf temperature on clear midsummer days in the Snowy Mountains, south-eastern Australia. *Acta Oecol, Oecol Plant* 4:117–124
- Körner Ch, Cochran PM (1985) Stomatal responses and water relations of *Eucalyptus pauciflora* in summer along an elevational gradient. *Oecologia* 66:443–455
- Körner Ch, Larcher W (1988) Plant life in cold climates. In: Long SF, Woodward FI (eds) *Plants and temperature* (Symp Soc Exp Biol 42). The Company of Biol Ltd, Cambridge, pp 25–57
- Körner Ch, Mayr R (1981) Stomatal behaviour in alpine plant communities between 600 and 2600 metres above sea level. In: Grace J, Ford ED, Jarvis PG (eds) *Plants and their atmospheric environment*. Blackwell, Oxford, pp 205–218
- Körner C, Pelaez Menendez-Riedl S (1989) The significance of developmental aspects in plant growth analysis. In: Lambers H, Cambridge ML, Konings H, Pons TL (eds) *Causes and consequences of variation in growth rate and productivity of higher plants*. SPB Academic Publishers, The Hague, pp 141–157
- Körner Ch, Woodward FI (1987) The dynamics of leaf extension in plants with diverse altitudinal ranges. 2. Field studies in *Poa* species between 600 and 3200 m altitude. *Oecologia* 72:279–283
- Körner Ch, Allison A, Hilscher H (1983) Altitudinal variation in leaf diffusive conductance and leaf anatomy in heliophytes of montane New Guinea and their interrelation with microclimate. *Flora* 174:91–135
- Körner Ch, Bannister P, Mark AF (1986) Altitudinal variation in stomatal conductance, nitrogen content and leaf anatomy in different plant life forms in New Zealand. *Oecologia* 69:577–588
- Körner Ch, Farquhar GD, Wong SC (1991) Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. *Oecologia* 88:30–40
- Körner Ch, Perterer J, Altrichter Ch, Meusburger A, Slovák S, Zöschg M (1995) Ein einfaches empirisches Modell zur Berechnung der jährlichen Schadgasaufnahme von Fichten- und Kiefernnadeln. *Allg Forst Jagdz* 166:1–9
- LaMarche VC, Mooney HA (1972) Recent climatic change and development of bristlecone pine (*P. longaeva* Bailey) krummholz zone, Mt. Washington, Nevada. *Arct Alp Res* 4:61–72
- LaMarche VC, Graybill DA, Fritts HC, Rose MR (1984) Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. *Science* 225:1019–1021
- Larcher W (1963) Zur spätwinterlichen Erschwerung der Wasserbilanz von Holzpflanzen an der Waldgrenze. *Ber Naturwiss-Med Verein Innsbruck* 53:125–137
- Larcher W (1975) Pflanzenökologische Beobachtungen in der Parametstufe der venezolanischen Anden. *Anz Math-naturwiss Klasse, Oesterr Akad Wiss* 11:194–213
- Larcher W (1985) Winter stress in high mountains. In: Turner H, Tranquillini W (eds) *Establishment and tending of subalpine forest: research and management*. Ber Eidg Anst Forstl Versuchswes 270:11–20
- Lauer W (1988) Zum Wandel der Vegetationszonierung in den Lateinamerikanischen Tropen seit dem Höhepunkt der letzten Eiszeit. In: Buchholz HJ, Gerold G (eds) *Jahrbuch der Geog-*

- raphischen Gesellschaft zu Hannover, Lateinamerikaforschung, Hannover. Geographischen Gesellschaft, Hannover, pp 1–45
- Lauer W, Klaus D (1975) Geoecological investigations on the timberline of Pico di Orziba, Mexico. *Arct Alp Res* 7:315–330
- Lauscher F (1976/1977) Ergebnisse der Beobachtungen an den nordchilenischen Hochgebirgsstationen Collahuasi und Chuquicamata. *Jahresber Sonnblickver 1976–1977*:43–67
- Leuschner Ch (1996) Timberline and alpine vegetation on the tropical and warm-temperate oceanic islands of the world: elevation, structure and floristics. *Vegetatio* 123:193–206
- Loris K (1981) Dickenwachstum von Zirbe, Fichte und Lärche an der alpinen Waldgrenze/Patscherkofel. *Ergebnisse der Dendrometermessungen 1976–79*. Mitt Forstl Bundesversuchsanst Wien 142:416–441
- Löve D (1970) Subarctic and subalpine: where and what? *Arct Alp Res* 2:63–73
- Malyshev L (1993) Levels of the upper forest boundary in northern Asia. *Vegetatio* 109:175–186
- Marchand PJ (1991) *Life in the cold*. University Press of New England, Hannover
- Marchand PJ, Chabot BF (1978) Winter water relations of tree-line plant species on Mt. Washington, New Hampshire. *Arct Alp Res* 10:105–116
- McCracken IJ, Wardle P, Benecke U, Buxton RP (1985) Winter water relations of tree foliage at timberline in New Zealand and Switzerland. In: Turner H, Tranquillini W (eds) *Establishment and tending of subalpine forests: Research and management*. Ber Eidg Anst Forstl Versuchswes 270:85–93
- Michaelis P (1934) Ökologische Studien an der alpinen Baumgrenze. IV. Zur Kenntnis des winterlichen Wasserhaushaltes. *Jahrb Wiss Bot* 80:169
- Miehe G (1989) Vegetation patterns on Mount Everest as influenced by monsoon and föhn. *Vegetatio* 79:21–32
- Miehe G, Miehe S (1994) Zur oberen Waldgrenze in tropischen Gebirgen. *Phytocoenologia* 24:53–110
- Mikola P (1962) Temperature and tree growth near the northern timber line. In: Kozlowski TT (ed) *Tree growth*. Ronald, New York, pp 265–274
- Mooney HA, Wright RD, Strain BR (1964) The gas exchange capacity of plants in relation to vegetation zonation in the White Mountains of California. *Am Midl Nat* 72:281–297
- Moser M (1966) Die ektotrophe Ernährungsweise an der Waldgrenze. *Allg Forstz* 77:120–127
- Munn LC, Buchanan BA, Nielsen GA (1978) Soil temperatures in adjacent high elevation forests and meadows of Montana. *Soil Sci Am J* 42:982–983
- Nicolussi K, Bortenschlager S, Körner Ch (1995) Increase in tree-ring width in subalpine *Pinus cembra* from the central Alps that may be CO₂-related. *Trees* 9:181–189
- Noble IR (1980) Interactions between tussock grass (*Poa* spp.) and *Eucalyptus pauciflora* seedlings near treeline in South-Eastern Australia. *Oecologia* 45:350–353
- Norton DA, Schönenberger W (1984) The growth forms and ecology of *Nothofagus solandri* at the alpine timberline, Craigieburn Range, New Zealand. *Arct Alp Res* 16:361–370
- Ohsawa M (1990) An interpretation of latitudinal patterns of forest limits in South- and East-Asian mountains. *J Ecol* 78:326–339
- Ohsawa M, Nainggolan PHJ, Tanaka N, Anwar C (1985) Altitudinal zonation of forest vegetation on Mount Kerinci, Sumatra: with comparisons to zonation in the temperate region of east Asia. *J Trop Ecol* 1:193–216
- Oswald H (1963) Verteilung und Zuwachs der Zirbe (*Pinus cembra* L.) der subalpinen Stufe an einem zentralalpinen Standort. *Mitt Forstl Versuchswes Österreichs* 60:437–499
- Ott E (1978) Über die Abhängigkeit des Radialzuwachses und der Oberhöhen bei Fichte und Lärche von der Meereshöhe und Exposition im Lötschental. *Schweiz Z Forstwes* 3:169–193
- Pisek A, Winkler E (1958) Assimilationsvermögen und Respiration der Fichte (*Picea excelsa* Link) in verschiedener Höhenlage und der Zirbe (*Pinus cembra* L.) an der alpinen Waldgrenze. *Planta* 51:518–543
- Pisek A, Winkler E (1959) Licht- und Temperaturabhängigkeit der CO₂-Assimilation von Fichte (*Picea excelsa* Link), Zirbe (*Pinus cembra* L.) und Sonnenblume (*Helianthus annuus* L.). *Planta* 53:532–550
- Rada F, Azocar A, Briceno B, Gonzalez J, Garcia- Nunez C (1996) Carbon and water balance in *Polylepis sericea*, a tropical tree-line species. *Trees* 10:218–222
- Rochefort RM, Little RL, Woodward A, Peterson DL (1994) Changes in sub-alpine tree distribution in western North America: a review of climatic and other causal factors. *Holocene* 4:89–100
- Rundel PW (1994) Tropical alpine climates. In: Rundel PW, Smith AP, Meinzer FC (eds) *Tropical alpine environments*. Cambridge University Press, Cambridge, pp 21–44
- Sakai A (1970) Freezing resistance in willows from different climates. *Ecology* 51:485–491
- Sakai A, Larcher W (1987) Frost survival of plants. Responses and adaptation to freezing stress (*Ecological studies*) 62. Springer, Berlin Heidelberg New York
- Schönenberger W, Frey W (1988) Untersuchungen zur Ökologie und Technik der Hochlagenaufforstung. *Forschungsergebnisse aus dem Lawinenanrissgebiet Stillberg*. Schweiz Z Forstwes 139:735–820
- Schröter C (1926) *Pflanzenleben der Alpen*. Albert Raustein, Zürich
- Schweingruber FH, Bräker OU, Schär E (1979) Dendroclimatic studies on conifers from central Europe and Great Britain. *Boreas* 8:427–452
- Schweingruber FH (1987) Flächenhafte dendroklimatische Temperaturrekonstruktionen für Europa. *Naturwissenschaften* 74:205–212
- Schweingruber FH, Bartholin T, Schaer E, Briffa KR (1988) Radiodensitometric-dendroclimatological conifer chronologies from Lapland (Scandinavia) and the Alps (Switzerland). *Boreas* 17:559–566
- Schulze ED, Mooney HA, Dunn EL (1967) Wintertime photosynthesis of bristlecone pine (*Pinus aristata*) in the White Mountains of California. *Ecology* 48:1044–1047
- Scott PA, Bentley CV, Fayle DCF, Hansell RIC (1987a) Crown forms and shoot elongation of white spruce at the treeline, Churchill, Manitoba, Canada. *Arct Alp Res* 19:175–186
- Scott PA, Hansell RIC, Fayle DCF (1987b) Establishment of white spruce populations and responses to climatic change at the treeline, Churchill, Manitoba, Canada. *Arct Alp Res* 19:45–51
- Scuderi LA (1987) Late Holocene upper timberline variation in the southern Sierra Nevada. *Nature* 325:242–244
- Scuderi LA, Schaaf CB, Orth KU, Band LE (1993) Alpine treeline growth variability: simulation using an ecosystem process model. *Arct Alp Res* 25:175–182
- Shanks RE (1956) Altitudinal and microclimatic relationships of soil temperature under natural vegetation. *Ecology* 37:1–7
- Slatyer RO (1976) Water deficits in timberline trees in the Snowy Mountains of south-eastern Australia. *Oecologia* 24:357–366
- Slatyer RO (1978) Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. VII. Relationship between gradients of field temperature and photosynthetic temperature optima in the Snowy Mountains area. *Aust J Bot* 26:111–121
- Slatyer RO, Ferrar PJ (1977) Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. V. Rate of acclimation to an altered growth environment. *Aust J Plant Physiol* 4:595–609
- Slatyer RO, Noble IR (1992) Dynamics of montane treelines. In: Hansen AJ, Castri F di (eds) *Landscape boundaries. Consequences for biotic diversity and ecological flows* (*Ecological studies* 92). Springer, Berlin Heidelberg New York, pp 346–359
- Smith WK, Carter GA (1988) Shoot structural effects on needle temperatures and photosynthesis in conifers. *Am J Bot* 75:496–500
- Sonesson M, Hoogesteger J (1983) Recent tree-line dynamics (*Betula pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman) in

- northern Sweden. In: Morisset P, Payette S (eds) Tree-line ecology (Collection Nordicana 47, Centre d'études nordiques). Université Laval, Quebec, pp 47–54
- Sowell JB, Koutnik DL, Lansing AJ (1982) Cuticular transpiration of whitebark pine (*Pinus albicaulis*) within a Sierra Nevada timberline ecotone, USA. *Arct Alp Res* 14:97–103
- Stevens GC, Fox JF (1991) The cause of treeline. *Annu Rev Ecol Syst* 22:177–191
- Sveinbjörnsson B, Kauhanen H, Nordell O (1996) Treeline ecology of mountain birch in the Torneträsk area. *Ecol Bull* 45:65–70
- Takahashi K (1944) Die Baum- und Waldgrenze im Hida-Gebirge (japanische Nordalpen). Ein Beitrag zur Baum- und Waldgrenze Ostasiens. *Jpn J Bot* 13:269–343
- Tranquillini W (1963) Climate and water relations of plants in the sub-alpine region. In: Rutler AJ, Whitehead FH (eds) The water relations of plants. Blackwell, Oxford, pp 153–167
- Tranquillini W (1979) Physiological ecology of the alpine timberline. Tree existence at high altitudes with special references to the European Alps (Ecological studies 31). Springer, Berlin Heidelberg New York
- Tranquillini W (1982) Frost drought and its ecological significance. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopedia of plant physiology 12B, physiological plant ecology II. Springer, Berlin Heidelberg New York, pp 379–400
- Tranquillini W, Platter W (1983) Der winterliche Wasserhaushalt der Lärche (*Larix decidua* Mill.) an der alpinen Waldgrenze. *Verhandl Ges Oekol Göttingen* 11:433–443
- Troll C (1961) Klima und Pflanzenkleid der Erde in dreidimensionaler Sicht. *Naturwissenschaften* 9:332–348
- Troll C (1973) The upper timberlines in different climatic zones. *Arct Alp Res* 5:A3–A18
- Tschager A, Hilscher H, Franz S, Kull U, Larcher W (1982) Jahreszeitliche Dynamik der Fettspeicherung von *Loiseleuria procumbens* und anderen Ericaceen der alpinen Zwergstrauchheide. *Oecol Plant* 3:119–134
- Turner H (1968) Ueber "Schneeschliff" in den Alpen. *Wetter und Leben* 20:192–200
- Turner H, Schönenberger W (1981) Environmental factors affecting radial growth in afforestations near timberline. *Mitt Forstl Bundesversuchsanst Wien* 142:357–365
- Vogt KA, Grier CC, Meier CE, Edmonds RL (1984) Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in Western Washington. *Ecology* 63:370–380
- Walter H (1973) Vegetation of the earth in relation to climate and eco-physiological conditions. English University Press, London
- Walter H, Medina E (1969) Die Bodentemperatur als ausschlaggebender Faktor für die Gliederung der subalpinen und alpinen Stufe in den Anden Venezuelas. *Ber Dtsch Bot Ges* 82:275–281
- Wardle P (1968) Engelmann spruce (*Picea engelmannii* Engel.) at its upper limits on the Front Range, Colorado. *Ecology* 49:483–495
- Wardle P (1971) An explanation for alpine timberline. *NZ J Bot* 9:371–402
- Wardle P (1974) Alpine timberlines. In: Ives JD, Barry RG (eds) Arct alp environments. Methuen, London, pp 371–402
- Wardle P (1981a) Winter desiccation of conifer needles simulated by artificial freezing. *Arct Alp Res* 13:419–423
- Wardle P (1981b) Is the alpine timberline set by physiological tolerance reproductive capacity, or biological interactions? *Proc Ecol Soc Aust* 11:53–66
- Wieser G (1997) Carbon dioxide gas exchange of cembra pine (*Pinus cembra*) at the alpine timberline during winter. *Tree Physiol* 17:473–477
- Wijmstra TA (1978) Palaeobotany and climate change. In: Gribbin J (ed) Climatic change. Cambridge University Press, Cambridge, pp 25–45
- Winiger M (1981) Zur thermisch-hygrischen Gliederung des Mount Kenya. *Erdkunde* 35:248–263
- Young KR (1993) Tropical timberlines: changes in forest structure and regeneration between two Peruvian timberline margins. *Arct Alp Res* 25:167–174
- Zukrigl K (1975) Zur Geschichte der Hochlagenwälder in den Seetaler Alpen (Steiermark). Eine pollenanalytische Untersuchung des kleinen Moores im Winterleitenkessel. *Cbl Ges Forstwes* 92:175–188