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ARTICLE

# A world-wide study of high altitude treeline temperatures

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## ABSTRACT

**Aim** At a coarse scale, the treelines of the world's mountains seem to follow a common isotherm, but the evidence for this has been indirect so far. Here we aim at underpinning this with facts.

**Location** We present the results of a data-logging campaign at 46 treeline sites between 68° N and 42° S.

**Methods** We measured root-zone temperatures with an hourly resolution over 1–3 years per site between 1996 and 2003.

**Results** Disregarding taxon-, landuse- or fire-driven tree limits, high altitude climatic treelines are associated with a seasonal mean ground temperature of 6.7 °C ( $\pm 0.8$  SD; 2.2 K amplitude of means for different climatic zones), a surprisingly narrow range. Temperatures are higher (7–8 °C) in the temperate and Mediterranean zone treelines, and are lower in equatorial treelines (5–6 °C) and in the subarctic and boreal zone (6–7 °C). While air temperatures are higher than soil temperatures in warm periods, and are lower than soil temperatures in cold periods, daily means of air and soil temperature are almost the same at 6–7 °C, a physics driven coincidence with the global mean temperature at treeline. The length of the growing season, thermal extremes or thermal sums have no predictive value for treeline altitude on a global scale. Some Mediterranean (*Fagus* spp.) and temperate South Hemisphere treelines (*Nothofagus* spp.) and the native treeline in Hawaii (*Metrosideros*) are located at substantially higher isotherms and represent genus-specific boundaries rather than boundaries of the life-form tree. In seasonal climates, ground temperatures in winter (absolute minima) reflect local snow pack and seem uncritical.

**Main conclusions** The data support the hypothesis of a common thermal threshold for forest growth at high elevation, but also reflect a moderate region and substantial taxonomic influence.

## Keywords

Climate, growth, forest limit, timberline, alpine ecology, mountains.

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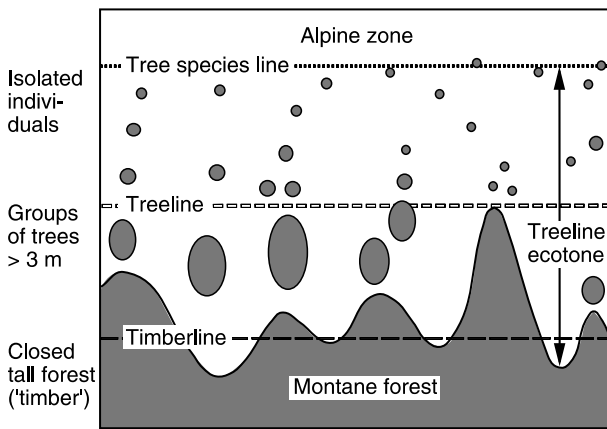
## INTRODUCTION

The high altitude limit of forests, commonly referred to as treeline, timberline or forest line (Fig. 1) represents one of the most obvious vegetation boundaries. In reality the transition from uppermost closed montane forests to the treeless alpine vegetation is commonly not a line, but a steep gradient of increasing stand fragmentation and stuntedness, often called the treeline ecotone or the treeline park land. Viewed from a great distance, the ecotonal transition is still quite abrupt, with groups of tall trees often found only 50 m below the limit of

isolated trees. South Hemisphere *Nothofagus* treelines often lack a gradual transition zone and form sharp boundaries (Wardle, 1998). The global high altitude treeline phenomenon calls for a common climatic driver, most likely a thermal one. This is the topic of this paper.

## Causes of treeline formation

Possible causes for the transition from forest to alpine shrub and grassland have been widely discussed (e.g. Däniker, 1923; Tranquillini, 1979; Wardle, 1993; Miehe & Miehe, 1994;



**Figure 1** A schematic representation of the high altitude treeline ecotone and the nomenclature used in this study. Note that such definitions are conventions for communication and do not deserve a major scientific debate.

Körner, 1998, 1999). Historically, too much weight has been given to regional peculiarities, which can overshadow the broader picture. Here we will strictly refrain from considering any aspect of anthropogenic influence (e.g. logging, burning, grazing) and situations where mechanical reasons make tree growth impossible (e.g. steep rocks, loose gravel, avalanche tracks, etc.). Also situations where moisture shortage prevents tree growth will be disregarded, because this is not a cause specific to high elevations. Hence the topic of this analysis is natural climatic treelines on mountains which receive sufficient moisture for tree growth, found at all latitudes between 70° N and 56° S.

For these treelines, a suite of explanations has been proposed over the years, falling into two categories: (1) general reasons, operating on all mountains, globally, and (2) modulating reasons of more regional significance. Unfortunately, most of the debate has circulated around the second. Continental temperate zone phenomena such as winter desiccation or ice blast require climates non-existent at treeline altitudes in most parts of the world. Variation in season length has been shown to affect tree performance within some temperate zone treeline ecotones (e.g. Baig & Tranquillini, 1976; Hadley & Smith, 1990), but globally, season duration at the treeline varies from 3 months (or shorter) in parts of the subarctic to a full year in the equatorial tropics, with little difference in the seasonal mean temperature, as far as this can be estimated from available meteorological data (Körner, 1998). Frost sensitivity has been dismissed many times as decisive for those species which passed the selection filter, although young above-ground tissue may become damaged occasionally (e.g. Sakai & Larcher, 1987; Körner, 1999). This also holds for roots in cold climates (Sutinen *et al.*, 1998). Where stands of crippled trees (krummholz) can be found above the treeline (which is most commonly the case), the lack of upright trees cannot plausibly be explained by reproductive failure. Furthermore,

tree seedlings are commonly found above the treeline, nested into the low stature alpine vegetation, but they do not become trees. Apparently viable seeds were available, but perhaps not enough to balance losses as young trees grow up, thereby preventing the establishment of closed stands in which individuals can protect each other mechanically, and, to a limited extent, climatically (for root zone temperatures such crowding is in fact negative, cf. Holtmeier & Broll, 1992).

It was geographers who pointed at the strikingly parallel elevational position of treeline and snowline across the globe (Hermes, 1955, see the detailed reference to his work in Körner, 1999). As the snowline is a purely physics-driven boundary, a common physical (possibly thermal) determinant of treeline altitude appears plausible, but biological mechanisms other than the ones mentioned above need to be identified. A thermal limitation of photosynthesis (carbon acquisition, source activity) is an unlikely explanation, according to Tranquillini's (1979) careful assessment. A thermal limitation of the investment of photo-assimilates into structural growth (sink activity) appears more likely (Däniker, 1923; Körner, 1998, 1999). But why should trees be affected more than shrubs and grasses, which do well at much higher elevations?

This is where microclimatology and plant architecture come in. Given their life form, trees themselves create the low tissue temperatures, which cause them to yield terrain to low stature vegetation, which in turn profits from life-form driven passive solar-energy use, facilitating canopy and soil heating. Treeline trees clearly experience a colder climate than adjacent low-stature alpine vegetation or krummholz-mats (Hadley & Smith, 1987; Grace, 1988; Körner, 1999; Körner *et al.*, 2003) and this has two reasons: the canopy is tightly coupled to atmospheric circulation and the root zone under a closed forest is screened from sun-driven soil heat flux, hence it is colder than the ground under low-stature vegetation, as will be documented here.

Three avenues had been proposed to sort out the sink or source related explanations of treeline formation (Körner, 1998): (1) an assessment of the actual growth temperatures in treeline forests world-wide, (2) a comparative study of the non-structural photo-assimilate pool of trees across the treeline ecotone and (3) *in situ* CO<sub>2</sub>-enrichment of treeline trees, which should stimulate sources rather than sinks, hence permit the test whether carbon is a limiting resource. The second avenue, explored over the last 3 years (Hoch *et al.*, 2002; Hoch & Körner, 2003), yielded clear evidence of increasing non-structural carbon charging of trees as one approaches the tree limit in the subarctic, the temperate and the subtropical zone. A free air CO<sub>2</sub>-enrichment project at the Swiss treeline is now entering its fourth year (Hättenschwiler *et al.*, 2002), with the first conclusive results to be expected soon. Results of a source-removal test at treeline (partial defoliation in pine) suggested that trees do not seriously suffer from C-limitation (Li *et al.*, 2002). The results of the temperature assessment project will be reported here.

### Why study treeline temperatures?

This global data collection campaign rests on the assumption that temperature is the key climatic factor which sets rather narrowly defined growth-physiological limits to plant life at high elevation in general and to trees in particular. The decisive biological processes involved may range from temperature-driven nutrient availability (Sveinbjörnsson, 2000; Karlsson & Weih, 2001), to developmental constraints (Körner & Peláez Menendez-Riedl, 1989; Häslér *et al.*, 1999) or effects on certain metabolic (Dahl, 1986) or synthetic pathways during structural growth (Körner, 1999).

The potential of temperature extrapolations from meteorological networks has been explored quite exhaustively (e.g. Lauer, 1986; Wardle, 1993 and earlier works, Körner, 1998; Jobbagy & Jackson, 2000) and left a broad margin of uncertainties, but there are still some useful guidelines. It seems from these analyses that the treelines of the world occur at seasonal mean air temperatures between 5.5 and 7.5 °C, with some noteworthy exceptions on islands and in the Southern Hemisphere (tree limits at higher temperatures). The 10 °C warmest month isotherm, a favoured correlate of earlier days, emerged to reflect the then geographical location of the research institutes active in this field (Alps, Rocky Mountains), with little predictive power on a global scale (Körner, 1998). Jobbagy & Jackson (2000) introduced a continentality index (allowing for thermal amplitudes) in combination with annual mean temperatures. This approach led to a better prediction of treeline altitude than simple treeline altitude-latitude correlates, but the ecological relevance is doubtful, because neither annual means nor temperature minima and winter conditions in general seem to matter, based on current wisdom (see the above reviews). Furthermore, any extrapolation from data by meteorological stations (commonly far away from treelines), carries with it the uncertainty to what extent they match actual temperatures experienced by trees. While there exist very detailed micrometeorological studies from within the treeline ecotone (e.g. Aulitzky, 1961a,b; Wardle, 1968; Lauer & Klaus, 1975; Turner & Schönenberger, 1981; Gross, 1989; Kessler & Hohnwald, 1998; Bendix & Rafiqpoor, 2001), standardized comparisons across mountain ranges and continents are missing. This paper aims at such a comparison.

### Why select root temperature?

The attempted global comparison requires a sharply defined measurement protocol and needs to be practical. Available technology now offers unique tools for collecting data from remote sites, but the rules of physics and thus the general problems with any temperature measurement remain the same. Every material exposed to solar radiation will heat, depending on its density and thermal conductivity, colour, wetness, ventilation, exposure and the size of the exposed structure. This makes data of a freely exposed temperature probe subject to a lottery, a problem well known to meteorologists, and the reason why air temperature measurements

(despite the technical simplicity of obtaining a signal) require delicate means of screening and ventilation, also leading to obvious installations, which need year-round protection. If perfectly done, we still do not know what temperatures conifer needles, a shoot or a root meristem might experience. Thus, air or canopy temperatures are not an appropriate choice for such a world-wide screening programme in remote places.

In addition to these aspects of practicality, four reasons led us to select root-zone temperatures for this project. (1) There is much evidence to show that the growth of roots is very sensitive to temperature (Körner, 1999, see also the discussion later); (2) ground temperature measured in 10 cm depth under a closed tree canopy (i.e. fully shaded) is a fairly good surrogate for daily mean canopy temperature (see results); (3) the basic physiological growth mechanisms which become critically constrained below a certain minimum temperature operate at the cellular level and are likely to be the same in all tissues and (4) root-zone temperatures also exert direct influences on above-ground metabolism (e.g. DeLucia, 1986; Day *et al.*, 1991). A draw back compared with canopy temperatures is that root-zone temperatures are buffered and do not mirror the actual extremes experienced by the shoot. However, given its atmospheric coupling, these diurnal excursions from the mean are much smaller in trees than in low-stature vegetation and we will present an analysis of canopy vs. ground temperature.

Root-zone temperatures obtained this way throughout 1 to 3 years from as many as possible treeline locations around the globe form the core of this data set. As 1 to 3 years cannot be considered fully representative of longer periods for a given site, except perhaps in the tropics, the year-to-year variation will contribute to the overall noise of the data. Therefore, we will not put too much weight on a single site's thermal regime, rather we focus on the cross-site patterns. A number of the sites were studied synchronously, but we consider the local climates across the globe to deviate randomly from their specific long-term means. The spatial replication across the globe should thus minimize any bias introduced by local climatic peculiarities of a given year. In a way, this procedure represents a space-for-time sampling on a global scale, which should make our conclusions rather robust. Additional temperature measurements in the canopy at selected sites and comparisons with adjacent treeless ground-temperatures help interpretation of the data. We will first present results of these more detailed studies, which underpin the meaning and usefulness of root-zone temperatures, and only then report the global patterns.

## METHODS AND STUDY SITES

All measurements presented here were obtained between 1996 and 2003 with single channel, fully water proof (in fact completely sealed) electronic data loggers equipped with an internal thermistor probe (Tidbits; Onset Computer Corporation, Cape Cod, MA, USA; -30 to + 70 °C, 0.2 K resolution, 3 cm diameter, 1.5 cm thickness, with the sensor placed in a

protruding nose and 2 mm below the surface of the polymer coat). Communication with these loggers at launching or downloading data is through a clear window using an IR beam (no plugs, no screw caps etc.), with signals transmitted to a laptop computer. The internal lithium battery lasts for c. 4 years. The measurement interval was set to 1 h. Prior and after exposure loggers were checked in an ice-water bath and at some higher temperatures, which confirmed a remarkable stability and absolute accuracy (deviation from zero <0.4 K, commonly <0.2 K). In one of 30 cases we detected unexplained deviations up to 1.4 K, which were corrected. The slope of the calibration curve was never found to be affected.

Loggers were buried in nearly horizontal ground, completely screened by the forest tree canopy during all times of the day and at 10 cm below the soil surface, with natural ground litter cover replaced after burying. A 10 cm depth was chosen because this provides enough microscale spatial integration (e.g. in the case of small sunflecks a shallower position could bias the readings), because at this depth temporal variations are sufficiently buffered at an hourly resolution, and because most roots occur in that depth or slightly above. A shallower position of say 5 cm, would have fallen into the soft raw humus layer in some sites, which we tried to avoid, also because root density is commonly higher just beneath the raw humus, and heat diffusion may become too dependent on patchy density differences of the organic material. Temperatures measured at treeline at various depth down to 50 cm commonly yield similar means, but show less temporal variation the deeper one goes (Wardle, 1968; Kessler & Hohnwald, 1998; Bendix & Rafiqpoor, 2001). As the excursions to higher and lower temperatures are certainly important for root functioning, we did not want to lose this information. However, as long as all sites are treated equal, absolute depth in this range should not significantly affect the global site comparison.

No visible installations or obvious site markers were used, avoiding curiosity searches by trespassers. A 2-mm nylon string was allowed protruding the soil, but covered under litter. This permitted spotting the logger after locating the position, using coordinates among nearby reference trees. Except for seven of the sites, loggers were placed by one of the authors, but were often recovered by local helpers and sent back to us. With loggers buried exactly following this protocol, we found no significant differences between data from various loggers buried at different places within the same site, hence there was no need for replication per site. However, wherever possible, we tried to expose loggers on at least two different sites in each region (e.g. on two different slopes of a valley), although it turned out later (see Results) that differences in ground temperature are still very small, provided loggers were buried at completely tree covered microsites and at the same elevation.

For a specific test of the relationship between root-zone and canopy temperature we selected a hump shaped mountain (Mt Patscherkofel, near Innsbruck, Austria), which has treelines in all four main compass directions within a 4 × 4 km area and mounted additional sensors in the tree canopy of *Picea abies*,

just above, where we buried the root-zone sensors (2–3 m above ground). Although sites were selected for their similarity, the four locations still differed somewhat in tree stature, slope inclination, microtopography and ground litter, a natural variation of conditions across which a relatively robust picture about root vs. canopy temperature relationships should be obtained. Canopy loggers were tied to the lower side of horizontal, north-exposed branches of 3–5 cm diameter, with dense, hanging branchlets also screening the logger from the side. The thermistor was c. 0.5–1 cm under the branch's stem. Any remaining radiative warming of the sensor should be rather similar to what the branch may experience naturally.

In a *post hoc* verification of ground temperatures, we used daily temperature amplitudes to ascertain that the above positioning criteria were met (this is particularly important where we did not place the loggers ourselves). A series of tests showed that the 24-h amplitude of temperature does not exceed 5.5 K if the ground was permanently shaded. If we noted greater excursions the data were carefully inspected for the regular recurrence of asymmetric diurnal courses (e.g. as a consequence of extensive sunflecks) and if such effects were identified, the data set was omitted (see also Results).

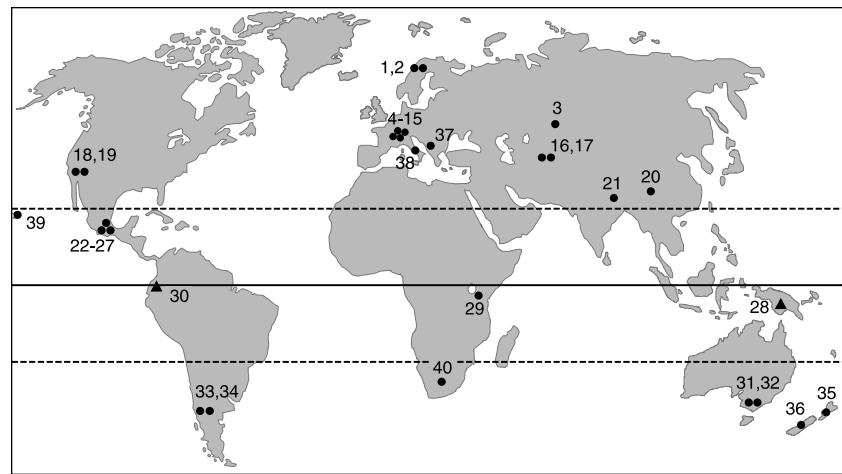
### Study sites

Only natural climatic treelines were considered. Whether a treeline is natural or not rests on two criteria: (1) the consistent highest position of tree stands in a region and (2) the visible, commonly rapid elevational deterioration of tree stature. For the purpose of this survey, the treeline was defined as the connecting line between the uppermost forest patches in an area (Fig. 1), with trees upright and at least 3 m in height and growing in groups. Loggers were placed in the deep shade of such stands, as close as possible to the treeline as defined above. The geographical positions of sites and their coordinates are shown in Fig. 2 and Table 1.

### Data analysis

Hourly readings for at least one full year represent a lot of information, which can be analysed in many ways, using different means, sums, frequency distributions etc. for selected periods or the whole year. We tested various ways of handling these data and finally adopted the following procedure: in the first step, we plotted the full time-series data. In the second step a threshold-based routine was used to identify the duration of the growing period. A comparison of an automatic procedure and visual inspection of the time-series data plus local site knowledge revealed that the best correspondence occurs when the beginning of the season was defined as that date at which the soil temperature at 10 cm depth exceeds 3.2 °C in spring. This is the ground temperature which corresponds to a weekly mean of canopy temperature of 0 °C (see Results). In most seasonal sites, winter ground temperatures remain at 0 °C for most of the time and snow melt produces a sharp thermal signal. Within a day or two

**Figure 2** Location of the test areas for treeline ground temperature measurements. Numbers refer to site numbers in Table 1. Cases where we use data from other sources are marked with triangles: Ecuadorian Andes, Rafiqpoor MD and Bendix J (pers. comm., unpubl. data); Papua New Guinea, data as referred to in Körner *et al.* (1983).



temperatures commonly exceed 5 °C. This sharp transition was even detectable in Mexico at 19° N. Also in the tropics, periods with continuous soil temperatures below 3.2 °C were regarded as ‘quasi stand still periods’ (c. 6 weeks in Ecuador during the peak of the rainy season) in order to retain comparability. The end of the growing season was defined as the date at which the ground temperature at 10 cm depth reached 3.2 °C for the first time in autumn.

After snow melt, surface soils warm more rapidly, whereas in autumn, surface soils cool faster than is recorded by the sensor at 10 cm depth. A sensitivity test of either including or excluding a few doubtful days in case of less sharp transitions, did not really affect the results for a given site (e.g. a 0.1 K difference of the season mean). As such transitions occur at different dates in different years we used mean dates for season length across years, where more than a year’s data were available. However, for the frequency distribution plots, we still assembled temperatures for hours only which fall in a specific year’s growing period (hence no period is considered twice). The averaging for mean annual courses is the reason why season boundaries in diagrams sometimes do not seem to match the above criteria.

Winter data were not further analysed, but we report the absolute minimum recorded for each site and discuss some special cases. Overall, soil temperatures below zero do not bear a lot of biological meaning, because where such temperatures occur at higher latitudes, trees are dormant irrespective of the actual temperature. Low temperature resistance always exceeds such minima, and late winter desiccation stress associated with frozen ground in some continental temperate zone treelines is a very local problem for very young trees (Körner, 1998, 1999) that is not relevant at the global scale considered here.

The third step was the statistical treatment of the growing-season data as defined above. We calculated the arithmetic mean and the median, the warmest month mean, and the day degrees above 0 and 5 °C for the whole growing season. In case of overlapping time courses of more than a year, these were condensed to a 12-month year by averaging any data obtained for the same part of the year. For the sake of comparability,

South Hemisphere data were plotted so that December lines up with June.

## RESULTS

Before discussing the global comparison we will first address three issues which relate to the usefulness of the data: (1) a *post hoc* analysis of temperature amplitudes in order to underpin the correct positioning of measurement points, (2) a test of the sensitivity of ground temperatures to slope exposure under a dense forest canopy and finally, (3) a discussion of the relationships and differences between root zone and canopy temperatures. All results from multiple sites will be presented by latitude, except for the data from six treeless test sites, which are ranked by ground-cover density.

### Root-zone temperatures and ‘radiation errors’

Although our ground sensors will not experience any direct impact of solar radiation, they may capture enhanced soil heat flux in cases where direct solar radiation hits the ground despite the precautions taken at burying. A few hours of sunshine on the ground surface, perhaps very early or late in the day when solar angles are low, would diminish comparability. Such periodic solar ground heating is, however, detectable in the data by an enhanced diurnal temperature amplitude. In the few cases where we could not bury loggers ourselves, this permitted a *post hoc* test. From sensors where we were absolutely confident that sun could never hit the ground surface, we know that the maximum 24-h amplitude ever measured at 10 cm depth and under complete solar screening by trees is 5.5 K.

Absolute maxima (the single largest amplitude in one to two seasons) averaged over various sites per geographical region are at around 3 K in the subarctic (N. Sweden) and subtropics (Mexico) and between 4 and 5 K in the temperate zone (Table 2). There are hardly any differences in mean 24-h amplitudes for the whole growing season across the globe (1.8 + 0.7 K) if sensors were correctly positioned. This in itself

**Table 1** Study sites for the worldwide treeline temperature assessment

| Region  | Latitude/longitude<br>N/S, E/W | Altitude<br>(m) | Dominant species<br>at treeline | Recording period<br>(d-m-y; from/to) |
|---|--------------------------------|-----------------|---------------------------------|--------------------------------------|
| Subarctic (Scandinavia)   |                                |                 |                                 |                                      |
| Kårsavagge, Abisko (N. Sweden)  | 68°23', 19°17'                 | 700             | <i>Betula pubescens</i>         | 23-04-98/20-07-99                    |
| Lapporten, Abisko (N. Sweden)   | 68°23', 19°17'                 | 700             | <i>Betula pubescens</i>         | 24-04-98/24-07-99                    |
| S-Boreal (N. Central Asia)  |                                |                 |                                 |                                      |
| Seminski Pass, Altai (Russia)   | 51°05', 85°40'                 | 1890            | <i>Pinus sibirica</i>           | 05-08-97/08-08-98                    |
| Cool-temperate zone (E. Alps)   |                                |                 |                                 |                                      |
| Patscherkofel N, Innsbruck (Austria)  | 47°13', 11°24'                 | 2050            | <i>Pinus cembra</i>             | 27-05-00/23-06-01                    |
| Patscherkofel E, Innsbruck (Austria)  | 47°13', 11°24'                 | 2070            | <i>Picea abies</i>              | 27-05-00/23-06-01                    |
| Patscherkofel S, Innsbruck (Austria)  | 47°13', 11°24'                 | 2065            | <i>Picea abies</i>              | 27-05-00/23-06-01                    |
| Patscherkofel W, Innsbruck (Austria)  | 47°13', 11°24'                 | 2065            | <i>Picea abies</i>              | 27-05-00/23-06-01                    |
| Glungezer, Hall (Austria)   | 47°20', 11°30'                 | 2130            | <i>Pinus cembra</i>             | 31-05-97/16-10-98                    |
| Poschach, Ötztal (Austria)  | 46°50', 11°00'                 | 2130            | <i>Pinus cembra</i>             | 23-05-97/16-10-98                    |
| Obergurgl, Ötztal (Austria)   | 46°50', 11°00'                 | 2280            | <i>Pinus cembra</i>             | 25-05-97/16-10-98                    |
| Cool-temperate zone (W. Alps)   |                                |                 |                                 |                                      |
| Titlis, Engelberg (Switzerland)   | 46°48', 08°24'                 | 1900            | <i>Picea abies</i>              | 06-07-00/04-07-01                    |
| Stillberg, Davos (Switzerland)  | 46°46', 09°52'                 | 2220            | <i>Larix decidua</i>            | 02-06-97/11-06-98                    |
| Mt Noble, Marena, Sion (Switzerland)  | 46°12', 07°30'                 | 2310            | <i>Pinus cembra</i>             | 26-09-96/27-09-00                    |
| Mt Noble, Planards, Sion (Switzerland)  | 46°12', 07°30'                 | 2240            | <i>Pinus cembra</i>             | 26-09-96/29-09-00                    |
| Mt Noble, Tour de Bonvin, Sion (Switzerland)  | 46°12', 07°30'                 | 2370            | <i>Pinus cembra</i>             | 26-09-96/26-09-00                    |
| Cool-temperate zone (Central Asia)  |                                |                 |                                 |                                      |
| Tien Shan SW (Kyrgyzstan)   | 41°30', 77°00'                 | 2920            | <i>Picea schrenkiana</i>        | 11-09-96/10-09-97                    |
| Tien Shan E (Kyrgyzstan)  | 41°30', 77°00'                 | 2750            | <i>Picea schrenkiana</i>        | 11-09-96/10-09-97                    |
| Mediterranean (N. America)  |                                |                 |                                 |                                      |
| Mt Gibbs SW, Yosemite NP (California)   | 37°53', 119°14'                | 3320            | <i>Pinus albicaulis</i>         | 22-08-97/16-08-98                    |
| Mt Gibbs N, Yosemite NP (California)  | 37°53', 119°14'                | 3200            | <i>Pinus albicaulis</i>         | 23-08-97/16-08-98                    |
| Warm-temperate (Central & E. Asia)  |                                |                 |                                 |                                      |
| Zhe Gu Shan, Min Mts., Sichuan (China)  | 31°53', 102°43'                | 3750*           | <i>Picea asperata</i>           | 18-08-00/12-12-01                    |
| Kijangjing Gompa 1, Langtang, Himalaya (Nepal)  | 28°12', 85°35'                 | 4010            | <i>Betula utilis</i>            | 07-08-99/02-08-00                    |
| Subtropical (Central America)   |                                |                 |                                 |                                      |
| Nevado de Toluca E (Mexico)   | 19°09', 99°46'                 | 4030            | <i>Pinus hartwegii</i>          | 17-03-97/18-03-98                    |
| Nevado de Toluca N (Mexico)   | 19°09', 99°46'                 | 3990            | <i>Pinus hartwegii</i>          | 31-03-00/22-04-01                    |
| Pico de Orizaba S (Mexico)  | 19°01', 97°16'                 | 4020            | <i>Pinus hartwegii</i>          | 14-03-97/15-03-98                    |
| Pico de Orizaba N (Mexico)  | 19°01', 97°16'                 | 4020            | <i>Pinus hartwegii</i>          | 14-03-97/15-03-98                    |
| Iztaccihuatl E (Mexico)   | 19°11', 98°38'                 | 3965            | <i>Pinus hartwegii</i>          | 15-03-97/14-03-98                    |
| Iztaccihuatl S (Mexico)   | 19°11', 98°38'                 | 3970            | <i>Pinus hartwegii</i>          | 15-03-97/14-03-98                    |
| Equatorial (SE. Asia, Africa, S. America)   |                                |                 |                                 |                                      |
| Pindaunde (Papua New Guinea)†   | 05°40', 145°01'                | 3800*           | Ericaceae                       | 1966/1972                            |
| Mweka S, Kilimanjaro (Tanzania)   | 03°05', 37°20'                 | 3800*           | <i>Erica</i> sp.                | 26-08-02/11-04-03                    |
| Papallacta Pass (Ecuador)‡  | 00°24', 78°07'                 | 4000            | <i>Gynoxis acostae</i>          | 13-07-01/07-06-02                    |
| Mediterranean, South Hemisphere (Australia)   |                                |                 |                                 |                                      |
| Charlotte's Pass S, Snowy Mountains (Australia)   | 36°26', 148°20'                | 2000*           | <i>Eucalyptus pauciflora</i>    | 23-12-98/01-03-00                    |
| Charlotte's Pass N, Snowy Mountains (Australia)   | 36°26', 148°20'                | 2000*           | <i>Eucalyptus pauciflora</i>    | 23-12-98/01-03-00                    |
| Temperate S-Hemisphere  |                                |                 |                                 |                                      |
| Termas de Chillán W, Concepcion (Chile)   | 36°40', 71°30'                 | 1950            | <i>Nothofagus pumilio</i>       | 04-01-00/13-12-01                    |
| Termas de Chillán E, Concepcion (Chile)   | 36°40', 71°30'                 | 1950            | <i>Nothofagus pumilio</i>       | 04-01-00/13-12-01                    |
| Urcin Track, Kaimanawa Mts., Turangi (New Zealand-N)  | 39°10', 175°51'                | 1350            | <i>Nothofagus solandri</i>      | 23-12-98/12-03-00                    |
| Springs Junction, Mt Haast (New Zealand-S)  | 42°20', 172°05'                | 1220            | <i>Nothofagus menziesii</i>     | 01-12-98/15-04-00                    |
| Additional sites not conforming to our<br>treeline criteria, because of lack of species or fire |                                |                 |                                 |                                      |
| Jakupica (Macedonia)  | 41°45', 21°22'                 | 1840            | <i>Fagus moesiaca</i>           | 05-11-98/01-09-00                    |
| Maiella E, Central Appennine (Italy)  | 42°10', 14°08'                 | 1820            | <i>Fagus sylvatica</i>          | 10-05-99/29-08-00                    |
| Mauna Loa N (Hawaii)  | 19°30', 155°40'                | 2590            | <i>Metrosideros polymorpha</i>  | 06-02-99/14-03-00                    |
| Sentinel Trail, Drakensberg (South Africa)  | 28°42', 28°54'                 | 2700*           | <i>Erica</i> sp.                | 19-05-00/09-06-01                    |

**Table 1** *continued*

| Region  | Latitude/longitude<br>N/S, E/W | Altitude<br>(m) | Dominant species<br>at treeline | Recording period<br>(d-m-y; from/to) |
|---|--------------------------------|-----------------|---------------------------------|--------------------------------------|
| Additional sites without tree cover at or close to treeline |                                |                 |                                 |                                      |
| Patscherkofel S, Innsbruck (Austria)                        | 47°13', 11°24'                 | 2065            | <i>Nardus</i> heath             | 27-05-00/23-06-01                    |
| Maiella NW, Central Appennine (Italy)                       | 42°10', 14°08'                 | 1820            | <i>Festuca</i> heath            | 10-05-99/29-08-00                    |
| Kyangjin Gompa 2, Langtang, Himalaya (Nepal)                | 28°12', 85°35'                 | 4010            | <i>Kobresia</i> heath           | 07-08-99/02-08-00                    |
| Kyangjin Gompa 3, Langtang, Himalaya (Nepal)                | 28°12', 85°35'                 | 3970            | <i>Rhododendron</i> krummholz   | 07-08-99/02-08-00                    |
| Mauna Loa S (Hawaii)  | 19°30', 155°40'                | 2590            | <i>Metrosideros polymorpha</i>  | 06-02-99/14-03-00                    |
| Nevado de Toluca W (Mexico)                                 | 19°09', 99°46'                 | 4000            | tussock grass                   | 31-03-00/22-04-01                    |

\*These altitudes had been adjusted for the position of actual remnants of treeline by using an adiabatic lapse rate of 0.55 K per 100 m (Zhe Gu Shan +70 m, Pindaunde +320 m, Mweka -200 m, Charlotte's Pass +60 m, Sentinel trail +200 m).

†Data by Hnatiuk *et al.* 1976.

‡Data by M.D. Rafiqpoor and J. Bendix (unpubl.).

**Table 2** Mean and maximum 24-h amplitude of root zone temperature (K) under a closed forest canopy at treeline during the whole growing season. In brackets the number of sites in each geographical region

| Region   | Seasonal mean<br>of the daily amplitude | Maximum daily amplitude<br>during the season |
|--|---|--|
| N. Scandinavia 68° N ( <i>n</i> = 2)   | 2.2 ± 0.3                               | 3.0 ± 1.2                                    |
| Eastern Alps 46°–47° N ( <i>n</i> = 7)   | 1.7 ± 0.3                               | 5.1 ± 0.6                                    |
| Western Alps 46°–47° N ( <i>n</i> = 6)   | 2.1 ± 0.4                               | 4.6 ± 0.7                                    |
| Mexico 19° N ( <i>n</i> = 6)   | 2.0 ± 0.7                               | 3.2 ± 1.0                                    |
| Southern Hemisphere 36°–39° S<br>(Australia, Chile, New Zealand; <i>n</i> = 6)   | 1.9 ± 0.3                               | 4.2 ± 0.3                                    |
| Mean for all sites ( <i>n</i> = 36; including<br>regions belonging to different<br>climates but represented<br>by only one or two sites) | 1.8 ± 0.7                               | 3.9 ± 1.2                                    |

is already an important result. Data, which exceeded the 5.5 K limit, are at risk and need detailed inspection. We detected three such cases. In the Alps this was a singularity created by a cold break in summer on one site (Mt Glungezer, max. amplitude 6.1 K). The second was in the Sierra Nevada of California (Yosemite, also 6.1 K) with a more regular occurrence of high amplitudes, which needs to be kept in mind when discussing the data. One important site from the tropical Andes, unfortunately, had to be dismissed (we did not see the site ourselves), because the data revealed regular amplitudes of 25 K, which is physically impossible at 10 cm depth. From our experience even uncovered ground cannot exceed a 24-h amplitude of 10 K at 10 cm soil depth at treeline altitudes, a value we detected below dark, completely bare, fully sunlit ground, *c.* 300 m below the potential treeline on Mauna Loa, Hawaii (see also Table 8).

The data presented in Table 2 make us confident that the measurement points used in this campaign meet our criteria and permit the comparisons we are aiming for. Amplitudes for those larger regions from which we have only one to two study sites (not included in Table 2) are within or below the ranges shown. Very low amplitudes were found in Nepal (mean 0.4 K, max 1.2 K) and on Kilimanjaro (0.6 and 1.2 K). In both cases the ground was very densely covered with litter and vegetation,

which may have added to the buffered signals. In any case, these are the actual diurnal temperature amplitudes that roots experience at treeline conditions.

### Root-zone temperature and slope exposure

We used three geographical regions for which we have a multitude of sites with contrasting slope exposure to test the influence of compass direction of the overall slope on a given site. Once loggers are positioned according to our protocol, slope exposure has no effect on either the maximum diurnal amplitude of root-zone temperature or its seasonal mean (Table 3). The variance among data for different sites in one geographical region seems to depend more on local peculiarities (microtopography, litter, canopy density, wind etc.) than on the main direction of slope. However, the overall variability among sites is surprisingly small (commonly <0.5 K), which will be discussed later in more detail. Within this overall variability, the slope-only effect (if there is any) is equal (E. Alps) or smaller (W. Alps, Mexico). Temperature amplitudes do not correlate with seasonal means, hence sites with a high maximum diurnal range are not necessarily warmer sites and vice versa.

The insignificance of exposure in large reflects the screening of the sun by the tree canopy. The fact that loggers were buried

| Region/parameter         | North     | East      | South      | West | all       |
|--------------------------|-----------|-----------|------------|------|-----------|
| E-Alps, Mt Patscherkofel |           |           |            |      |           |
| Max. amplitude (K)       | 5.0       | 4.4       | 5.5        | 4.4  | 4.8 ± 0.5 |
| Seasonal mean (°C)       | 7.3       | 6.7       | 6.9        | 7.4  | 7.0 ± 0.3 |
| W-Alps, various sites    |           |           |            |      |           |
| Max. amplitude (K)       | 4.7       | 4.4       | 4.6 ± 0.9* | 4.4  | 4.5 ± 0.2 |
| Seasonal mean (°C)       | 7.7       | 6.3       | 7.1 ± 0.2  | 7.3  | 7.1 ± 0.6 |
| Mexico, three sites      |           |           |            |      |           |
| Max. amplitude (K)       | 3.2 ± 0.3 | 3.1 ± 0.2 | 3.2 ± 1.5  | –    | 3.2 ± 0.1 |
| Seasonal mean (°C)       | 5.5 ± 0.4 | 6.4 ± 0.9 | 5.7 ± 0.2  | –    | 5.9 ± 0.5 |

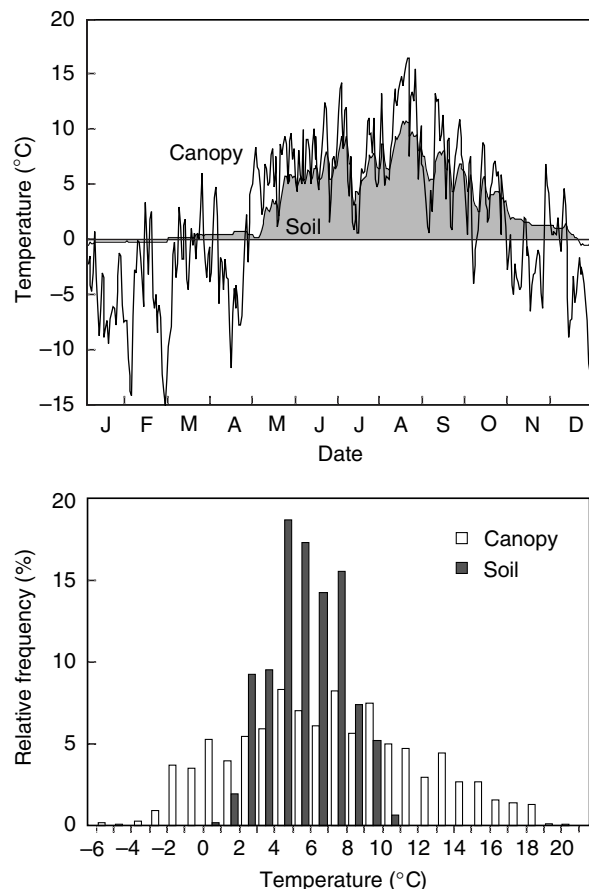
\*Mean and SD in cases where more than one (two to three) site was available per exposure type.

on nearly flat patches within the overall slope may have added to this. In the following we will treat all sites as independent replicates, irrespective of the site-specific slope direction. To our surprise, tree-canopy temperatures (not presented here in detail, but see the following section) also do not show slope effects, which agrees with statistics documenting no slope effects on treeline altitude in Mexico and the Alps (Beaman, 1962; Paulsen & Körner, 2001). The well known slope effects on radiation interception seem to be restricted to bare ground and low stature vegetation, but are neither seen below dense tree crowns nor within shaded parts of tree canopies. With their crowns, trees create their own interaction angles with solar radiation, irrespective of ground surface inclination and slope direction. The situation would be different in open woodlands, where ground heating could lead to thermic effects in isolated tree crowns during calms.

### Root-zone and canopy temperature

The correlation between root-zone temperature and tree-canopy temperature (which is often close to air temperature) during the growing season obviously depends on the integration period. It is well known that over very long periods deep (e.g. 1 m) soil temperatures 'store' mean air temperature. Our –10 cm root-zone temperature buffers much less and follows the day-by-day variation in air temperature with little (3–4 h) delay, but reduced amplitude (Fig. 3). For our test region (four sites in the E. Alps) there is little difference between 24 h ( $r^2=0.74$ ), 2 or 7 days ( $r^2 = 0.84$ ) integration periods (Table 4) and correlations for all sites are very similar. Hence we present pooled regressions (Fig. 4) and means and variance only. Soils are warmer than the air at low and cooler than air at high air temperatures, with the point of equality surprisingly invariant across the four sites at a mean of 6.5 °C. When 7-day means of canopy temperature are regressed to 0 °C, the 7-day mean soil temperature is 3.2 °C, hence, our definition of the beginning and end of the season (see Methods). Full-season means of hourly temperatures differ little between the root zone and the canopy (the canopy is *c.* 1 K warmer; the warmest month mean is 2 K higher), but the winter minima, the diurnal amplitudes and maxima during the growing season differ considerably

**Table 3** Exposure effects on root-zone temperature in the Alps and Mexico



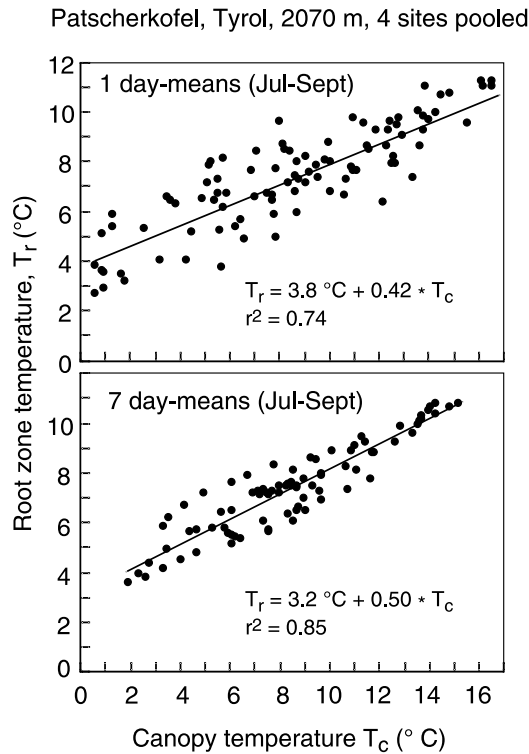
**Figure 3** The seasonal course of daily mean temperature and the frequency distribution of hourly temperatures during the 135-day growing season for the root zone and the tree canopy on an eastern slope of Mt Patscherkofel near Innsbruck, Austria, 2050 m. Data for the other three locations tested look very similar. For means and extremes across the four test sites see Table 5.

(Table 5). The higher frequency of hours with warmer temperatures in the canopy (Fig. 3) is also reflected in a 32% higher sum of degree hours above zero in the canopy, despite the colder night temperatures. Of course, the fully sunlit part of the canopy can periodically experience much higher temperatures, depending on branch architecture and wind



**Table 4** The correlation between root zone ( $T_r$ ) and canopy ( $T_c$ ) temperature of four different test sites ( $n = 4$  sites, i.e. N, E, S, W) at  $2050 \pm 20$  m in the Alps (Mt Patscherkofel)

| Integration period | $T_r$ at $T_c = 0$ °C | Temp. (°C) at $T_r = T_c$ | $r^2$ |
|--------------------|-----------------------|---------------------------|-------|
| 1 day (24 h)       | $3.8 \pm 0.7$         | $6.5 \pm 0.6$             | 0.74  |
| 2 days             | $3.7 \pm 0.7$         | $6.5 \pm 0.6$             | 0.75  |
| 7 days             | $3.2 \pm 0.8$         | $6.3 \pm 0.8$             | 0.85  |

**Figure 4** Linear regressions for root zone  $T_r$  and canopy temperature  $T_c$  at the treeline of Mt Patscherkofel with 1- and 7-day integration periods for any given date during the  $134 \pm 4$  days growing season in 2001 (data pooled from all four sites). See also Table 4.

speed (Gross, 1989; Wieser *et al.*, 2000; Gansert *et al.*, 2002), and also experiences substantial radiative cooling during clear nights, not reflected in our data. However, such phenomena are not tied to certain regions, and hence would apply anywhere, although perhaps with varying frequency. To capture such micrometeorological detail requires different methods, not applicable to the scale of our survey.

In summary, root-zone temperatures at 10 cm depth also mirror canopy temperatures on a daily to weekly basis and mean canopy temperatures can be predicted with a relatively high confidence using the equations presented with Fig. 4. Given the uniformity of diurnal amplitudes of shaded root-zone temperatures across the globe (see above), these relationships should also hold for other regions. For our global comparison of life conditions, root-zone temperature

**Table 5** Comparison of root zone ( $-10$  cm) and canopy ( $+2$  m) temperatures at treeline in a test area in the Central Alps (Mt Patscherkofel, Tirol, Austria)\*

| Type of temperature data          | Roots          | Canopy          | Difference (K) |
|-----------------------------------|----------------|-----------------|----------------|
| Seasonal mean temperature (°C)    | $7.1 \pm 0.3$  | $8.2 \pm 0.2$   | +1.1           |
| Absolute minimum temperature (°C) | $-1.1 \pm 1.1$ | $-16.7 \pm 0.4$ | -15.6          |
| Absolute maximum temperature (°C) | $12.1 \pm 0.7$ | $22.5 \pm 0.9$  | +10.4          |
| Mean daily amplitude (K)          | $1.6 \pm 0.3$  | $8.5 \pm 0.7$   | +6.9           |
| Warmest month mean (°C)           | $9.3 \pm 0.4$  | $11.3 \pm 0.2$  | +2.0           |
| Number of degree hours above 0 °C | $949 \pm 29$   | $1248 \pm 52$   | +299           |

\*Mean and SD for four sites in a  $4 \times 4$  km area, each site exposed to a different compass direction, namely exactly N, E, S and W at  $2050 \pm 20$  m altitude for a  $135 \pm 4$ -day-growing period, as defined by a  $3.2$  °C soil temperature threshold (21 May/2 June to 1/9 October). The data hardly differed between the four sites, hence we present mean  $\pm$  SD only.

thus also has some meaning for what trees experience above the ground.

### Global comparisons

In the following sections we will compare different parameters associated with the thermal regime experienced by treeline trees. The analysis of the data made it clear right from the beginning that we also collected information from sites that in retrospective do not represent climatic treelines. These are the sites with *Fagus* sp. and *Metrosideros polymorpha* in the Northern Hemisphere, and *Nothofagus* sp. and *Erica* sp. (Drakensberg) in the South Hemisphere, for which most values are far higher than anywhere else, from the subarctic to the equator. These treelines are thus probably species- or genus-specific boundaries, but not treelines in the sense that no other tree species could grow at higher elevation in the given area (evidence for North Hemisphere conifers growing well at several hundred metres above 'native' treeline in New Zealand and Hawaii, see Discussion). In the case of the Drakensberg in South Africa, there were simply no higher sites where trees could grow in the near to vertical escarpment. Although we do not consider these upper tree-limits as a climatic treeline, we still report these data for the sake of completeness, but treat them as a separate group not included in the treeline debate *per se*. A special problem is the data from Yosemite. The large winter snow pack releases those trees from snow only in July, right into the peak Mediterranean summer. During the 3 months growing period, ground temperatures become higher than in any other climatic treeline. The exceptional high seasonal mean amplitudes of 24 h ground temperature of 3.5 K (compared with the numbers in Table 2) may hint at incomplete canopy cover, but there may also be advective heat seeping into those forests. We retained the data,

**Table 6** Means, extremes and sums of growing-season ground temperatures for all sites grouped by climate region

| Site                               | Absolute minimum | Absolute maximum | Seasonal mean (median) | Mean of warmest month | Sum °h >0 °C | Sum °h >5 °C | Duration of growing season (d) |
|------------------------------------|------------------|------------------|------------------------|-----------------------|--------------|--------------|--------------------------------|
| Subarctic boreal                   |                  |                  |                        |                       |              |              |                                |
| 1                                  | -3.4             | 9.6              | 6.3 (6.8)              | 7.9                   | 645          | 181          | 102                            |
| 2                                  | -2.0             | 10.9             | 6.4 (6.5)              | 7.6                   | 655          | 169          | 103                            |
| Boreal                             |                  |                  |                        |                       |              |              |                                |
| 3                                  | -4.8             | 11.0             | 6.6 (6.6)              | 8.5                   | 700          | 210          | 106                            |
| Cool temperate E. Alps             |                  |                  |                        |                       |              |              |                                |
| 4                                  | -2.5             | 11.9             | 7.3 (7.1)              | 9.3                   | 944          | 307          | 130                            |
| 5                                  | -0.5             | 11.2             | 6.7 (6.5)              | 8.8                   | 925          | 263          | 139                            |
| 6                                  | -1.4             | 12.9             | 6.9 (6.8)              | 9.5                   | 936          | 302          | 136                            |
| 7                                  | 0.0              | 12.3             | 7.4 (7.4)              | 9.7                   | 991          | 346          | 134                            |
| 8                                  | -5.0             | 13.9             | 6.9 (7.0)              | 9.1                   | 909          | 315          | 132                            |
| 9                                  | -3.4             | 12.0             | 6.4 (6.4)              | 8.3                   | 825          | 233          | 129                            |
| 10                                 | -5.0             | 13.7             | 6.8 (6.8)              | 8.8                   | 892          | 290          | 132                            |
| Cool temperate W. Alps             |                  |                  |                        |                       |              |              |                                |
| 11                                 | -0.9             | 8.9              | 6.3 (6.1)              | 8.1                   | 902          | 201          | 145                            |
| 12                                 | -2.4             | 12.8             | 7.3 (7.1)              | 9.6                   | 1087         | 367          | 150                            |
| 13                                 | -4.9             | 13.7             | 7.7 (7.6)              | 9.3                   | 896          | 324          | 117                            |
| 14                                 | -1.7             | 12.8             | 7.4 (7.5)              | 10.4                  | 1121         | 403          | 152                            |
| 15                                 | -2.1             | 13.4             | 6.8 (6.4)              | 9.9                   | 837          | 264          | 123                            |
| Cool temperate Central Asia        |                  |                  |                        |                       |              |              |                                |
| 16                                 | -10.4            | 12.5             | 7.5 (7.3)              | 8.9                   | 950          | 329          | 125                            |
| 17                                 | -5.3             | 12.6             | 8.1 (8.0)              | 9.7                   | 1070         | 413          | 131                            |
| Mediterranean (California)         |                  |                  |                        |                       |              |              |                                |
| 18                                 | -5.0             | 15.0             | 9.4 (9.4)              | 11.2                  | 862          | 405          | 92                             |
| 19                                 | -2.9             | 13.6             | 8.0 (8.0)              | 9.6                   | 725          | 277          | 91                             |
| Warm temperate Central and E. Asia |                  |                  |                        |                       |              |              |                                |
| 20                                 | -4.0             | 11.9             | 7.1 (7.0)              | 8.9                   | 1016         | 322          | 143                            |
| 21                                 | -2.5             | 9.2              | 5.8 (6.8)              | 8.7                   | 895          | 279          | 142                            |
| Subtropical (Mexico)               |                  |                  |                        |                       |              |              |                                |
| 22                                 | 2.2              | 10.5             | 7.3 (7.5)              | 8.6                   | 1736         | 577          | 245                            |
| 23                                 | 0.4              | 9.4              | 5.1 (4.9)              | 5.8                   | 1017         | 94           | 199                            |
| 24                                 | 1.0              | 7.6              | 5.5 (5.6)              | 6.1                   | 1120         | 132          | 205                            |
| 25                                 | -1.7             | 9.2              | 5.9 (6.1)              | 7.0                   | 1211         | 229          | 205                            |
| 26                                 | 0.3              | 8.5              | 5.5 (5.5)              | 5.0                   | 1178         | 138          | 228                            |
| 27                                 | 1.3              | 9.7              | 5.8 (5.8)              | 6.3                   | 1345         | 233          | 243                            |
| Tropical                           |                  |                  |                        |                       |              |              |                                |
| 28                                 | -                | -                | 5.6                    | -                     | -            | -            | 365                            |
| 29                                 | 5.0              | 8.0              | 6.7 (6.6)              | 7.2                   | 1522         | 377          | 365                            |
| 30                                 | 1.3              | 6.3              | 4.5 (4.6)              | 5.4                   | 1485         | 39           | 314                            |
| Australia                          |                  |                  |                        |                       |              |              |                                |
| 31                                 | -2.0             | 13.1             | 7.9 (7.7)              | 9.4                   | 1212         | 455          | 153                            |
| 32                                 | -1.7             | 12.6             | 7.8 (7.8)              | 9.4                   | 1198         | 443          | 153                            |
| Other sites (see text)             |                  |                  |                        |                       |              |              |                                |
| 33                                 | -0.6             | 14.8             | 8.7 (9.0)              | 10.1                  | 1352         | 585          | 154                            |
| 34                                 | 0.0              | 15.7             | 9.1 (9.3)              | 10.5                  | 1969         | 899          | 215                            |
| 35                                 | 1.2              | 16.0             | 10.7 (11.0)            | 12.7                  | 2398         | 1277         | 224                            |
| 36                                 | 0.7              | 12.8             | 8.2 (8.1)              | 9.6                   | 1504         | 589          | 183                            |
| 37                                 | -0.9             | 12.8             | 8.2 (8.2)              | 10.6                  | 1635         | 653          | 200                            |
| 38                                 | 0.2              | 15.6             | 10.5 (10.5)            | 13.0                  | 1716         | 902          | 163                            |
| 39                                 | 5.2              | 12.6             | 9.0 (8.8)              | 11.2                  | 3287         | 1457         | 365                            |
| 40                                 | 0.4              | 15.8             | 11.1 (11.2)            | 13.0                  | 2485         | 1365         | 224                            |

For six additional sites without tree cover see Table 8.

**Table 7** Summary of root-zone temperature data from climatic treelines for 10 bioclimatic regions (mean  $\pm$  SD; in brackets number of sites per region)

|                                 | Absolute minimum | Absolute maximum | Seasonal mean | Warmest month  | Sum °h >0 °C   | Sum °h >5 °C  | Season length (days) |
|---------------------------------|------------------|------------------|---------------|----------------|----------------|---------------|----------------------|
| Subarctic (2)                   | -2.7 $\pm$ 0.7   | 10.3 $\pm$ 0.6   | 6.4 $\pm$ 0.1 | 7.7 $\pm$ 0.1  | 650 $\pm$ 5    | 175 $\pm$ 6   | 102 $\pm$ 1          |
| Boreal (1)                      | -4.8             | 11.0             | 6.6           | 8.5            | 700            | 210           | 106                  |
| N-cool temperate (Alps) (12)    | -2.5 $\pm$ 1.8   | 12.5 $\pm$ 1.4   | 7.0 $\pm$ 0.4 | 9.2 $\pm$ 0.7  | 939 $\pm$ 89   | 301 $\pm$ 56  | 135 $\pm$ 10         |
| N-cool temperate (Asia) (2)     | -7.9 $\pm$ 2.6   | 12.5 $\pm$ 0.1   | 7.8 $\pm$ 0.3 | 9.3 $\pm$ 0.3  | 1010 $\pm$ 60  | 371 $\pm$ 42  | 128 $\pm$ 3          |
| Mediterranean (California) (2)* | -4.0 $\pm$ 1.0   | 14.3 $\pm$ 0.7   | 8.7 $\pm$ 0.7 | 10.4 $\pm$ 0.8 | 794 $\pm$ 68   | 341 $\pm$ 64  | 92 $\pm$ 0           |
| N. warm temperate (Asia) (2)    | -3.2 $\pm$ 0.8   | 10.6 $\pm$ 1.4   | 6.5 $\pm$ 0.7 | 8.8 $\pm$ 0.1  | 956 $\pm$ 61   | 301 $\pm$ 22  | 142 $\pm$ 1          |
| Subtropical (6)                 | 0.6 $\pm$ 1.3    | 9.2 $\pm$ 1.0    | 5.9 $\pm$ 0.7 | 6.6 $\pm$ 1.1  | 1268 $\pm$ 253 | 234 $\pm$ 177 | 221 $\pm$ 21         |
| Tropical (2–3)                  | 3.2 $\pm$ 1.9    | 7.2 $\pm$ 0.9    | 5.6 $\pm$ 0.9 | 6.3 $\pm$ 0.9  | 1504 $\pm$ 19  | 208 $\pm$ 170 | 348 $\pm$ 24         |
| S. temperate (Australia) (2)    | -1.9 $\pm$ 1.0   | 12.9 $\pm$ 0.2   | 7.8 $\pm$ 0.1 | 9.4 $\pm$ 0.0  | 1205 $\pm$ 7   | 449 $\pm$ 5   | 153 $\pm$ 0          |
| S-cool temperate (4)†           | 0.3 $\pm$ 0.8    | 14.8 $\pm$ 1.4   | 9.2 $\pm$ 1.1 | 10.7 $\pm$ 1.4 | 1806 $\pm$ 474 | 838 $\pm$ 328 | 194 $\pm$ 32         |
| Mean across biomes (8)          | -2.4 $\pm$ 3.1   | 10.8 $\pm$ 1.8   | 6.7 $\pm$ 0.8 | 8.2 $\pm$ 1.1  | 1029 $\pm$ 288 | 281 $\pm$ 87  | 167 $\pm$ 77         |

\*Season restricted to mid summer by exceptional snow pack, not considered in biome means.

†*Nothofagus* treeline, not considered a climatic treeline (a taxon treeline).

but suggest that they are interpreted cautiously. In most cases, we will bypass these data when we discuss the global patterns.

### Season length and thermal sums at the climatic treeline

The mean length of the growing season at the treeline as defined here, varies surprisingly little across a 40° latitude range from the arctic circle to the edge of the subtropics (c. 100–150 days, mostly around 135 days; Table 6, 7, Fig. 5). In fact, the shortest treeline growing season of only 92 days occurs in the Sierra Nevada of California in the Mediterranean climate zone (Yosemite National Park). This extreme, but also the overall variation seen in the data reflect local snow pack (hence winter precipitation) rather than latitude. Season length increases very rapidly towards the subtropics (two-third of the year) and the tropics, but even in the tropics there may be periods presumably too cold for tree growth. For instance, the data from Ecuador include a continuous period of 51 days with 10 cm ground temperature below 3 °C (down to 1.2 °C) which corresponds to the peak of the rainy season (July–September) with soaked wet soils and a continuous thick cloud cover (cf. Bendix & Rafiqpoor, 2001). With an amplitude of 92–365 days, season length has no explanatory power for the elevational position of the treeline.

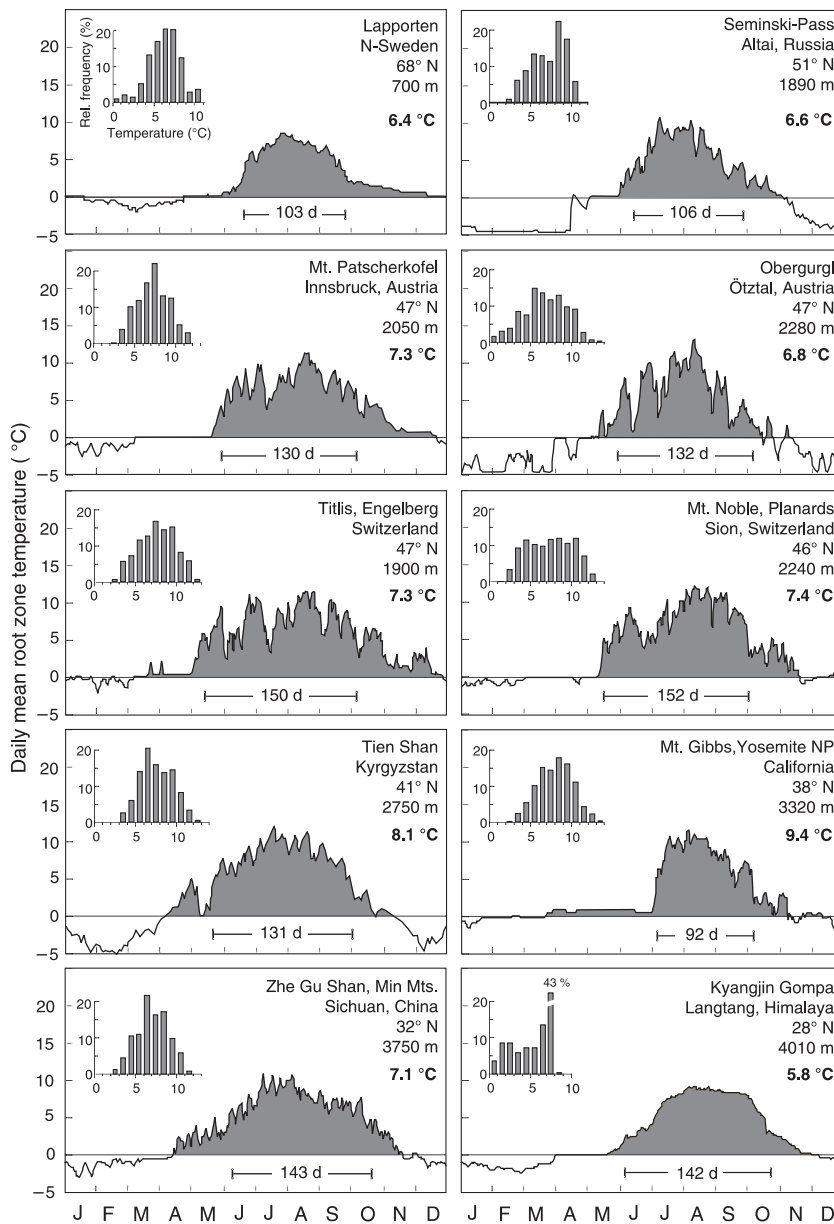
Thermal sums above 0 °C or any other threshold (e.g. 5 °C) are the combined result of season length and the actual temperature during the growing season. However, as can be seen in Table 6, season length is the dominant driver. For instance, a 102-day season in the arctic and a 92-day season in Yosemite arrive at similar, i.e. 650 and 800 degree hours above zero per season, whereas the 221 days season in Mexico creates c. 1300 degree hours. With a threefold range from 650 to nearly 2000 degree hours at the treelines included in this survey, thermal sums during the growing period do not correlate with treeline position. The situation gets worse if one uses a 5 °C

instead of a 0 °C threshold, because temperatures above 5 °C are rare at tropical treelines, and thermal sums above 5 °C may vary between 94 and 577 within one region (Mexico). However, within one geographical region, sums above zero can provide a very consistent correlate as can be seen for the eastern and western Alps, where numbers across a multitude of sites are very similar.

In summary, neither season length (even within the temperate to subarctic zone) nor thermal sums seem to have much to do with the position of the treeline across the globe. The upper limit of tree growth must therefore be tied to more direct influences of temperature, at least as long as the season length is not shorter than 3 months (which was never observed).

### Extremes of treeline root-zone temperature

From the seasonal courses of root-zone temperature such as those shown in Fig. 5, one can depict the absolute lowest and highest hourly reading (Tables 6 and 7). While the single highest value at 10 cm soil depth has little biological meaning (but still permits a climatological comparison among sites), the minimum could theoretically exceed freezing resistance and it indicates whether or not soils ever get frozen at this depth. Observed minima range from -10.4 °C in the Tien Shan to +5 °C in the tropics, but soil freezing at -10 cm depth under trees is a possibility anywhere outside the equatorial zone. The most common absolute minimum temperatures across the extratropical sites are 0 to -3 °C. Only a few sites show temperatures as low as -5 °C or below. There is a lot of variation within latitudinal zones and the year-to-year variation (not covered here for any site) must be large. However, given the many locations this survey includes, a space-for-time approach may, to some extent, also cover a great deal of the temporal variation across sites. In summary, the data show very moderate minima, very different from what is known to be damaging to



**Figure 5** Examples of the annual course of root zone temperature for the various bioclimatic regions. Histograms are for the relative frequency of temperatures within the growing period. For extremes, means and sums of all sites see Tables 6 and 7. The bold number is the seasonal mean of the individual location.

hardened tissue (Sutinen *et al.*, 1998), and there is no obvious trend across latitudes, except for the higher minima in the tropics. Most likely depending on snow pack, soils at 10 cm depth may never freeze at some temperate sites or may freeze to this depth even in the subtropics. Clearly these data do not offer a common global denominator signal for treelines.

Irrespective of latitude, soils under forest trees at the climatic treeline never get warmer than 15 °C, which is a single extreme value recorded at the Yosemite treeline. A common upper limit is 13 °C. Significantly lower absolute maxima at 10 cm depth were recorded in the subtropics (10.5 °C) and the equatorial tropics (8.0 °C). However, in fragmented stands or in the case of isolated trees, roots could explore warmer ground under low-stature vegetation as will be shown below.

### Mean root-zone temperatures

Among the various measures of treeline temperature, the mean temperature during the growing season as defined above shows the smallest variation across the globe (Table 7, Fig. 6). Between 30° and 68° N, seasonal mean root-zone temperature per region varies between 6.4 and 7.8 °C (Table 7). Given that the variation in any single region covers a similar range (the 12 sites in the Alps alone vary from 6.4 to 7.7 °C), a common 7 °C threshold for these higher latitudes seems like a very reasonable approximation. There is a clear trend of reduced seasonal mean temperatures as one enters the subtropics exemplified by Mexico and near the equator, where means of around 5 °C with a rather narrow mean variation have been found.

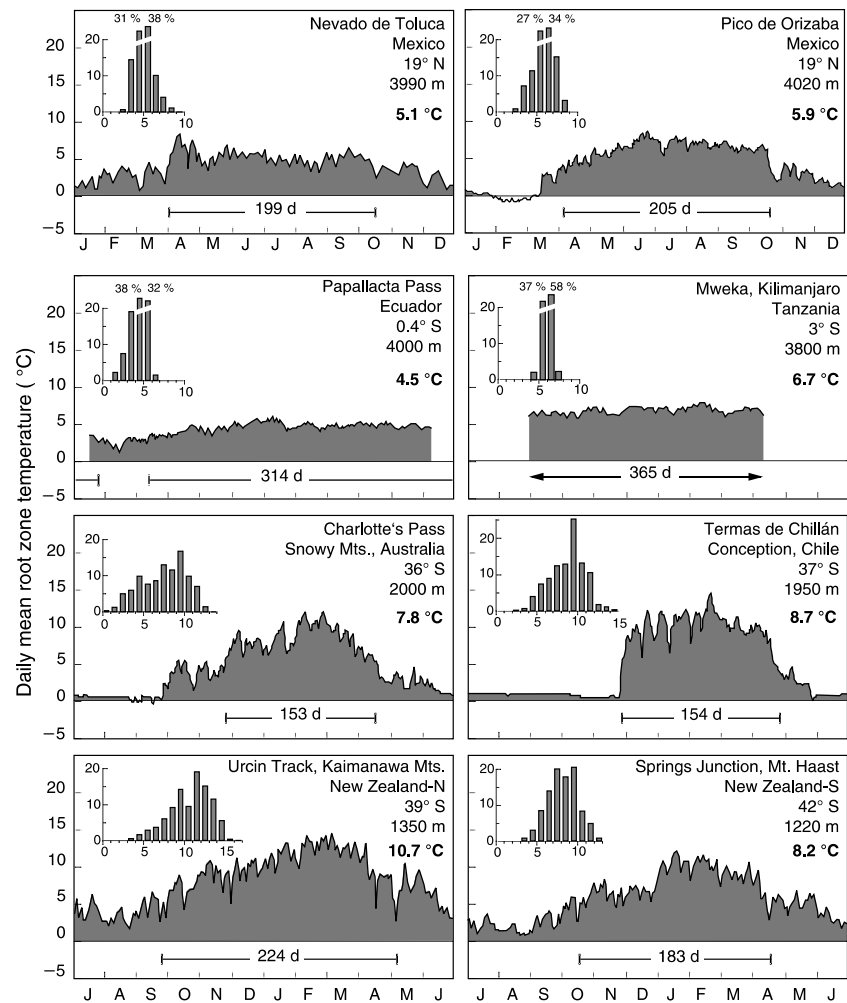


Figure 5 continued.

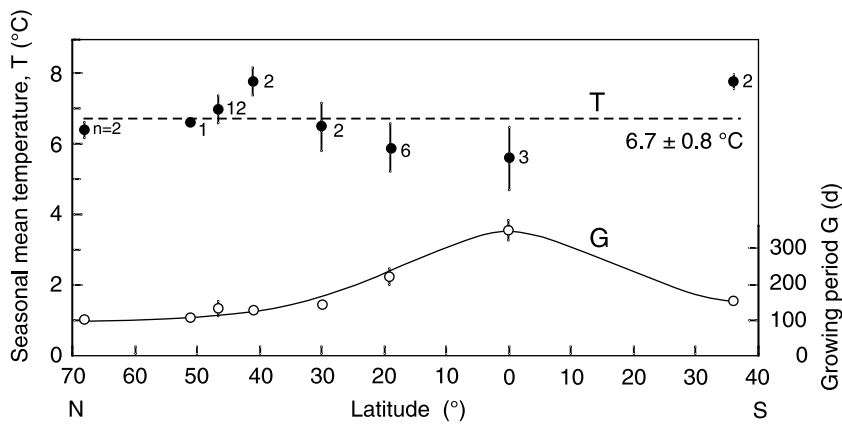
The warmest month temperature parallels this trend at *c.* 1–2 K higher temperatures (7.7–9.3 °C north of 30° N; 6.3–6.6 °C in the subtropics and tropics), with a global amplitude for the means of all individual sites of 5.0–10.4 °C (disregarding Yosemite and the taxon-specific treelines). Thus, the warmest month mean is a less useful correlate than the seasonal mean, although our data will be more robust against season to season variation than against month to month variation. The ‘month’ is also an artificial time segment, because the warmest 30-day period may fall across two calendar months and thus can be diluted by a cold ‘tail’.

In the Northern Hemisphere, August was the warmest month in all sites outside the tropics. The only sites in the Southern Hemisphere outside the tropics which line up with Northern Hemisphere trends are the two sites in the Australian Snowy Mountains, with a seasonal mean similar to that found in the Tien Shan and within the variance range over several of the warmer sites in the Alps. Temperatures during the extremely short Mediterranean summer at Yosemite are 1 K above the remaining 19 Northern Hemisphere sites outside the subtropics and tropics, but there is one site in the W. Alps (Planards) which reaches a similar

10.4 °C warmest month mean. It remains open whether these high temperatures in Yosemite reflect a peculiarity of the chosen logger positions or reflect a more general situation. The truncation of the season by the typically long snow-pack duration in the Californian Sierra Nevada to the hottest period may contribute to the above-average season mean (missing the cooler early part of the summer). The four *Nothofagus* sites in New Zealand and Chile, and the two Mediterranean *Fagus* sites fall way out of the data for all other sites and thus should be considered genus-specific (seasonal mean 9.2 °C, warmest month 10.7 °C, with three sites, namely North Island of New Zealand, Jakupica in Macedonia and Maiella in Italy reaching 12.7–13.0 °C). The Drakensberg’s warmest month also reaches 13 °C with a season mean of 11.1 °C, twice that of Mexico, clearly evidencing that there is no climatic treeline, with the same genus doing well at a seasonal mean of 6.7 °C (warmest month 7.2 °C) on Kilimanjaro.

#### Ground temperatures without tree cover

In a few sites across the globe we recorded temperatures at the treeline under bare ground, grass or low-stature shrub



**Figure 6** Seasonal mean root zone temperature at treeline across latitudes. Data for the Sierra Nevada (California) and for the *Nothofagus* treelines are not shown (see Table 7 and the text). Numbers indicate the replication of sites within one climate region.

**Table 8** Ground temperatures at treeline, but outside tree cover (low stature, often sparse vegetation)

| Site number                              | Absolute minimum | Absolute maximum | Seasonal mean | Mean of warmest month | Sum °h >0 °C | Sum °h >5 °C | Duration of growing season (days) |
|--|------------------|------------------|---------------|-----------------------|--------------|--------------|-----------------------------------|
| 41 Patscherkofel S, heath                | 0.1              | 14.9             | 9.3           | 11.7                  | 1391         | 643          | 150                               |
| 42 Maiella NW, <i>Festuca</i> grassland  | -2.3             | 20.7             | 12.3          | 15.0                  | 2009         | 1195         | 163                               |
| 43 Langtang 2, <i>Kobresia</i> grassland | -4.3             | 17.8             | 12.5          | 14.6                  | 2081         | 1252         | 170                               |
| 44 Langtang 3, <i>Rhododendron</i>       | -4.3             | 12.5             | 9.7           | 11.3                  | 1588         | 779          | 163                               |
| 45 Mauna Loa S, bare*                    | 6.0              | 22.8             | 12.8          | 16.5                  | 4689         | 2859         | 365                               |
| 46 Nevado de Toluca W, tussock grassland | -3.0             | 12.1             | 6.5           | 8.1                   | 1291         | 393          | 199                               |

\*At the *Metrosideros* treeline, but *c.* 300 m below the climatic treeline; the sensor was placed 2 m near a 3 m tall tree.

vegetation, areas into which individual trees may expand their roots. These examples should illustrate the effect of a closed tree cover on ground temperature, but also the benefits that roots of isolated trees may gain from stand fragmentation at the tree limit. In contrast to temperatures under closed tree canopies, such temperatures are very sensitive to slope direction. Here we present data for flat ground or SW exposed slopes in the Northern Hemisphere (on N slopes effects of plant cover may become zero depending on inclination). Evidently, soils get much warmer without a tree cover, but the degree of ground-warming depends on the density and height of the ground cover (Table 8). Even at 10 cm depth, bare ground (Hawaii) or ground very sparsely covered with grass (Maiella) can heat up to >20 °C at altitudes near the treeline. A dense short grass cover still permits soil warming up to 15 and 18 °C (Patscherkofel, Langtang), whereas tall tussocks (Mexico) or dense *Rhododendron* shrub (Langtang) permit maxima of *c.* 12 °C, similar to soils under trees. All other parameters follow the same pattern with higher temperatures or heat sums, the shorter and more open the ground cover is.

## DISCUSSION

With close to 50 data sets from around the globe, the treeline temperature data presented here cover a fair range of variability and permit some generalizations about the thermal

growth conditions at treeline altitudes (Fig. 6). The following may be the key findings of this survey:

1. Parameters relating to the duration of periods favourable for tree growth appear to have no predictive value for treeline altitude at a global scale (season length, thermal sums above 0 or 5 °C).
2. Mean root-zone temperatures for the growing period vary between 5.4 and 7.8 °C. Extremes range from -5 °C (one extreme case of -10.4 °C in central Asia) to 13 °C during the whole year.
3. Tropical treelines occur at 1–2 K lower temperatures (near 5 °C) than extratropical treelines, highest seasonal mean temperatures are found in the temperate and Mediterranean treelines (7–8 °C), with subarctic and subtropical treelines holding an intermediate position (6–7 °C). Hence there is no consistent latitude effect on ground temperature.
4. A number of treelines, particularly in Mediterranean regions and in the Southern Hemisphere are not climatic treelines in the sense of a life-form boundary, but represent taxon specific or topography controlled upper tree limits (missing species, substrate or influence of fire).
5. Trees have a strong negative influence on temperature when compared with low-stature vegetation. Tree absence causes a substantial increase of root-zone (and presumably canopy) temperature. Stand fragmentation at treeline increases root-zone temperature, depending on ground cover.

We have tested a set of other descriptors of treeline temperature (e.g. median instead of mean, warmest month temperature, thermal sums above 7 °C) but none came close to the relative consistency seen in seasonal means. It comes as a surprise that thermal sums vary by 3 to 4 across the world's treelines. In large this is because the underlying duration of favourable periods for growth seems to be irrelevant for native taxa, once a minimum of 3 months is reached.

### Comparison with regionally available data

The range of ground temperatures observed here match well with the results of a series of local studies. For instance, Karlsson & Weih (2001) report a 6.6 °C seasonal mean for 10 cm soil depth at their 650 m *Betula* treeline site in N-Sweden (our 700 m value is 6.4 °C). Kessler & Hohnwald (1998) studied ground temperature under *Polylepis* thickets at 4050 m in Bolivia for two 3-month and one 6-week period, and their means and extremes come very close to the data reported here for other tropical treelines. Means did not differ significantly between 5, 12.5, 15 and 17.5 cm depth, and amplitudes below 5 cm never exceeded 2 K (mostly around 1 K). They observed extended periods with ground temperatures of only 2–3.5 °C even at 15–17.5 cm depth and the means over their test periods were between 4 and 5 °C and always cooler under trees than in adjacent open land. More than 2 years' data for the Ecuadorian treeline at c. 4000 m by Bendix & Rafiqpoor (2001) indicate a 4.3 °C mean under *Gynoxis* thickets (0.5 m soil depth; including a several week cold spell with <3.2 °C, which would not be considered 'growing season' in our analysis) with a 5.6 °C mean under adjacent tussock grassland. For the same area Lauer & Rafiqpoor (2000) suggest that the 6 °C isotherm marks the upper *Polylepis* limit (at 4100 m). These temperatures are significantly lower than those of 7–8 °C suggested by Walter & Medina (1969) for the tropics, presumably, because fire-driven, depressed treelines were taken as a reference (Winiger, 1981). For *Hagenia* shrub at 3350 m elevation on Mt Kenya, Winiger (1979) reports a 7 °C ground temperature mean, which scales to 5.5 °C at the presumed climatic treeline at about 3800 m (0.55 K/100 m), almost identical to the value documented here for Kilimanjaro. There is no evidence in the literature that freezing low temperature extremes are decisive for treeline formation (see Discussion in Körner, 1998, 1999), but for the upper limits of certain types of montane forest below the treeline (e.g. evergreen broad leaved) such thresholds were found critical (Ohsawa, 1991).

The range of mean air temperatures at treeline of 5.5–7.5 °C (global mean 6.7 °C), extrapolated previously from data from meteorological stations (Körner, 1998, 1999) comes very close to the current results for the –10 cm root zone. Given that the point of equilibrium between soil and air (canopy) temperature is at 6.5 °C (Table 4) the close correspondence of the means of the two independent assessments is perhaps not surprising.

Our study is one more in a series of studies that document for high elevations that the root zone under a closed forest canopy is significantly cooler than under low-stature vegetation (Shanks, 1956; Wardle, 1968; Ballard, 1972; Munn *et al.*, 1978; Holtmeier & Broll, 1992; Kessler & Hohnwald, 1998; Körner, 1999, Körner *et al.*, 2003; Bendix & Rafiqpoor, 2001). The common opening of forests as they approach their thermal limit also opens warm terrain for roots to explore and hence may permit trees to grow at higher elevations as they could in closed stands.

A number of 'outlier' sites deserve comment. It had been shown previously that *Nothofagus* treelines are climatically depressed (Wardle, 1998). This finds full support by the current data for four sites in New Zealand and central Chile. Wardle also concluded that the discrepancy between the potential climatic treeline and the *Nothofagus* treeline is greater in New Zealand than in Chile, which is not reflected in our data (mean for New Zealand sites 9.5 °C, for Chile sites 8.9 °C). Two locations in a specific region are not enough to ascertain such trends, nevertheless, both treelines are at least 200 m lower (Wardle even mentioned 500 m for New Zealand) than to be expected from treeline temperatures elsewhere. Successful establishment of *Pinus contorta* c. 300 m above the *Nothofagus* treeline in New Zealand supports this conclusion (Wardle, 1985, 1998). Although phylogenetically not as closely related as previously thought, the same applies to *Fagus* sp. where they form treelines in southern Europe. It remains to be explained why regionally available conifer taxa did not occupy the terrain above the deciduous *Fagus* forest.

The situation in Hawaii and South Africa (Drakensberg) permits a more straight forward explanation. Hawaii simply misses appropriate taxa, hence the *Metrosideros* limit does not mark the climatic treeline as is impressively demonstrated by c. 20 m tall Mediterranean Eucalypts and a series of Northern Hemisphere conifer species around the Mauna Kea observatory visitor centre and tall, fruiting *Picea abies* stands on Haleakala, both several hundred metres above the *Metrosideros* limit. For the Drakensberg, our temperature records illustrate that locations inhabitable for trees are simply not high enough and where the escarpment approaches 3000 m as in our test area near Witsishoek, there are only steep cliffs or regularly burned drifts, restricting the establishment of trees beyond where we found the uppermost thickest on a blockfield.

Temperatures were not found to differ with direction (exposure) of forested slopes, which seems to reflect old wisdom for regions that lack strong moisture contrasts. Across seasons Innerebner (1933) had already documented the same air temperatures in shade, 2 m above ground, on N and S slopes in the central Alps. Slope contrasts come into play in low-stature plant cover (see Introduction) and when oceanicity, snow pack or general moisture gradients are important, as was shown for subarctic birch treelines (Kjällgren & Kullmann, 1998) and as can be seen in some very dry parts of central Asia (Esper *et al.*, 1995) or northern Chile (Troll, 1968).

### Evidence for temperature-limited tree growth

The relatively narrow range of temperatures at the global high altitude forest limits raises the question of a common mechanistic explanation. With current knowledge, explanations related to carbon acquisition seem to be poorly founded, given that the temperature response of photosynthesis is so well tuned that a temperature driven shortage of assimilates seems close to impossible (see the extensive Discussion in Tranquillini, 1979; Körner, 1998, 1999 and the Introduction). There is, however, compelling evidence for a direct link between temperature and the structural growth of trees, i.e. the investment of photo-assimilates.

Research on tree-rings at high elevation reveal a number of examples underlining the dominant role of temperature for tree growth, with reports dating back to the early part of the last century (e.g. Däniker, 1923; Huber, 1948; Hustich, 1949; Glock, 1955), and with a series of more recent works (e.g. Schweingruber *et al.*, 1979; Sonesson & Hoogesteger, 1983; Grace & Norton, 1990; Rolland *et al.*, 1998; Paulsen *et al.*, 2000). Temperature effects on tree growth are also well established for warm vs. cool periods of the Holocene (e.g. Innes, 1991; Luckman, 1996; Kullman, 1998; Biondi, 2001).

However, such long term integrated signals of growth may still co-reflect positive effects on photosynthetic carbon gain or be autocorrelated with more sunshine hours. Therefore, immediate growth responses to temperature are more instructive as they were shown for shoots (e.g. Scott *et al.*, 1987; James *et al.*, 1994) and roots (e.g. Kajimoto *et al.*, 1998; Häsler *et al.*, 1999), confirming the tight coupling between warmth and meristematic activity, as was suggested by Däniker (1923). James *et al.*'s data show for *Pinus sylvestris* a zero growth threshold for extension growth of shoots between 6 and 7.5 °C. Not surprisingly, several authors have predicted that even a minute warming at the treeline should enhance tree growth (e.g. Grace *et al.*, 2002) as was evidenced for the last 100 years in the Alps (Rolland *et al.*, 1998; Paulsen *et al.*, 2000). Remote sensing may develop to even detect effects on treeline positions where temperatures have been rising (Shugart *et al.*, 2001), although such responses are commonly much delayed.

There is also a wealth of experimental evidence demonstrating the key role that temperature plays in cold environments for tissue formation (reviewed in Körner, 1999). For roots and their functioning, temperature is considered to be the major determinant (e.g. Tryon & Chapin, 1983; Lopushinsky & Max, 1990; Weih & Karlsson, 2001). Constraints for structural investments at low temperature are so dominant that mobile carbohydrates (e.g. starch) accumulate (Domisch *et al.*, 2001), which seems to be a general response to low temperature (Fitter & Hay, 2002, p. 68) and is reflected in the increasing non-structural carbon compound concentrations as one approaches the cold climate tree-limit (Hoch *et al.*, 2002; Hoch & Körner, 2003). Night-time temperatures (no solar canopy warming) may be particularly critical. Treeline trees, when compared with trees at lower elevation, may 'lose' nights for above-ground tissue formation because most nights at

treeline are cooler than 5 °C. For *Picea engelmannii* Hellmers *et al.* (1970) showed that night-time temperature is the key factor for seedling growth, and a number of studies have shown that ground temperatures also directly (in part linearly) affect above-ground tree metabolism until a temperature of about 7 °C is reached (e.g. Havranek, 1972, see review in Körner, 1999). So, there is no doubt that temperature has an immediate and direct effect on formation of new tissue, irrespective of whether other influences such as, for instance, nutrient absorption become affected in places, as was shown for *Betula* at the subarctic treeline (Karlsson & Nordell, 1996; Sveinbjörnsson *et al.*, 1996).

### Implications

The treelines of the world are perhaps the best bioclimatic boundary against which other thermal life zones can be defined, irrespective of latitude. As such it is of great significance to know the factors that permit the modelling of treeline position, once moisture limitation had been eliminated as a driver. The equations derived from Fig. 4 permit a linkage with modelled air temperatures, and the trends with latitude as summarized in Fig. 6 can assist a global application of the findings presented here. This may help reconstructing past land-surface changes by comparing the potential with the actual elevational distribution of trees. Such a predictive tool can also assist in estimating potential future changes of treeline position.

The analysis presented here aimed at detecting the general linkages between the high-elevation limit of trees and temperature. However, given the many (regionally differing) modulating forces which operate on top of the presumed basic thermal driver, temperature might not explain the actual treeline position any better than  $\pm 50$  m of altitude. The modulating influences within this boundary are to be understood at a regional scale, but their absence will unlikely change the predicted treeline position by more than 100 m in most places.

It is a challenging research agenda to explain also the critical biological mechanisms involved. It seems that these are of general nature and not specific to trees. It is only the architecture of trees, which makes them particularly sensitive and more directly coupled to atmospheric conditions than other plant life-forms. In other words, the thermal reasons for treeline formation are in large tied to the stature and size of trees and not to any particular shortcomings in their physiology, compared with other plant types. Short-stature plants, i.e. the alpine plants growing above treeline should face similar thermal limitations, but reach these, thanks to their morphology, at higher elevations and can operate with much shorter season duration because of their faster leaf turnover and their meristems being nested near or below soil surface where heat accumulation reaches a maximum.

A remarkable analogy exists between the thermal threshold range for trees documented here and the well established general thermal limits in temperate zone agriculture. The US



Department of Agriculture considers 6 °C the 'zero point' of crop growth (Smith, 1920) and very similar 6 °C rules have been published over the last century for the UK and Germany (Gensler, 1946). Hence, the thermal tree limit at high altitude may just represent a rather visible case of an otherwise general phenomenon.

## ACKNOWLEDGMENTS

This 7-year campaign would not have been possible without many helpers who recovered the data loggers and sent them back to us. In a few cases loggers were also buried following our instructions. We sincerely thank the following persons for their cooperation and advice: A. Andonovsky and A. Mihajlovski (Skopje, Macedonia), M. McClaran and Peggy Moore (Tucson/Yosemite NP, US), L. Cavieres and E. Ruiz (Concepcion, Chile), L. Cullen (Lincoln, NZ), S. Hättenschwiler (Basel/Hawaii), A. Hemp (Bayreuth, Germany/Moshi, Tanzania), A. Lehmann (Hamilton, NZ), Liu Xing-Liang and Mai-He Li (Beijing/Sichuan/Basel), B. Scholes (Pretoria, SA), F. Schweingruber (Birmensdorf/Zürich), U. Müller (Bishkek, Kyrgyzstan), O. Huturnoi (Tomsk, Russia), M. Strobl (Obergurgl/Innsbruck, Austria), J.-P. Teurillat (Geneva) and A. Stanisci (Rome), H. Vibrans (Toluca/Mexico City), B. Wellington and S.C. Wong (Canberra, Australia), H. Von Wehrden (Marburg, Germany/Nepal). D. Rafiqpoor (Bonn) provided unpublished data from Ecuador. We also thank Susanna Peláez-Riedl for graphical work and cross-checking of data.

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## BIOSKETCHES

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