



How accurately can minimum temperatures at the cold limits of tree species be extrapolated from weather station data?



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ABSTRACT

Most plant physiological processes act on micro-geographic scales within meters or less and on temporal scales of minutes or less. Yet, most studies relating species distribution to climate used typical resolutions of kilometers and months at best. Commonly available climate records from weather stations or freely available coarse-resolution geographic climatic layers thus, do not reflect local climatic conditions. In this study we selected sites where eight temperate deciduous tree species are growing at their cold upper elevational and latitudinal limits in the Swiss Alps (from 1165 m a.s.l. to 1804 m a.s.l.) and in Sweden (from 58°18'N to 59°27' N). At each site, temperature was recorded for 1–2 years in different conditions: at understory height (50 cm), 2-m above ground, in the top of tree canopies and at 10 cm depth in the soil. We compared these biologically meaningful temperatures with the closest weather station data after correction for elevation. The data evidence that in mountain terrain, scaling from weather station data to on-site forest conditions requires month-specific lapse rates of temperatures, separated for means and extremes (e.g. minima). Besides best elevation-correction procedures, monthly absolute minimum temperatures predicted from near weather stations remained 1.4 ± 0.2 K (mean \pm se, 12 sites) cooler than *in situ* conditions during growing season (2.0 ± 0.2 K cooler during the non-growing season). At the time when 2-m air temperature reached its absolute monthly minimum, the top of the tree canopy was found 0.4 ± 0.1 K cooler (mean \pm se, 12 sites) during growing season and 0.9 ± 0.1 K during the non-growing season. These systematic deviations of low temperature extremes from those predicted from weather stations close the gap between geographical range limits of species, their physiological limits (e.g. freezing resistance) and meteorological information. The “thermal niche” concept of species range limits needs to account for such deviations of life conditions from meteorological data, should the niche boundaries have a functional meaning rooted in plant biology.

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1. Introduction

The distributional limits of tree species at high latitude or high elevation are likely associated with particular manifestations of low temperature (Sakai and Larcher, 1987; Von Humboldt and Bonpland, 1807; Woodward, 1987). While mean growing season temperatures are critical for the position of the climatic tree-line (Körner, 2012; Körner and Paulsen, 2004), the range limits of non-treeline species are more likely associated with their freezing tolerance (Sakai and Larcher, 1987) and thus, the occurrence of freezing events. However, temperature data are rarely recorded

where species reach their distributional limits. Hence any inferences of species-range-climate associations rely on climate records from surrounding weather stations or spatially interpolated climatic layers derived from station networks. Absolute minima of temperature or other expressions of extremes are rarely reported (but see Zimmermann et al., 2009) and not offered by geographic climatic layers, such as from WorldClim (Hijmans et al., 2005), Climate Research Unit (New et al., 2002) or Tyndall Centre for Climate Change Research (Mitchell et al., 2004): It remains unclear, to which extent such measurements from weather stations or data obtained from climatic layers reflect the actual life conditions that trees experience at their range limit.

Three major constraints must be overcome for accurately inferring temperatures acting on trees at their limits: (1) the geographical position of weather stations which is often distant from species boundaries, (2) the deviation of forest microclimate from weather station conditions and (3) the spatial and temporal resolution of the temperature parameter provided by e.g. the geographic climatic layer.

Abbreviations: $meteoT_{Air}$, 2-m air temperature of the weather station; $meteoT_{Air}^*$, elevation corrected 2-m air temperature of the weather station; $on-siteT_{Air}$, 2-m air temperature on the tree; $on-siteT_{Ustorey}$, temperature in the understory; $on-siteT_{Soil}$, temperature in the soil; $on-siteT_{Crown}$, temperature in the top of the crown.

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First, weather stations are sparsely distributed and are often restricted to low elevation. This is critical when predicting climate variables for higher elevation sites (e.g. at a tree species' upper elevational limit), as the error is expected to increase with elevational distance.

Second, due to their intrinsic structure, forests generate their own microclimate (Geiger et al., 2003). The structure of tree canopies affects the radiation regime and the wind profile (Van Eimern and Riedinger, 1986). The resistance of the associated aerodynamic boundary layer causes air temperatures in the forest to deviate from those measured under standardized conditions in a weather station, commonly placed on an open field (Larcher, 1975). The same tree individual can be exposed to very different thermal conditions from roots to the top of the canopy. Similarly, tree seedlings and saplings in the understorey may experience different temperatures from both the tree canopy and standard weather station data. In addition to heat convection, radiative cooling can cause temperatures of exposed tissues to depart from air temperatures measured two meters above ground in a shelter (Jones, 1992).

The third problem arises when using geographic climatic layers due to broad spatial and temporal resolution of the climate data obtained from them. Here, accuracy decreases because temperatures were interpolated across a gridded landscape and/or averaged to mean conditions of a large area (e.g. a pixel that represents 1 km² or more); this has been shown to provide inaccurate/false species range shifts in mountain regions where elevational gradients are important (Randin et al., 2009; Scherrer et al., 2011). Further, many processes related to tree survival operate at a minute to an hourly time scale (e.g. freezing damage). In contrast, climatic layers offer long-term series of climate records as monthly averages only, whereas in reality, extreme events (singularities) exert significant ecological impact (Easterling et al., 2000; Parmesan et al., 2000; Stenseth et al., 2002). Most likely, these unknown extremes are decisive for species boundaries. For instance, late frost events in spring affect new leaves and active meristems of trees. A single frost event in a 50-year period can kill all trees in an area and thus, might constrain a species limit. Similarly, absolute temperature minima during winter can set the species limit (Sakai and Larcher, 1987; Till, 1956). Unsurprisingly, Zimmermann et al. (2009) showed that species distribution models improved their predictive power by including standard deviation of climate variables as a proxy of extreme climatic events. There is, thus, an urgent need for providing a proper assessment of deviations between weather stations/climatic layers and *in situ* temperatures that trees experience at their distributional limits (as done for the soil surface microclimate by Graae et al., 2012).

We focused on monthly mean, monthly mean minima and monthly absolute minimum temperatures because mean temperatures are likely to control growth rate whereas absolute minimum temperatures affect survival. The broad spectrum of taxa (and thus locations) included here should buffer our findings against local climatic peculiarities.

Thus, we were addressing the following tasks: (1) A quantification of the extent of deviations between *in situ* minimum temperatures recorded directly on trees growing at their presumed thermal limit and temperatures derived from weather stations which were scaled to the same elevation using regional lapse rates (as commonly used in most high-resolution modeling studies). (2) An assessment of the temperature differences across a vertical profile in the forest at the same species-specific elevational and latitudinal limit. By means of (1) and (2) we provide (3) factors for scaling meteorological information to temperatures experienced by trees from roots to the top.

2. Methods

2.1. Species and study sites

We selected eight widely distributed deciduous tree species: *Acer pseudoplatanus* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Laburnum alpinum* (Mill.) Bercht. & J. Presl, *Prunus avium*, *Quercus petraea* (Matt.) Liebl., *Sorbus aria* L. and *Tilia platyphyllos* Scop. We used data from the Swiss National Forest Inventory (NFI) from two inventory periods, which were sampled during the years 1983–1985 (NFI1) and 1995–1997 (NFI2) on a regular 1-km grid (1.4 km grid for NFI2). Additional tree occurrences in Switzerland were derived from the forest plots database (Wohlgemuth, 1992). This resulted in $n=22,130$ observations for all Switzerland. This database allowed us to identify the highest elevation reached for each study species. All eight taxa reached their highest elevation in two regions, one in the Western Alps of Switzerland centered on Martigny (46°6'N, 7°4'E) and the other one centered on Chur in the Eastern Swiss Alps (46°51'N, 9°32'E, Fig. 1). Based on the Swedish national forest inventory data (Nilsson and Cory, 2011) and explorations in the field, we identified the latitudinal limits of a subset of four species in Sweden (South Scandinavia) between Göteborg (57°42'N, 11°57'E) and Arvika (59°39'N, 12°36'E, Fig. 1).

For each species, we selected one adult tree among others within the regional uppermost (Alps) or northernmost (South Scandinavia) margin of distribution and within closed forest stands. So we did not select the single highest individual (such outposts may reflect a peculiar microclimate), but rather placed our sensors where several reproductive individuals marked the limit. When two or more species shared the same distributional limits (within 10 m of elevational difference or 1 km in latitude), we selected only one common site for our measurements related to these species. This resulted in four replicate measurement sites (trees) in each of the three regions (Table 1). A later population study in the Alps (Vitasse et al., 2012) revealed that some isolated individuals may be found in certain microhabitats at (several tenth of meters higher) elevation, but their reproductive success is unknown.

2.2. Temperature records and experimental design

At each monitored site, we placed four temperature loggers (Tidbit v2 Temp UTBI-001, Onset Computer Corporation) at different positions within the forest:

One logger was placed on the north-facing side of the stem of a tall tree (d.b.h. >0.3 m) at 2 m above the ground, under a major branch, and hence completely shaded by the host tree's canopy and stem during the growing season and by the stem and surrounding branches during the coldest part of the year (called hereafter on-site T_{Air}). We were using the loggers to obtain minimum temperatures of the air inside the forest. However, by choosing such location we avoided direct effect of sunshine and night-time radiative cooling during the non-growing season. Further, low solar elevation angle and short day length make radiation errors due to direct sunshine impossible. This is particularly true in Sweden and in the valleys in the Alps where surrounding mountains screen the horizon. These air temperature records were used to compare with 2-m air temperature from the nearest standard weather stations. A second data logger was buried 10 cm under the soil surface, 10 cm north of the stem (called hereafter on-site T_{Soil}) to reflect temperature in the upper root zone. Such soil temperatures collected in deep shade are known to correlate well with weekly mean air temperature records (Körner and Paulsen, 2004). A third logger was positioned at c. 50 cm above ground in the understorey to reflect temperature at the seedling/young sapling height (called hereafter on-site $T_{Ustorey}$). This logger was intentionally not sheltered and may periodically have been exposed to solar radiation

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