

Original document stored on the publication server of the University of Basel
edoc.unibas.ch

This work is licenced under the agreement „Attribution Non-Commercial No Derivatives –
2.5 Switzerland“. The complete text may be viewed here:
creativecommons.org/licenses/by-nc-nd/2.5/ch/deed.en



Attribution-Noncommercial-No Derivative Works 2.5 Switzerland

You are free:



to Share — to copy, distribute and transmit the work

Under the following conditions:



Attribution. You must attribute the work in the manner specified by the author or licensor (but not in any way that suggests that they endorse you or your use of the work).



Noncommercial. You may not use this work for commercial purposes.



No Derivative Works. You may not alter, transform, or build upon this work.

- For any reuse or distribution, you must make clear to others the license terms of this work. The best way to do this is with a link to this web page.
- Any of the above conditions can be waived if you get permission from the copyright holder.
- Nothing in this license impairs or restricts the author's moral rights.

Your fair dealing and other rights are in no way affected by the above.

This is a human-readable summary of the Legal Code (the full license) available in German:
<http://creativecommons.org/licenses/by-nc-nd/2.5/ch/legalcode.de>

Disclaimer:

The Commons Deed is not a license. It is simply a handy reference for understanding the Legal Code (the full license) — it is a human-readable expression of some of its key terms. Think of it as the user-friendly interface to the Legal Code beneath. This Deed itself has no legal value, and its contents do not appear in the actual license. Creative Commons is not a law firm and does not provide legal services. Distributing of, displaying of, or linking to this Commons Deed does not create an attorney-client relationship.

Bioclimate and reproductive potential
at the cold limit
of European deciduous tree species

INAUGURALDISSERTATION

zur

Erlangung der Würde eines Doktors der Philosophie

vorgelegt der

PHILOSOPHISCH-NATURWISSENSCHAFTLICHEN FAKULTÄT

der Universität Basel

von

CHRIS KOLLAS
aus Berlin, Deutschland

Berlin, 2013

Genehmigt von der Philosophisch-Naturwissenschaftlichen Fakultät auf Antrag von

Prof. Dr. Christian Körner
Prof. Dr. Martine Rebetez

Basel, den 13. November 2012

Prof. Dr. Jörg Schibler
Dekan

„Nur wenn sie in engster Fühlung mit der experimentellen Physiologie verbleibt, wird die Ökologie der Pflanzengeographie neue Bahnen eröffnen können, denn sie setzt eine genaue Kenntnis der Lebensbedingungen der Pflanze voraus, welche nur das Experiment verschaffen kann“ – Schimper, 1898

Acknowledgements

First of all I would like to thank Christian Körner, not only for teaching me Ecophysiology, but also for supporting me during these past three and a half years and for proof-reading of many manuscripts.

Thanks to Martine Rebetez for co-examining my thesis.

I am happy to thank Christophe Randin, Yann Vitasse, Günter Hoch and Armando Lenz for excellent cooperation within our project, for valuable advice, stimulating discussions and tough field work.

There was an enormous amount of fieldwork within the TREELIM project, a big deal arising from the common garden experiment. Thanks go to all the people who assisted with fieldwork: Koostella, Roger, Martin, Fernando, Julia, Helina, Chantal, Pascale, Denis, Tobi, Jonas, Miriyam, Jessica, Sämi, Anna, Juliana, Luzi, Maria, Jamil, Jasmin and Remo.

I wish to thank the members of the Botanical Institute and the gardeners of the Botanical garden for help and advice on field work and for creating a very inspiring & cosy working environment.

Funding came from the European Research Council (ERC) grant 233399 (project TREELIM).

I would like to thank you Nina for all the support you provided during these years, for being patient when I came home full of questions, for listening and encouraging me when things did not go so well. Finally, I thank my parents, they supported me in nearly all I have ever done.

Contents

1	General Introduction	3
2	Do elevational limits of deciduous tree species match with their thermal latitudinal limits?	13
3	How accurate can weather stations predict temperatures at tree species limits?	31
4	Critical temperatures determining the elevational and latitudinal range limits of European broad-leaved trees	49
5	Unrestricted quality of seeds in European broad-leaved tree species growing at the cold boundary of their distribution	67
6	Tree recruitment of European tree species at their current upper elevational limits in the Swiss Alps	77
7	Extended summary	91
A	Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species	99

Chapter 1

General Introduction

General Introduction

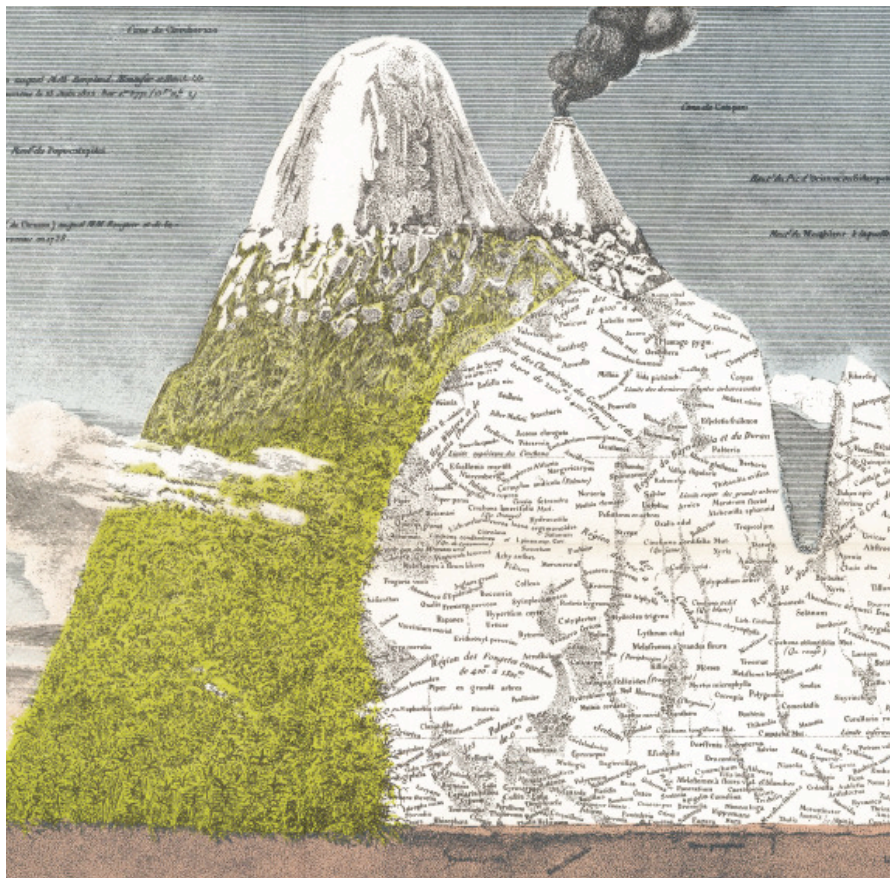


Figure 1: Profile of the volcano Chimborazo (Ecuador), visualisation of climatic and vegetation zones (Von Humboldt and Bonpland, 1807)

Foundation of Biogeography

200 years ago plant geography emerged when Alexander von Humboldt published a profile of the volcano Chimborazo (Ecuador) including data on plant species distribution, geology and thermal bands (Fig. 1, Von Humboldt and Bonpland, 1807). Since then, biogeographers began to illustrate and study the causes of species distribution. Augustin-Pyrame de Candolle first described both, barriers (like mountains) and the presence of other plants as limiting factors of the distribution of species (de Candolle, 1856). Correlative approaches for assessing the link between plant species distribution and climatic conditions provided a first framework of climate based plant biogeography (Grisebach, 1872; Merriam, 1894; Walter, 1931). At the

same time, the first ecophysiological studies of plant responses to climatic conditions emerged (Schimper, 1898). While the first do not reveal mechanisms, the second often fall short in scale. One example where a mechanistic understanding could be scaled to a global dimension is the high elevation treeline. Because both, the upper elevational and polar latitudinal treeline form one of the most drastic terrestrial borders between vegetation types, it attracted ecologists and biogeographers from the beginning. Today, the cold-climate treeline phenomenon and the underlying physiological mechanisms are reasonably well understood (Körner, 2012). In contrast, the low temperature limits of non-treeline forming tree species still await ecophysiological explanations.

The environmental niche & climate equilibrium concepts

As sessile organisms, plant species rely on certain combinations of environmental conditions to maintain their population at a given location. These requirements have been termed the ecological niche (Hutchinson, 1957). The fundamental niche of a given species is obtained by taking together all the abiotic constraints that shape the species distribution, such as temperature and water availability. In contrast, the realized niche describes that fraction of the fundamental niche that the species is actually occupying, given biotic constraints such as pathogens and competition with other plant species and historical factors like landuse- and migration history. When a species reaches the limit of its fundamental niche, it is considered “in equilibrium”. Disequilibria arise when species are unable to expand as fast as the environmental conditions (e.g. climate) change. For example, dispersal limitation that inhibits tracking climatic warming after the last glaciation is often attributed to such mismatch between the species (observed) range limit and its fundamental thermal limit. It is assumed that most European broad-leaved tree species did not reach their latitudinal thermal limit (Svenning and Skov, 2004). To test this hypothesis, elevational and latitudinal gradients that comprise the cold distribution limits of the same tree species provide an excellent tool to study the success of species in reaching its climatic niche limits.

Local adaptation to temperature

In contrast to central and rear populations, a species’ upper elevational and northern latitudinal thermal limit is assumed to consist of a leading edge (migrating) population. Such cold edge populations are under greater abiotic constraints (e.g. due to a short growing seasons) than central populations. Thus, the degree of genetic adaptation and phenotypic plasticity in populations at the leading edge will control species survival under harsh (and changing) climates (Aitken et al., 2008). In tree species, a strong population differentiation in fitness traits has been shown since the early provenance trials 200 years ago (review in Langlet, 1971) until

now (Savolainen et al., 2007). In general, population fitness is highest at the populations’ origin (local adaptation). Thus, profound knowledge of genetic adaptation and phenotypic plasticity among central and leading edge populations is required to understand species dynamics and their adaptive ability at the limit.

Factors limiting tree species distribution

The range limits of species are controlled by biotic and abiotic factors. However, there is limited support for the role of biotic factors, such as competition, predation (herbivory) or diseases in controlling species limits (Sexton et al., 2009), nevertheless these factors were shown to modulate species abundance on a regional scale (Bullock et al., 2000). Among the abiotic factors, soil nutrients are not expected to control tree species limits. As the limits of broad-leaved tree species regarded here (from 1165 to 2160 m a.s.l.) fall inside the closed deciduous forest belt (with one exception, *S. aucuparia*) and many tree species occupy lower and higher elevations, soil nutrient availability is unlikely restricting species expansion. However, climatic (abiotic) factors that change consistently with altitude, are most likely candidates responsible for tree species limits in mountain regions (Körner, 2007). Globally, wind speed shows no consistent change with elevation (Barry, 1981; Grace, 1977), nor does precipitation (Flohn, 1974; Lauscher, 1976). Clear sky solar radiation increases with altitude, but at the same time the relative frequency of cloud cover increases with altitude, counteracting this trend (Körner, 2007). The atmospheric pressure declines with increasing altitude but the mixing ratio of CO₂ and O₂, does not change. Low CO₂ partial pressure cannot be assumed responsible for tree species limits since plants were shown to cope with such low levels during the last glaciation at low elevation or latitude when partial pressure of CO₂ was as low as 180 ppm (Rundgren and Ingolfsson, 1999). Further, high latitude limits at low elevation should be much further north if the higher partial pressure of CO₂ had a positive effect. Only the mean atmospheric temperature declines worldwide consistently with both increasing altitude and latitude worldwide and

thus, is most likely controlling broad-leaved tree species limits towards higher elevation and latitude. Yet, it is unclear which facet of temperature is decisive.

Any influence of temperature depends on the developmental state of a plant. In the case of extremely low temperatures it makes a big difference whether a plant is dormant or actively growing. Hence, climatic impacts interact with development, which in itself is driven by climatic factors such as sufficient winter chilling, photoperiod and temperature. Thus, plant phenology (seasonal activity driven by environmental factors) is a key trait. In harsh climates at the species limit for instance, the timing of bud break represents a trade-off between maximizing the length of the growing season and avoiding damages by late freezing events.

Temperature conditions at the species limit

Mature trees at the low temperature species limit integrate the species' minimum climatic requirements for reproduction and survival over past decades or even centuries. Their presence indicates that no threshold had been surpassed during their life span. On the reverse, the absence of species does not necessarily mean that such extremes had occurred. The species may be absent for other reasons. Longer warm periods should facilitate upslope excursions of recruits as was evidenced by Lenoir et al. (2009).

However, it is hard to tell which temperature at which period of the year is decisive for such migration and the establishment of the species limit. Further, weather stations are not commonly placed at the edge of a species elevational or latitudinal limit, hence in situ climate conditions during the life cycle of trees are needed. Thus, there are two issues to be re-

solved: (1) The in situ temperature conditions at the species limits need to be known and (2) the critical temperature needs to be identified, with means least and extremes most likely decisive.

Climatic descriptions of species distributional boundaries typically rely on large scale approximations derived from climate databases. The geographic climatic layers calculated from such databases are grid matrices that include a geo-reference and the associated climate information. Such gridded data are derived by interpolating irregular point data from climate stations. That way derived estimates of site temperature may not reflect biologically meaningful climate conditions (Scherrer and Körner, 2011). Despite these obstacles, averaged and coarse-scale climatic data are frequently used in studies examining species distribution (Dirnböck et al., 2011; Engler et al., 2011). Thus, microclimatic measurements at the species limits will allow to quantify the deviations between weather station (or geographic climatic layers) temperature and in situ temperatures at the trees.

Long-term temperature records at the species limits enable distinguishing facets of temperature that might constrain tree species at these limits. The most likely mechanism by which cold temperature can affect tree growth and survival can be grouped into three classes: (1) The annual absolute minimum temperature during the non-growing season could act lethally on crucial plant tissues such as meristems in buds or the cambium (Sakai and Larcher, 1987). (2) Late spring frost events during bud-break and shortly after may damage vulnerable plant tissue such as leaves and flowers. (3) The requirement of a minimum amount (or length) of warm temperature during the growing season could not be met, implying that tissue maturation, seed ripening or the establishment of seedlings and saplings could not be achieved.

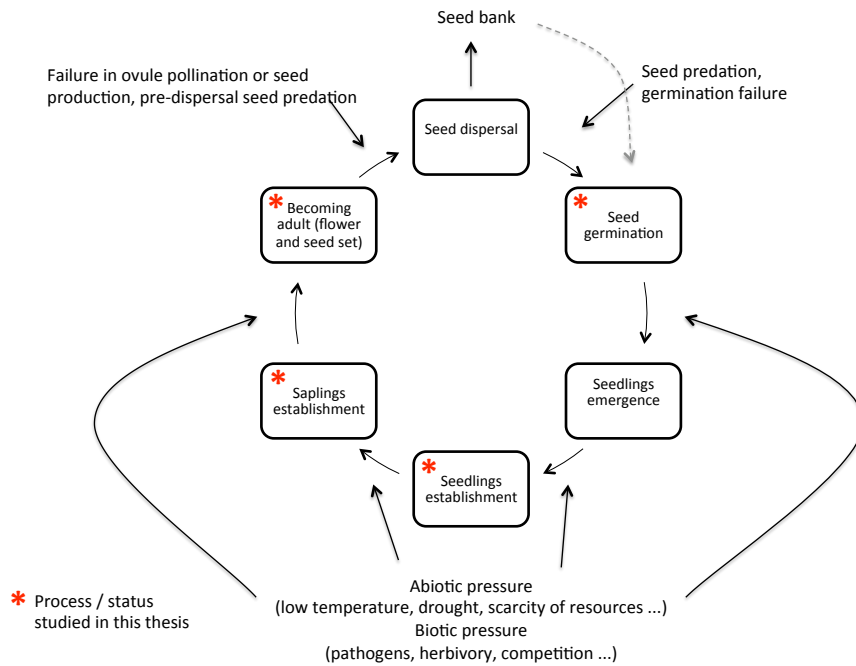


Figure 2: Tree life cycle and stage-specific hazards

Range dynamics at the upper limit of tree species: reproduction & recruitment

Due to changes in the environment, “species ranges are highly mobile, often shifting, expanding and contracting over time” (Sexton et al., 2009), as currently shown by some (climate change induced) upward and poleward shifts of tree species (Lenoir et al., 2009). These dynamics are tightly coupled to the life cycle of trees (Fig. 2). Each life stage may play a key role in maintenance and reproduction of the species. The successful cycle consists of decades of growth to become adult, well-synchronized time of flowering, sufficiently long growing season for seed ripening, seed germination, seedling development and sapling-to-adult growth. At each particular stage biotic and abiotic hazards may interrupt the life cycle (Fig. 2) and thus modify the species limit. Failure of pollination, fertilization or seed ripening are likely to prevent successful reproduction (Chuine, 2010; Pigott and Huntley, 1981). Seeds from high elevation provenances may lack viability, may be poor in reserves or fail to germinate in time, due to late

spring at high elevation or high latitude.

The establishment of seedlings and the growth into saplings can be a further critical step in successful reproduction. If tree recruits can exclusively be found below the species’ limit of mature trees, this could reflect unsuitable climate conditions in the recent past that prevented successful reproduction at the upper distribution limit. These unsuitable conditions may consist of recent occurrences of climatic extreme events such as severe drought or killing frost, both more effective on juvenile individuals than on adults. On the other hand, if tree recruits are found well above the limit of adult trees of the same species (without failures in other age classes), this might be indicative for recent optimal reproductive conditions and, provided the trend continues, upslope migration of the species. Thus, detailed demographic studies at the species leading edge are essential tools to determine the mechanisms responsible in shaping the cold limits (Vitasse et al., 2012) and to assess current retreats and advances of the local species ranges. All these questions are currently explored in an interdisciplinary approach as part of the TREELIM project at the Institute of Botany in Basel.

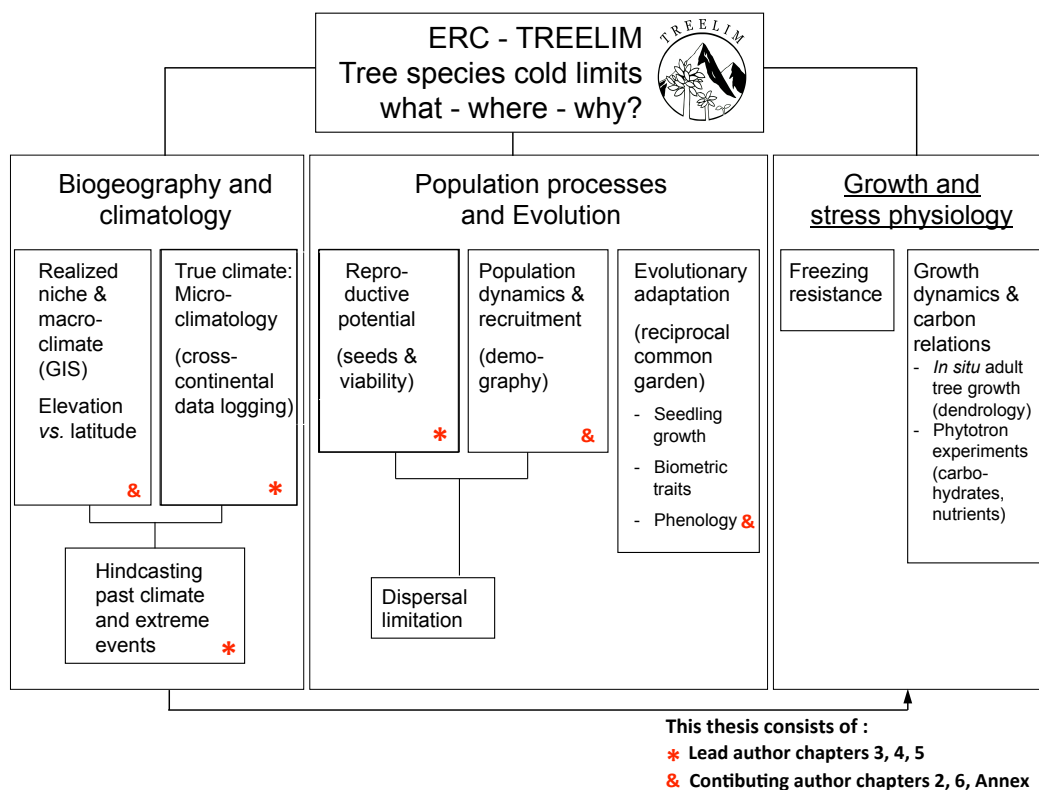


Figure 3: TREELIM project working packages

Aim of this thesis within the TREELIM framework

The TREELIM project aims at arriving at functional explanations of the distributional limits of prominent European broad-leaved tree species. In its **first** working package (Biogeography & Climatology, Fig. 3) the project aims to assess the current low temperature limits of tree taxa at their upper elevational and latitudinal limits, using existing databases of species occurrences, literature review and site visits. Further, the pattern found are/will be correlated with bioclimatic information at large scale (using weather station data) and at smaller scales (using data from a data logging campaign). The **second** work package (population processes and evolution) aims to examine the potential of reproduction (quality of seeds) and recruitment (establishment of seedlings and saplings) of temperate tree species at their current elevational limits in the Swiss Alps along with their plasticity of growth and phenology shift to temperature change. Finally, within the **third** work pack-

age (Growth and stress physiology) hypotheses of causes of growth limitation and stress survival are/will be tested using dendrological analysis along elevational gradients and ecophysiological experiments, such as an assessment of the freezing resistance of buds in spring (most vulnerable period for trees) and an examination of tree growth in climate chambers simulating temperatures that trees experience at their upper elevational limits.

This doctoral thesis focuses on topics belonging to the first two working packages within the framework of TREELIM. The work consists of the lead author studies on the accuracy of temperature predictions by weather stations for tree species limits (**Chapter 3**), on critical temperatures determining these tree species limits (**Chapter 4**) and on seed quality at the same tree species limits (**Chapter 5**). Further, I contributed to a study comparing the elevational and latitudinal limits of broad-leaved trees (Chapter 2), to a survey of tree recruitment at the species cold limits (Chapter 6) and

to an assessment of the elevational adaptation and plasticity in tree seedlings' growth and phenology (Annex).

In detail, I aimed at comparing the species elevational limits in Switzerland with their latitudinal limits in Scandinavia (**Chapter 2**, *Global Ecology and Biogeography*, in press). As these species limits are mainly controlled by temperature, lags between a species' elevational and latitudinal limit would indicate incomplete range filling due to non-thermal reasons. This was accomplished by conducting a cross-continental study, using a geographical information system to combine tree species occurrence databases, geographic climatic/elevational layers and a treeline model (Körner and Paulsen, 2004).

In **Chapter 3** I aimed at quantifying the deviations between temperature recorded *in situ* at tree species' elevational and latitudinal limits and nearest weather station temperature. In addition, I explored vertical temperature profiles in the same trees to characterize life conditions at the upper root zone, in the understory and at the crown level (Fig. 4, *Agricultural and Forest Meteorology*, submitted).

On that basis, I generated long-term *in situ* temperature series at the tree species limits (**Chapter 4**, in prep for *Journal of Biogeography*) to disentangle three temperature related hypothesis of broad-leaved tree species limits: (1) Freezing resistance during dormancy in deep winter, (2) late frost events during the period of bud burst and/or (3) the growing season length may constrain the spreading of species into the cold (in prep for *Journal of Biogeography*). For this purpose, I installed miniature datalogging devices (Fig. 5) at tree species limits in the Alps and South Sweden (Fig. 6). These measurements were then compared and linked to standard weather station data to derive at long-term species-specific temperature series.

In **Chapter 5** and **6** I studied stages within the life-cycle of broad-leaved tree species at their elevational limits in the Swiss Alps to address the question of whether (and if so, why) tree's reproductive cycle is interrupted at certain stages.

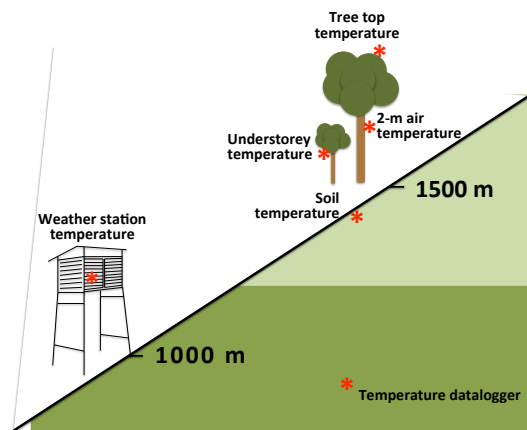


Figure 4: Datalogging study design



Figure 5: Miniature data-logging device TidbiT



Figure 6: Study areas of this thesis: Western & Eastern Swiss Alps, South Sweden

More specifically, I first analyzed whether broad-leaved tree species high elevation seed sources exhibit lower seed quality and lower germination success compared to seed sources from lower elevations (**Chapter 5**, published 2012 in *Annals of Botany*). To answer this question, I collected seed provenances of broad-leaved tree species from two regions and two contrasting elevations (Fig. 7, upper part), measured their physiological traits (weight, size, concentration of nitrogen and non-structural carbohydrates, viability) and conducted a seed germination experiment.

Second, by means of an *in situ* survey I investigated the presence of broad-leaved tree species below, at and above their elevational limits within the Swiss Alps (**Chapter 6**, published 2012 in *Journal of Biogeography*).

Further, I quantified the genetic adaptation and phenotypic plasticity of fitness related traits such as phenology in seedlings from central and marginal populations (**Annex**). For this, we set up a large common garden experiment (Fig. 7) comprising eight common gardens in the Western and Eastern Swiss Alps and ca. 5000 potted seedlings of seven broad-leaved tree species were grown and studied under standardized conditions.

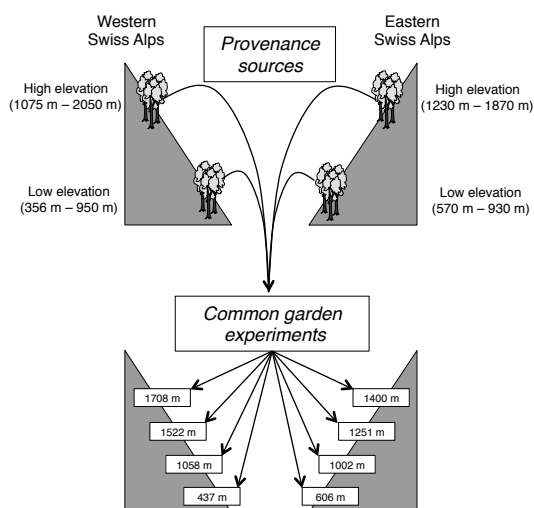


Figure 7: Design of the common garden experiment: Seeds from 8 broad-leaved tree species were collected at low and high elevation in both regions (Western & Eastern Swiss Alps). Hereafter, seedlings grown from seeds were transplanted to 8 common gardens situated along an elevational gradient in each of the two study regions (Y. Vitasse).

Studied species & study region

We selected ten broad-leaved tree species (*Acer pseudoplatanus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Laburnum alpinum*, *Prunus avium*, *Quercus petraea*, *Sorbus aria*, *Tilia platyphyllos*, *Sorbus aucuparia*, *Ilex aquifolium*, within a broad spectrum of plant families. The study regions encompassed the Western Swiss Alps near Martigny, the Eastern Swiss Alps near Chur and the South of Sweden (Fig. 6).

References

- Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T.L. and Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1 (1), 95-111.
- Barry, R.G., 1981. *Mountain weather and climate*. [Methuen], London, 313 S. pp.
- Bullock, J.M., Edwards, R.J., Carey, P.D. and Rose, R.J., 2000. Geographical separation of two *Ulex* species at three spatial scales: does competition limit species' ranges *Ecography* 23 (2), 257-271.
- Chuine, I., 2010. Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B* 365 (1555), 3149-3160.
- de Candolle, A., 1856. *Géographie botanique raisonnée*.
- Dirnböck, T., Essl, F. and Rabitsch, W., 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology* 17 (2), 990-996.
- Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araujo, M.B., Pearman, P.B., Le Lay, G., Piedallu, C., Albert, C.H., Choler, P., Coldea, G., De Lamo, X., Dirnböck, T., Gegout, J.C., Gomez-Garcia, D., Grytnes, J.A., Heegaard, E., Hoistad, F., Nogues-Bravo, D., Normand, S., Puscas, M., Sebastia, M.T., Stanisci, A., Theurillat, J.P., Trivedi, M.R., Vittoz, P. and Guisan, A., 2011. 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology* 17 (7), 2330-2341.
- Flohn, H., 1974. Contribution to a comparative meteorology of mountain areas. In: J. Ives and B. RG (Editors), *Arctic and Alpine environments*, London pp. 55-71.
- Grace, J., 1977. *Plant response to wind*. *Experimental botany*. Academic Press, London ; New York ; San Francisco, XI, 204 S. pp.
- Grisebach, A., 1872. *Die vegetation der Erde nach ihrer klimatischen Anordnung. Ein Abriss der vergleichenden Geographie der Pflanzen*. W. Engelmann, Leipzig.

- Hutchinson, G.E., 1957. Population Studies - Animal Ecology and Demography - Concluding Remarks. *Cold Spring Harbour Symposium* 22, 415-427.
- Körner, C., 2007. The use of 'altitude' in ecological research. *Trends in Ecology & Evolution* 22 (11), 569-574.
- Körner, C., 2012. *Alpine treelines*. Springer, Basel.
- Körner, C. and Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* 31 (5), 713-732.
- Langlet, O., 1971. Two Hundred Years Genecology. *Taxon* 20 (5/6), 653-721.
- Lauscher, F., 1976. *Weltweite Typen der Höhenabhängigkeit des Niederschlags. Wetter und Leben*.
- Lenoir, J., Gégout, J.-C., Pierrat, J.-C., Bontemps, J.-D. and Dhôte, J.-F., 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). *Ecography* 32 (5), 765-777.
- Merriam, C., 1894. Laws of temperature control of the geographic distribution of terrestrial animals and plants. *National Geographic Magazine* 6, 229-238.
- Pigott, C.D. and Huntley, J.P., 1981. Factors Controlling the Distribution of Tilia-Cordata at the Northern Limits of Its Geographical Range .3. Nature and Causes of Seed Sterility. *New Phytologist* 87 (4), 817-839.
- Rundgren, M. and Ingolfsson, O., 1999. Plant survival in Iceland during periods of glaciation? *Journal of Biogeography* 26 (2), 387-396.
- Sakai, A. and Larcher, W., 1987. *Frost survival of plants: Responses and adaptation to freezing stress*, 62. Springer, Berlin.
- Savolainen, O., Pyhajarvi, T. and Knurr, T., 2007. Gene flow and local adaptation in trees. *Annual Review of Ecology Evolution and Systematics* 38, 595-619.
- Scherrer, D. and Körner, C., 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography* 38 (2), 406-416.
- Schimper, A.F.W., 1898. *Pflanzengeographie auf phys-iologischer Grundlage*, Jena.
- Sexton, J.P., McIntyre, P.J., Angert, A.L. and Rice, K.J., 2009. Evolution and Ecology of Species Range Limits. *Annual Review of Ecology Evolution and Systematics* 40, 415-436.
- Svenning, J.C. and Skov, F., 2004. Limited filling of the potential range in European tree species. *Ecology Letters* 7 (7), 565-573.
- Vitasse, Y., Hoch, G., Randin, C.F., Lenz, A., Kollas, C. and Körner, C., 2012. Tree recruitment of European tree species at their current upper elevational limits in the Swiss Alps. *Journal of Biogeography*, 1-11.
- Von Humboldt, A. and Bonpland, A., 1807. *Ideen zu einer Geographie der Pflanzen nebst einem Naturgemälde der Tropenländer*. Cotta, Tübingen.
- Walter, H., 1931. *Die Hydratur der Pflanze*. Gustav Fischer, Jena.

Chapter 2

Do elevational limits of deciduous tree species match with their thermal latitudinal limits?

Christophe F. Randin, Jens Paulsen, Yann Vitasse, Chris Kollas, Thomas Wohlgemuth, Niklaus E. Zimmermann, Christian Körner
Global Ecology and Biogeography (2012), in press

Do elevational limits of deciduous tree species match with their thermal latitudinal limits?

Christophe F. Randin^{a*}, Jens Paulsen^a, Yann Vitasse^a, Chris Kollas^a, Thomas Wohlgemuth^a,
Niklaus E. Zimmermann^a, Christian Körner^a

^a *Institute of Botany, University of Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland*

**Corresponding author. Tel.: +41 61 267 3506; fax: +41 61 267 2980; E-mail address: Christophe.Randin@unibas.ch*

Summary

Aim We compared the upper limits of eighteen deciduous tree species along elevation in Switzerland and latitude in Europe. We hypothesized that species exhibit the same relative position along elevation and latitude, which can be expected if species have reached their thermal cold limit along both latitude and elevation.

Location Europe and Switzerland.

Methods We developed a method to identify a least-biased estimate of the elevational and latitudinal cold temperature limits and for comparing relative rank positions along these two limits. We applied an algorithm to calculate the elevation of the potential treeline for each point in the gridded landscape of Europe and Switzerland. For each occurrence of each species, elevation was extracted from digital elevation models. The vertical distance between elevation of the potential regional climatic treeline and uppermost species occurrences was calculated and used for comparisons between elevation and latitude.

Results We found a strong relationship between the thermal latitudinal and the elevational distance of species' cold limits to the potential treeline with only marginally significant different rank positions ($P=0.057$) along elevational and latitudinal gradients. A first group of nine species showed very similar thermal distances to the potential treelines along elevation and latitude. Among them, eight showed a significant decrease of their elevational limits towards high latitude across mountain regions of Europe. A second group of seven species occupied climatic niche closer to the treeline at their latitudinal range edge and only two species did not fill their thermal niche.

Main conclusions Our study provides support for the common concept of the species range–environment equilibrium. Notably, we did not find stronger deviation in filling thermal niches at the latitudinal limits as compared to the elevational limits, although the former involve a species to cover much more geographic distance. Thermal equilibrium seems therefore decoupled from equilibrium in the geographic space.

Keywords:

Deciduous trees, Europe, Swiss Alps, elevation, latitude, leading edge, climate equilibrium, postglacial history

Introduction

Tree species show specific upper elevational and polar latitudinal limits. Few species reach the life form limit of trees at the treeline. Most species do not, but find an upper limit well below the tree limit for mostly unknown reasons. The fact that the upper limit of tree species is reached at lower elevations at higher latitudes, ranging from >4800 m near the equator to sea level at polar latitudes (Hoch and Körner, 2005) has long attracted ecologists and suggests a common, temperature related explanation. For the high elevation or high latitude margins of the life form ‘tree’ in general, low temperature is considered to represent the main constraint (Huntley et al., 1989; Körner, 1998; Mellert et al., 2011). However, the mechanisms controlling the elevational or latitudinal limits of tree species that do not reach the tree limit are still poorly understood and so far, there are very few studies focusing on upper elevational limits of broad-leaved species (but see Mellert et al., 2011). Several temperature-driven limitations may affect these limits. For treeline formation (the life form limit, irrespective of species) freezing resistance is clearly not an issue (e.g. Sakai and Larcher, 1987; Körner, 1998). The best explanatory power is associated with a mean growing season temperature of 6.4 °C and a minimum duration of the growing season of 94 days, both critically constraining growth and development of trees (and newer data in Körner and Paulsen, 2004; Körner et al., 2011). However, for species reaching an upper or polar limit below the treeline, freezing tolerance may well be a significant constraint (Sakai and Weiser, 1973; Sakai and Wardle, 1978). Extreme low temperature related causes may include limited sexual reproduction during the flowering phase (e.g. *Tilia cordata*; see Pigott and Huntley, 1981; Woodward, 1990), lack of seed viability (Chuine, 2010) or failure of seedling establishment.

The postglacial migration-lag hypothesis

Although climate is considered the prime determinant for the distribution of temperate tree species from global to sub-continental scales

(Woodward, 1990), historical factors at the continental scale may also affect tree species ranges through time-lagged range expansion or more persisting dispersal limitation (Johnstone and Chapin, 2003). Naturalization of tree species or planted trees beyond their native range in Europe indicates the importance of dispersal and establishment constraints or competition effects on tree species range patterns. In this context, Svenning and Skov (2004) suggested that European tree species ranges may be affected by dispersal constraints during post-glacial expansion, with the effect that many species currently only fill a part of their potential climatic niche, their geographic range or both environmental and geographical spaces.

In contrast to the hypothesized gap between potential and realized species’ northern latitudinal limits, the discrepancy between realized and potential upper elevational limits of tree species in mountainous regions of Central Europe can be expected to be small or zero, because of the short distance between the center and the upper limit of species’ elevational distribution. If all species are at equilibrium with climate, their range limits should exhibit similar rank positions along both elevational and latitudinal temperature gradients. Indeed, tree species should have reached their climatic boundary at least occasionally, with the connecting line between those “outposts” representing the potential range limits as set by climatic factors only. Latitude thermal limits lower than expected from elevation thermal limits would suggest a thermal non-equilibrium as well as well a non-equilibrium geographic range due to an expansion lag to the north, thus meaning that competitive exclusion, inappropriate soils, pathogens, poor dispersal capacity, low propagule pressure or disturbance effects must have caused such lags. Similar latitudinal and elevation thermal limits, however, suggest a thermal equilibrium that may or may not coincide with geographic range equilibrium. Hence, for some species thermal equilibrium might occur despite showing non-equilibrium in geographic ranges.

Climatic, and more specifically temperature-driven factors explaining cold range limits of major deciduous tree species of European that do not reach treeline are not well studied to date. In contrast, the treeline as a physiognomic

boundary had been found to follow a surprisingly uniform mean growing season temperature despite enormous regional variation in its positioning and nature. Its predictability (Körner and Paulsen, 2004; Körner, 2007b) makes the natural treeline position and its associated growing season mean temperature an ideal biogeographic reference-line for comparisons and ranking of non-treeline species limits across latitude and elevation. Although the mechanisms of tree-line formation and those responsible for the limits of non-treeline forming tree species are likely different, the elevational and latitudinal treeline isotherm still provides a bioclimatic boundary against which the position of other species' limits can be compared in relative terms.

Although it is known for years that elevational and latitudinal range limits of taxa are likely correlated (e.g. Humboldt 1817), a systematic and fact-based assessment of this assumption has not yet been carried out. This study thus aims at first comparing the upper elevation limits of eighteen European deciduous tree species in the mountainous regions of Switzerland and the latitudinal limits in Europe. The elevation-for-latitude temperature model predicts a proportional reduction in temperature with increasing elevation or latitude. If tree species are mainly controlled by temperature-related drivers, their maximum elevation is expected to decrease with latitude. Therefore, elevation changes in species ranges along latitudinal gradients should follow regular, predictable patterns, paralleling the reduction in treeline elevation with increasing latitude, which has been described as Humboldt's Law (Humboldt, 1817). Thus, testing this law constitutes a second way of verifying the effect of temperature on tree cold limits across latitude and elevation. More specifically, we hypothesize that species exhibit the same rank position along elevation and latitude gradients, which translates to similar temperature constraints. If this hypothesis is correct, the regional elevational limits (and its associated temperatures) of all dominant deciduous species will decrease with latitude. Conversely, a latitudinal thermal limit lagging behind the elevational limit would be expected for species that have not yet reached their potential highest latitudinal position because of other than temperature-related factors such as large-scale

dispersal limitation during post-glacial recolonization from refugia during the Holocene.

Methods

Comparisons between elevational and latitudinal limits of broadleaved species

Study regions and species

The study was conducted across latitudinal gradient in Europe (40° N – 72° N, 24° W – 34° E ; Fig. 1a-b) and across an elevation gradient in Switzerland (45°40' – 47°50' N, 5°50' – 10°30' E; c. 41284 km²; elevation range: 197 to 2361 m above sea level ; Fig. 1a). We selected eighteen broad-leaved tree species that have wide distribution ranges in Europe (Table 1). Our data on tree distribution in Europe originate from the Level I data set of the International Co-operative Programme (ICP) on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests Level 1; Lorenz, 2010) and from the GBIF database (<http://www.gbif.org/>). The ICP Forests Level I database contains information on individual trees of every species occurring in predefined plots. The plots are distributed on systematic national grids of 16×16 km throughout Europe, covering 6046 plots. The number of individuals per species was recorded in four sub-plots at a distance of 25 m from the center grid point (Eichhorn et al., 2006) and the latitude and longitude coordinates correspond to the center of the geo-referenced plots. In addition, we sequentially selected GBIF tree species occurrences with (1) geographic positions from observation and specimen records only and (2) a horizontal uncertainty of the geographic coordinates of <100 m. The precision of the geographic coordinates (as defined in Chapman, 2005) was estimated with custom codes in R version 2.12.2 (R Development Core Team, 2011) by taking into account the number of decimal digits of the latitude and longitude and the position on the earth with the Harvesine formula. Occurrences of each species across Europe were visually inspected in a GIS and compared to georeferenced distribution maps from Meusel et al. (1964) to check for consistency with expert knowledge.

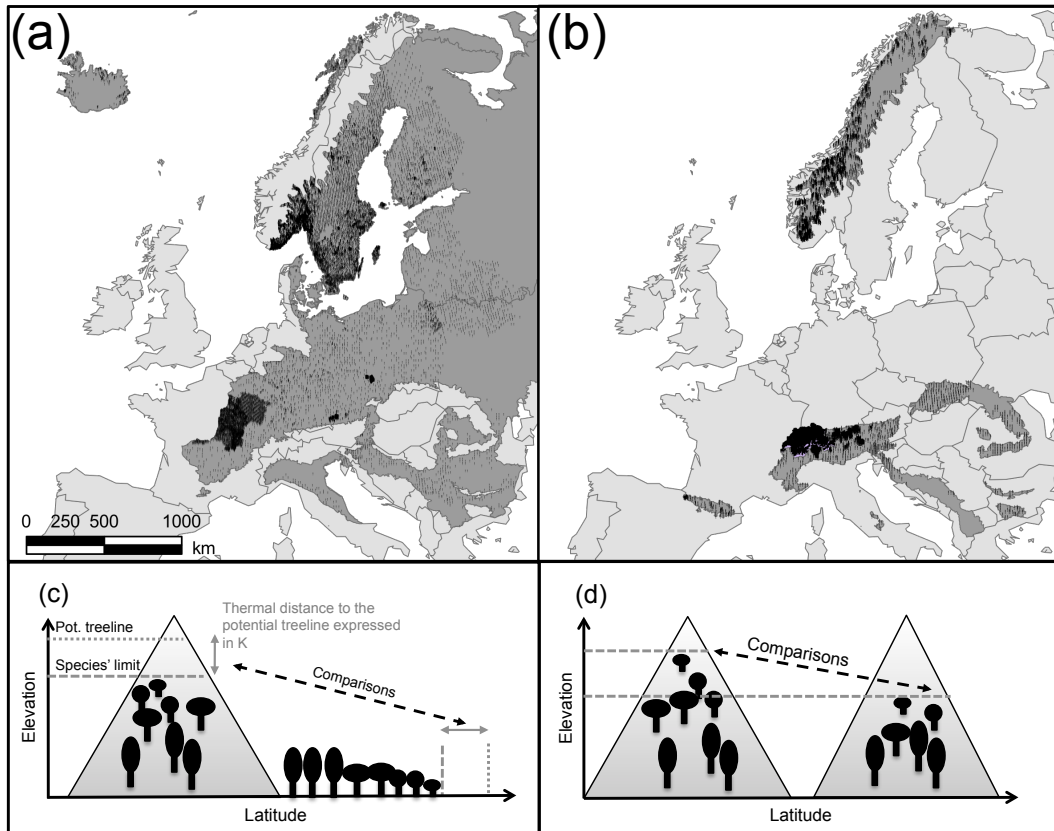


Figure 1: Location of the regions considered for the analyses. (a) Biogeographic regions (continental, boreal and arctic; in dark grey) and observations (black dots) used along latitude in Europe. (b) Mountainous regions of Europe (alpine biogeographic regions; in dark grey) selected to test the Elevation-for-latitude hypothesis (including observations along elevation in Switzerland). Conceptual views of the two analytical designs used to compare the upper elevational limits of the eighteen European deciduous tree species in the mountainous regions of Switzerland with the latitudinal limits in N-Europe (c; data from (a)) and to verify the elevation-for-latitude correspondence model (d; data from (b)).

Ultimately, we only considered Continental, Boreal and Arctic biogeographic regions of Europe (European Environment Agency 2001) for our analysis and thus excluded the belts of Atlantic, Alpine, Steppic and Mediterranean biogeographic regions (Fig. 1a). We removed these Atlantic regions to exclude upper limits of tree species controlled partly by a mild climate generated by ocean streams and not by climate only. This was done to improve comparisons between Fennoscandia and Switzerland as suggested by results from Grace (1997). We also excluded Alpine regions of Europe because we wanted to exclude the regions where the effect of elevation would be strongest and to capture the most northern limits. Finally we did not consider Mediterranean and Steppic regions to avoid the influence of drought on species limits.

In Switzerland, we used data from the Swiss National Forest Inventory (NFI) from two in-

ventory periods, which were sampled during the years 1983–1985 (NFI1) and 1995–1997 (NFI2) on a regular 1-km grid (1.4km grid for NFI2). Additional tree occurrences in Switzerland were derived from the forest plots database (Wohlge-muth, 1992). This resulted in $n = 21634$ observations for the selected biogeographic regions of Europe (excluding Switzerland) and $n = 22130$ observations for Switzerland.

Calculating the potential climatic treeline as a cold limit reference

Here we present a method to identify a least-biased estimate of the elevational and latitudinal cold temperature limits of broad-leaved tree species, and to compare species' rankings between these two limits. We first calculated the elevation of the potential treeline for

each cell in a gridded landscape (30×30 arcseconds = 1×1 km for Europe and 25×25 m for Switzerland) with custom code within the R environment. For Europe, we used geographic layers of monthly mean temperature and the digital elevation model (DEM) of the Worldclim dataset (Version 1.4, <http://Verdion.1.4.www.worldclim.org>; Hijmans et al., 2005). For Switzerland, we used monthly mean temperature layers derived from the national meteorological networks of Switzerland (MeteoSwiss ; method of computation are described in Zimmermann and Kienast, 1999) and a digital elevation model from Swisstopo (see more details below). In each cell, we derived daily values from monthly values of temperature with the aspline function of the akima library in R. These daily values were then projected for values of elevation ranging from 0 to 5000 m.a.s.l. with a 10-m interval using monthly lapse rates derived from moving windows of 5×5 km around the focal cell . The position of the potential climatic treeline was finally defined by the combined action of a minimum length of the growing season of 94 days (constrained by the first and last transition of a weekly average of daily mean air temperature of 0.9 °C) and a mean air temperature during that period of at least 6.4 °C (Körner et al., 2011).

Finally, for each occurrence in Europe, elevation was extracted from a 100×100 m digital elevation model, which was built from the 90 m SRTM Digital Elevation Model (version 4.1) and the 30 m ASTER Global Digital Elevation Model (north of 60° N). Elevation of tree occurrences in Switzerland was extracted from the 25 m DEM of Switzerland (from the federal office of topography).

For each species, the difference (i.e. vertical distance in m) between the elevation of the potential regional climatic treeline and each observed elevation of occurrences was calculated for Europe and Switzerland (Fig. 1c). Only the quantiles of 0% to 5% (with 0.5% increments) of these distances were tested for further analysis. Here, the 0% quantile of a species represents the one occurrence that is closest to the potential climatic treeline. Since elevation as such is meaningless for plants, we express this position as a thermal distance in K rather than in meters. We chose a lapse rate of 0.55 K for a vertical dis-

tance of 100 m to the potential climatic treeline.

The relation between the corresponding thermal distance to the potential climatic treeline in Switzerland and in Europe was tested using Pearson correlation tests for each quantile. This correlation between thermal distances to elevational and latitudinal treelines was significant for all quantiles tested (quantiles 0% to 5%: P-values < 0.05), with the correlation for the 2.5% quantile being the highest. We therefore based further analyses of the ranking of species using the 2.5%-quantile. Since the uppermost limits of tree species are likely in equilibrium with climate along elevation gradients, we chose the elevational thermal distance to the potential treeline as a reference and we tested if rankings from latitudinal distribution limits matched with those from elevational limits. Latitudinal records corresponding to the 2.5%-quantile were located at the northern-cold limits of all species (see Appendix S1).

Estimation of error in the analytical framework

We estimated the potential error that accumulated from different sources when calculating the distance to the potential treeline and we composed the error sum from three main components:

$$\varepsilon_{\text{Total}} = \sum (\varepsilon_{\text{DEM}} + \varepsilon_{\text{Elevation range within plots}} + \varepsilon_{\text{Treeline model}}) \quad (1)$$

The first source of error (ε_{DEM}) originates from the vertical error of the digital elevation model from which the plot elevation was extracted in Switzerland and in Europe. The vertical error of the 25×25 m DEM in Switzerland is 8m in mountain regions (http://www.swisstopo.admin.ch/internet/swiss_topo/fr/home/products/height/dhm25.html). The 100×100 DEM of Europe is a combination of the SRTM90 (90×90 m; up to 60° N) and ASTER GDEM (30×30 m; from 60° to 83° N) resampled to a 100×100 m resolution. ASTER has an estimated accuracy of 20 meters at 95 % confidence for vertical data (ASTER GDEM Validation Team) whereas the vertical absolute height error shall be less than 16 m for 90% of the data for the SRTM DEM (Rodriguez et al.

2009). Here, we took the value of 20m corresponding to the accuracy of the ASTER DEM.

The second error component ($\varepsilon_{\text{Elevation range within plots}}$) is an estimate of the range of elevations from the DEM that can be observed within a typical plot (plus the location error) from which tree occurrence data were extracted. Here we first generated buffers with radius of 100m for Europe and 25m in Switzerland. This corresponds to the maximum error generated by the precision of the coordinates in Europe and to the sum of the error of from the GPS (or from map) and of the plot size in Switzerland ($\sim 10\text{m} + 10\text{m}$: rounded to 25m so that it corresponds to a shift of one pixel in each direction from the measured coordinates). We then extracted the minimum and maximum elevation values within buffers around the plots for both Europe and Switzerland and summarized these values to a mean species-specific range. These ranges vary between 4m and 15m in Switzerland and 4m and 12m for Europe among the species. The third error component ($\varepsilon_{\text{Treeline model}}$) corresponds to the vertical mismatch in elevation provided by the model of potential treeline. This was evaluated to $< 50\text{m}$ (with data from Paulsen & Körner, 2001). The sum of the three components was then converted to K with the same lapse rate of $0.55 \text{ K} \times 100\text{m}^{-1}$ as was used previously.

Testing the elevation-for-latitude temperature model

Study regions and species

We used the same species occurrence dataset as for the previous analysis at the European scale. However, only mountainous regions of Europe were considered and Swiss occurrences from mountainous regions were combined with the European dataset in order to include all parts of the Alps (Fig. 1b and d). These regions were selected by extracting species occurrences within the Alpine biogeographic regions of Europe (European Environment Agency 2001).

Statistical analyses

Latitude and elevation from the 100m DEM were first extracted for each occurrence. Second, the maximum elevation reached for each species was recorded from 41° N to 71° N within a 0.5°

interval. Finally, the elevation was regressed as a function of latitude for each species with linear regressions. Here we hypothesized that the maximum elevation reached by a species for a given latitude decreases towards its northernmost limit in a linear and predictable manner because its upper-northernmost limit is controlled mainly by temperature (Fig. 1d).

Results

We found a strong relationship ($R^2 = 0.65$; P-value < 0.001 ; Fig. 2) and a marginally significant difference (Paired t-test; P-value = 0.057; $df = 17$) between the thermal latitudinal and elevational distances of species' cold limits. In addition, we found a strong and very significant relationship between the rank positions of species along the elevational and latitudinal gradients ($\rho = 0.620$; P-value = 0.007). The thermal distance in K to treeline was often smaller in the north along latitude (twelve species) than in the Alps along elevation (six species). *Sorbus aucuparia* was found to be closest to the potential climatic treeline at both elevation and latitudinal limits (Table 1). We distinguish three groups of species in our comparison between elevational and latitudinal rankings (Fig. 3). A first group (*Sorbus aucuparia*, *Acer pseudoplatanus*, *Betula pendula*, *Fagus sylvatica*, *Fraxinus excelsior*, *Prunus avium*, *Carpinus betulus*, *Castanea sativa* and *Tilia platyphyllos*; Table 2), representing half of the studied species, showed very similar thermal distances to the potential climatic treeline at both high elevation and high latitude (absolute difference between elevational and latitudinal distances $< 1.2\text{K}$). The first five of these listed nine species, together with *T. platyphyllos*, showed a significant decrease in maximum elevation limits with increasing latitude across the mountainous regions of Europe (Table 2; P-values < 0.05). Four species (*Prunus avium*, *Carpinus betulus*, *Tilia platyphyllos* and *Castanea sativa*) showed no significant trends. A second group of species (*Ulmus glabra*, *Populus tremula*, *Acer platanoides*, *Quercus petraea*, *Tilia cordata*, *Quercus robur* and *Ostrya carpinifolia*) had a smaller thermal distance to the treeline at high latitude compared to the high elevation treeline. Among these, three exhibited a significant decrease in

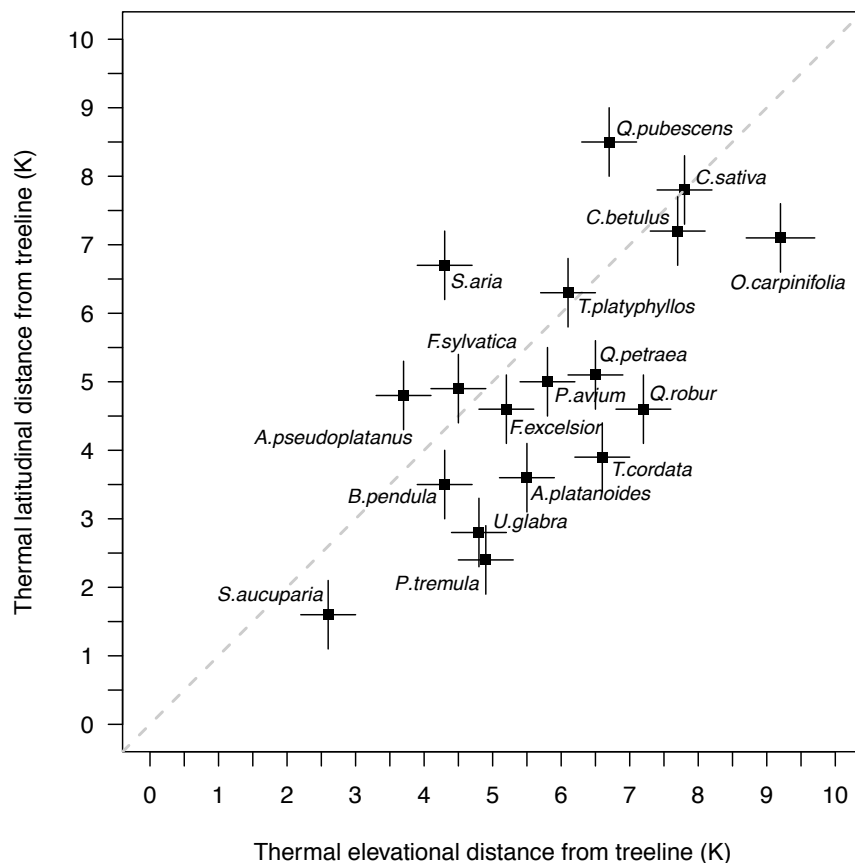


Figure 2: Relationships between the 2.5 % quantile of the distance from the potential regional treeline (elevation difference expressed in K) for the eighteen species in Europe and the Swiss Alps only (Pearson correlation coefficient: 0.652; P-value: 0.002). The dashed line represents a perfect agreement between elevational and latitudinal distances. Horizontal and vertical error bars represent the cumulative error (described by equation 1) of the distance to the treeline along elevation and latitude.

their high elevation limits with increasing latitude (*U. glabra*, *P. tremula* and *A. platanoides*; Table 2; P-value < 0.05) and one showed a marginally significant trend (*Q. petraea*; adjusted $R^2 = 0.13$; P-value = 0.087). Only two species (*Sorbus aria* and *Quercus pubescens*) belong to the third group and showed an opposite pattern to the second group. They exhibited a smaller thermal distance to the high elevation compared to the high latitude treeline (Fig. 3 and Table 2). We found no significant decrease in elevation limits with increasing latitude for this last group of species.

Discussion

Our results illustrate that the poleward thermal limits of half of the eighteen studied deciduous tree species matches the upper thermal limits in

the Swiss Alps well. Among them, eight showed a negative relationship between elevation and latitude across the different mountain regions of Europe including the Alps, which indicates that temperature is a key control of the upper elevation and poleward latitudinal limits of these deciduous tree species (Sakai and Weiser, 1973; Huntley et al., 1989). For seven out of the eighteen species our results suggest that these tree species currently fill their climatic niche closer to the treeline at their latitudinal edge of the distribution than at their elevational distribution edge. Only two species seem to lag behind their thermal niche at the latitudinal range edge, namely *S. aria* and *Q. pubescens*. All other species are filling their thermal niches at their latitudinal edge of distribution well, compared to their elevation limit in the more southern European mountains.

Table 1: Ranking of the eighteen species by their thermal distance between species' elevational (on the extreme left of the table) and latitudinal (on the extreme right) cold limits and the potential regional climatic treeline. The thermal distance is expressed in K. Scientific names follow the nomenclature of the Atlas Florae Europaeae (Lahti & Lampinen, 1999).

Elevation (Swiss Alps)				Latitude (Europe)		
Thermal distance (K)	Error (K)	Species	Ranking	Species	Error (K)	Thermal distance (K)
2.6	0.4	<i>Sorbus aucuparia</i> L.	1	<i>Sorbus aucuparia</i> L.	0.5	1.6
3.7	0.4	<i>Acer pseudoplatanus</i> L.	2	<i>Populus tremula</i> L.	0.5	2.4
4.3	0.4	<i>Betula pendula</i> Roth.	3	<i>Ulmus glabra</i> Huds.	0.5	2.8
4.3	0.4	<i>Sorbus aria</i> (L.) Crantz	4	<i>Betula pendula</i> Roth.	0.5	3.5
4.5	0.4	<i>Fagus sylvatica</i> L.	5	<i>Acer platanoides</i> L.	0.5	3.6
4.8	0.4	<i>Ulmus glabra</i> Huds.	6	<i>Tilia cordata</i> Mill.	0.5	3.9
4.9	0.4	<i>Populus tremula</i> L.	7	<i>Quercus robur</i> L.	0.5	4.6
5.2	0.4	<i>Fraxinus excelsior</i> L.	8	<i>Fraxinus excelsior</i> L.	0.5	4.6
5.5	0.4	<i>Acer platanoides</i> L.	9	<i>Acer pseudoplatanus</i> L.	0.5	4.8
5.8	0.4	<i>Prunus avium</i> L.	10	<i>Fagus sylvatica</i> L.	0.5	4.9
6.1	0.4	<i>Tilia platyphyllos</i> Scop.	11	<i>Prunus avium</i> L.	0.5	5.0
6.5	0.4	<i>Quercus petraea</i> Liebl.	12	<i>Quercus petraea</i> Liebl.	0.5	5.1
6.6	0.4	<i>Tilia cordata</i> Mill.	13	<i>Tilia platyphyllos</i> Scop.	0.5	6.3
6.7	0.4	<i>Quercus pubescens</i> Willd.	14	<i>Sorbus aria</i> (L.) Crantz	0.5	6.7
7.2	0.4	<i>Quercus robur</i> L.	15	<i>Ostrya carpinifolia</i> Scop.	0.5	7.1
7.7	0.4	<i>Carpinus betulus</i> L.	16	<i>Carpinus betulus</i> L.	0.5	7.2
7.8	0.4	<i>Castanea sativa</i> Mill.	17	<i>Castanea sativa</i> Mill.	0.5	7.8
9.2	0.5	<i>Ostrya carpinifolia</i> Scop.	18	<i>Quercus pubescens</i> Willd.	0.5	8.5

History and dispersal limitations

Numerous authors have stressed that large-scale contemporary plant species distribution ranges may be strongly controlled by large-scale historical constraints, in addition to controls by climate (McGlone, 1996; Hewitt, 1999; Ricklefs, 2004). More specifically, Svenning and Skov (2004) showed by combining atlas data with distribution models that the majority of European tree species seems to be filling less than 50% of their potential climatically suitable range. They attributed this low range filling to large-scale dispersal limitation of the post-glacial recolonization from the ice age refugia. In particular, the following percentages of potential range filling for five of our study species were given: *C. sativa* (14.4%), *C. betulus* (68.5%), *F. sylvatica* (73.7%), *Q. petraea* (83.3%) and *B. pendula* (92.8%). Except for *B. pendula* (which seems to fill its range), we found a comparable coverage of the thermal niche at both their latitudinal and elevational range limits and therefore, we did not observe a thermal non-equilibrium at their latitudinal range edge. Hence, these species may thus have non-equilibrium geographic ranges de-

spite being at thermal niche equilibrium. However, in their study, Svenning and Skov used minimal rectilinear envelopes to define the potential suitable niche of their species, which inflated artificially the size of the potential suitable habitats over Europe. In addition, such a modeling approach assumes no interaction between the bioclimatic variables considered in the determination of the species' potential range limits.

In line with our results, the presence of cryptic refugia in northern, central and eastern Europe, as proposed by Birks and Willis (2008), may have provided an ideal basis for rapid spreading of these trees from micro-refugia during the Holocene. For instance, the available combined palaeobotanical and molecular data for *Fagus sylvatica* suggest that its main spread occurred from populations in central and eastern Europe rather than from major refugia south of the Alps (Magri et al., 2006). By measuring patterns of covariation between species assemblages (rather than the ratio between observed and modeled distributions as Svenning and Skov in 2004), Araujo and Pearson (2005) found results that also support the hypothesis

Table 2: Coefficients of linear regressions of the maximum elevation reached by each of the eighteen species as a function of latitude within alpine and arctic biogeographic regions of Europe. P-values for species with a significant relationship are highlighted in bold. N indicated the number of observations used for the regressions.

Species	b_1 *Latitude (decimal degrees)	Standard deviation b_1	Adjusted R^2	P value	N
<i>Acer platanoides</i>	-45.6*(Lat.)	10.3	0.54	< 0.001***	17
<i>Acer pseudoplatanus</i>	-54.6*(Lat.)	8.6	0.60	< 0.001***	27
<i>Betula pendula</i>	-43.2*(Lat.)	11.4	0.33	< 0.001***	28
<i>Carpinus betulus</i>	-54.3*(Lat.)	34.3	0.10	0.136	15
<i>Castanea sativa</i>	+90.4*(Lat.)	148.1	-0.10	0.564	8
<i>Fagus sylvatica</i>	-46.6*(Lat.)	18.8	0.22	0.024*	19
<i>Fraxinus excelsior</i>	-45.4*(Lat.)	10.3	0.43	< 0.001***	26
<i>Ostrya carpinifolia</i>	NA	NA	NA	NA	4
<i>Populus tremula</i>	-19.1*(Lat.)	6.8	0.16	0.008**	37
<i>Prunus avium</i>	-15.7*(Lat.)	13.9	0.02	0.271	19
<i>Quercus petraea</i>	-26.7*(Lat.)	14.7	0.13	0.087	17
<i>Quercus pubescens</i>	-234.5*(Lat.)	145.5	0.21	0.168	7
<i>Quercus robur</i>	+4.0*(Lat.)	12.2	-0.05	0.746	20
<i>Sorbus aria</i>	+6.8*(Lat.)	59.8	-0.12	0.912	10
<i>Sorbus aucuparia</i>	-40.5*(Lat.)	7.1	0.48	< 0.001***	35
<i>Tilia cordata</i>	+5.6*(Lat.)	15.2	-0.05	0.712	19
<i>Tilia platyphyllos</i>	-146.4*(Lat.)	59.2	0.42	0.048*	8
<i>Ulmus glabra</i>	-25.6*(Lat.)	9.7	0.17	0.013*	29

that plants are often more mobile than is conventionally thought. Yet, and in defense of Svenning and Skov's (2004) approach, we only tested the general distance from regional upper limits to the potential treeline in each region. We did not test, however, whether this identical or even more advanced cold limit in the North is actually achieved over larger areas and occurred along a single population front or only in some particular regions, with long dispersal events producing outlier populations (Cain et al., 2000). Still, our results demonstrate that species, which have reached their elevational or latitudinal cold limits, may be at a thermal equilibrium at least in some part of their geographical distribution range in both regions. More recently, Svenning et al. (2010) found a broad support for the effect of accessibility to explain current local species richness. They concluded that local tree assemblages in Europe often fail to realize a large proportion of the potential richness, partially reflecting their geographical, historical, and environmental circumstances such as fragmentation and accessibility to recolonization. Further analysis should identify the geographic regions and the drivers of such thermal disequilibrium (see examples of

such analysis in Ohlemüller et al., 2011).

Based on our analysis, geographic barriers or dispersal and recruitment limitations may explain the lagging thermal position of *S. aria*, and *Q. pubescens*. For the latter species, Svenning and Skov (2004) found a potential range filling of only 49.6%, in line with our results. Geographic barriers such as edaphic conditions could be one explanation for *Q. pubescens* since this species grows mostly on limestone (Rameau et al., 1989; Lepais and Gerber, 2011). It has also been reported that *Q. pubescens* has a poor ability to survive in pine understories (Kunstler et al., 2004), which suggest that forest management and interspecific competition could also have modified its high latitude limits. Ultimately, when comparing the seed dispersal vectors of the eighteen species, *S. aria* and *Q. pubescens* are the two species that may lack an obvious vector (man or birds) that could have accelerated its spread over long distances especially over fragmented habitats. *S. aria* has non-persistent fruits that fall to the ground when ripe (Herrera, 1989) and therefore might not benefit as much as *S. aucuparia*, of birds as agents of seed dispersal.

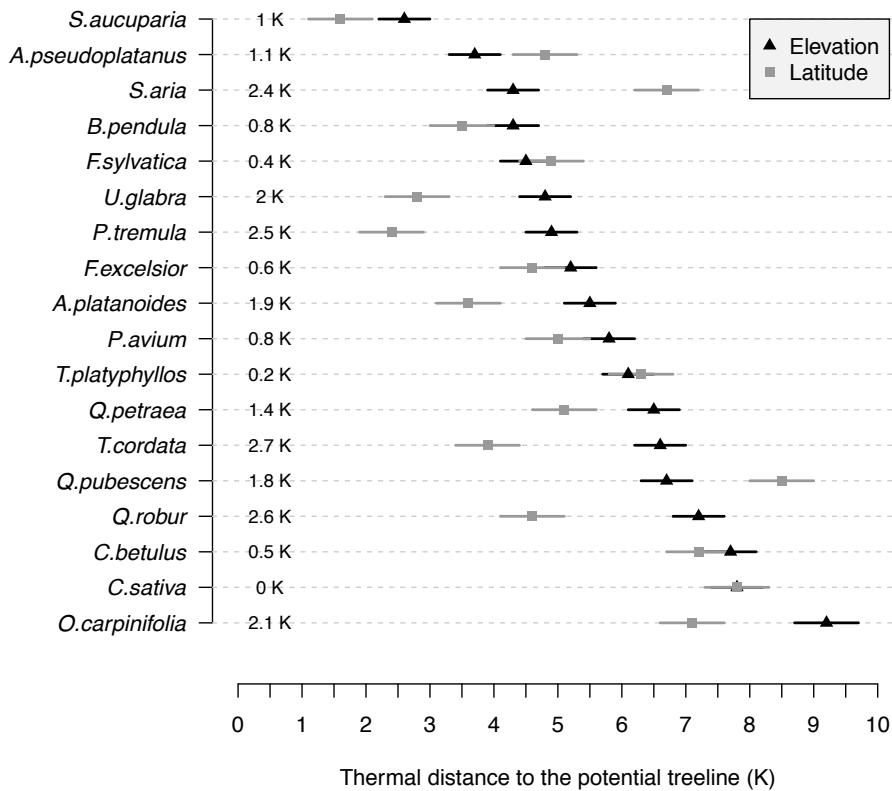


Figure 3: Thermal distances (in K) to the potential regional treeline along elevation and latitude. Species are ranked according to their elevational distance and arrows indicate the deviation of the latitudinal distances from the elevational distances. Absolute differences (Δ in K) between elevational and latitudinal distances are indicated on the left. Horizontal error bars represent the cumulative error (described by equation (1)) of the distance to the treeline along elevation (black lines) and latitude (grey lines).

Postglacial history and ecological preferences may also partly explain the latitudinal lag of *Q. pubescens*. Evidence from genetic markers showed that this lowland species originates from the Balkan and the Italian Peninsula. In contrast, *Q. petraea* is currently found at relatively high elevation and a possible postglacial colonization scenario assumes that one of its primary refugia was located in Slovenia (Petit et al., 2002). Therefore, the ecological tolerance of *Q. petraea* in combination with the locations of its refugia may have favored its migration to the Baltic countries.

Regional edaphic conditions could also explain the lower thermal limit in Switzerland and the important difference of 2.7 K between the high elevation limit in the Swiss Alps and the high latitude limit in North of Europe for *Q. robur* (see Table 1). The wide range of this species in contrast to *Q. petraea* in the south of Sweden may be related to the acidic substrate

occurring throughout Scandinavia and the disjunctive occurrence of calcareous bedrock. It has also been reported that *Q. robur* occurs in rich and deep soils that are often associated with crystalline rocks in this region since such bedrock has a very low porosity (Carlsson and Ejdeling, 1979). Conversely, *Q. petraea* is found on poorer and dryer soils often associated with karstic limestone bedrocks. At the northernmost distribution range in Sweden, bedrock is dominated by gneiss and igneous belts, which is more favorable to *Q. robur*, while younger sedimentary rock is more sparsely distributed (Korhonen et al., 1998). Finally, *Q. robur* is a post-pioneer capable of colonizing open land, whereas *Q. petraea* is a late-successional species that grows in stable and well-established forest environments (Lepais and Gerber, 2011). This generally suggests a better competitive capability of *Q. robur*.

Other potential causes of mismatch between Europe and the Alps

Although we generally found good agreement between the two distribution limits, elevation and latitude do not seem to represent perfect analogues. Climate gradients are steeper along elevation than along latitude (Billings, 1973). Important environmental factors, such as precipitation, cloudiness, length of the growing season, snowpack and seasonal temperature extremes may also impose different patterns and trends in relation to increasing elevation and latitude (Billings, 1973; Körner, 2003). Although oceanic regions were excluded from the European datasets for the latitude vs. elevation comparisons, climate in Switzerland is driven by different weather systems than those affecting the climate in the North (representing non-analogous climate). For our analysis, we applied the same adiabatic lapse rate to elevation and latitude for a given distance to the tree-line expressed as a difference in elevation. Although records from weather stations show similar lapse rates, this could be a source of bias. In addition, the thermal range is compressed to a smaller zone and the distance between the edges and the optimum of a species distribution is shorter along elevation of mountain ranges (Körner, 2003). Overall, in mountain regions, the available land area is rapidly decreasing with increasing elevation (Körner, 2007a). In summary, steeper climatic gradients acting jointly with decreasingly available land area towards higher elevation may actually increase competition among species and prevent the less competitive tree species to fully fill their thermal niche in mountain regions.

We based our ranking and comparison on the assumption that the same mechanisms control tree species' upper and poleward distribution limits and that species' limits relate to a temperature variable that exhibits a similar relationship to treeline temperature conditions. In fact, this may not be entirely so and several reasons could explain why we get similar but marginally-significant different rank positions. For instance, if minimum annual temperature were the key factor for a given species, this would affect the relationship of this factor with growing season temperature along a latitudinal gradient versus an elevational gradient in the Alps. As a conse-

quence, tree species with wide distribution areas might then have adapted differentially to the local growing conditions in different parts of the range (Savolainen et al., 2004).

Therefore, although the rank order for most species might be similar, we can also expect systematic discrepancies from this pattern that would arise where tree species' cold limits were not determined by the same mechanisms as for the treeline as a biome boundary. Thus, latitudinal limits lower than expected from elevation limits do not necessarily suggest expansion lags to the North.

These thermal species limits may also be controlled by thermal extremes, less correlated with the temperature means adopted from climate databases to calculate the potential climatic treeline. This effect of extremes on modifying tree distribution patterns has been demonstrated in a recent study (Zimmermann et al., 2009). Additionally, the deviation between means and extremes will likely be bigger in continental than in oceanic climates and different in the North of Europe compared to the Swiss Alps.

Macroclimate, edaphic conditions and intra-specific competition are plausible explanations of lower thermal limits of species in the Swiss Alps. However, we cannot exclude the effect of long-term and human management in the Alps despite the fact that our results are based on presence data and the highest occurrences recorded along elevation. Last, we cannot exclude the effects of strong elevational variations across the biogeographic regions selected for our analysis (high mountains falling at the cold limits of our species) combined with under-represented areas in our occurrence dataset.

Implications for climate-based distribution models

Our findings have important implications for projections of climate-change impacts on plant species that are using correlative approaches (e.g. Species Distribution Models; SDMs; see Guisan and Thuiller, 2005). Such models generally rely on the "equilibrium assumption", i.e. that a species' climatic niche can be estimated from a species' geographic distribution (Guisan and Zimmermann, 2000). Here we showed that

the validity of this assumption, at least for a thermal equilibrium, varies across our study species and between elevation and latitude. We found the assumption clearly supported for nine species. For seven species this assumption might only be met across latitudes, while the assumption is clearly violated for two species. Thuiller et al. (2004) showed that restricting the environmental range of data strongly influenced the estimation of response curves in SDMs, especially towards upper and lower distribution limits along environmental gradient. If some species are not at the thermal equilibrium at their cold limits, as suggested by our results for nine species, this may then lead to more conservative scenarios in terms of changes in distribution projections.

Conclusion

Our results demonstrate that half of the studied tree species have reached the thermal limits of their northern latitudinal (poleward) temperature niches compared to the elevational niche limits following postglacial re-colonization, even when evidence suggest that they have non-equilibrium geographic ranges. These results also provide a quantitative test of the common assumption of the species range–environment equilibrium that is generally used as a prerequisite assumption for climate change projections using species distribution models. While most of the remaining species come closer to filling their thermal niches in the North, than in the Alps, we found only two species that seem to lag clearly behind filling their thermal niches in the North compared to the Alps (*S. aria*, *Q. pubescens*).

Acknowledgements

The research leading to these results has been funded by European Research Council (ERC) grant 233399 (project TREELIM). NEZ has received funding from the 6th and 7th EU Framework Programme Grants GOCECT-2007-036866 (ECOCHANGE) and ENVCT-2009-226544 (MOTIVE). Finally, we thank GBIF and ICP Forests for access to tree species data of the Level I network.

References

- Araujo, M.B., Pearson, R.G. (2005) Equilibrium of species' distributions with climate. *Ecography* 28: 693-695.
- Billings, W.D. (1973) Arctic and Alpine Vegetations: Similarities, Differences, and Susceptibility to Disturbance. *BioScience* 23: 697-704.
- Birks, H.J.B., Willis, K.J. (2008) Alpines, trees, and refugia in Europe. *Plant Ecology & Diversity* 1: 147-160.
- Carlsson, L., Ejdeling, G. (1979) Geohydrological Properties of Tectonic Zones in Hard Rocks Obtained from Artificial Recharge Tests and Numerical Modeling. *Nordic Hydrology* 10: 49-62.
- Chapman, A.D. (2005) Principles of Data Quality, version 1.0. Report for the Global Biodiversity Information Facility. In: *Global Biodiversity*. GBIF, Copenhagen.
- Chuine, I. (2010) Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B-Biological Sciences* 365: 3149-3160.
- Grace, J. (1997) The oceanic tree-line and the limit for tree growth in Scotland. *Botanical Journal of Scotland* 49: 223-236.
- Guisan, A., Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147-186.
- Guisan, A., Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8: 993-1009.
- Herrera, C.M. (1989) Frugivory and seed dispersal by carnivorous mammals and associated fruit characteristics in undisturbed mediterranean habitats. *Oikos* 55: 250-262.
- Hewitt, G. (1999) Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society* 68: 87-112.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965-1978.
- Hoch, G., Körner, C. (2005) Growth, demography and carbon relations of *Polylepis* trees at the world's highest treeline. *Functional Ecology* 19: 941-951.
- Humboldt, A.v. (1817) Des lignes isothermes et de la distribution de la chaleur sur le globe. *Mémoires de Physique et de Chimie de la Société d'Arcueil* 3: 462-602.
- Huntley, B., Bartlein, P.J., Prentice, I.C. (1989) Climatic control of the distribution and abundance of beech (*Fagus* L) in Europe and North America. *Journal of Biogeography* 16: 551-560.
- Johnstone, J.F., Chapin, F.S. (2003) Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biology* 9: 1401-1409.
- Jones, E.W. (1945) *Acer* genus L. *Journal of Ecology* 32: 215-219.

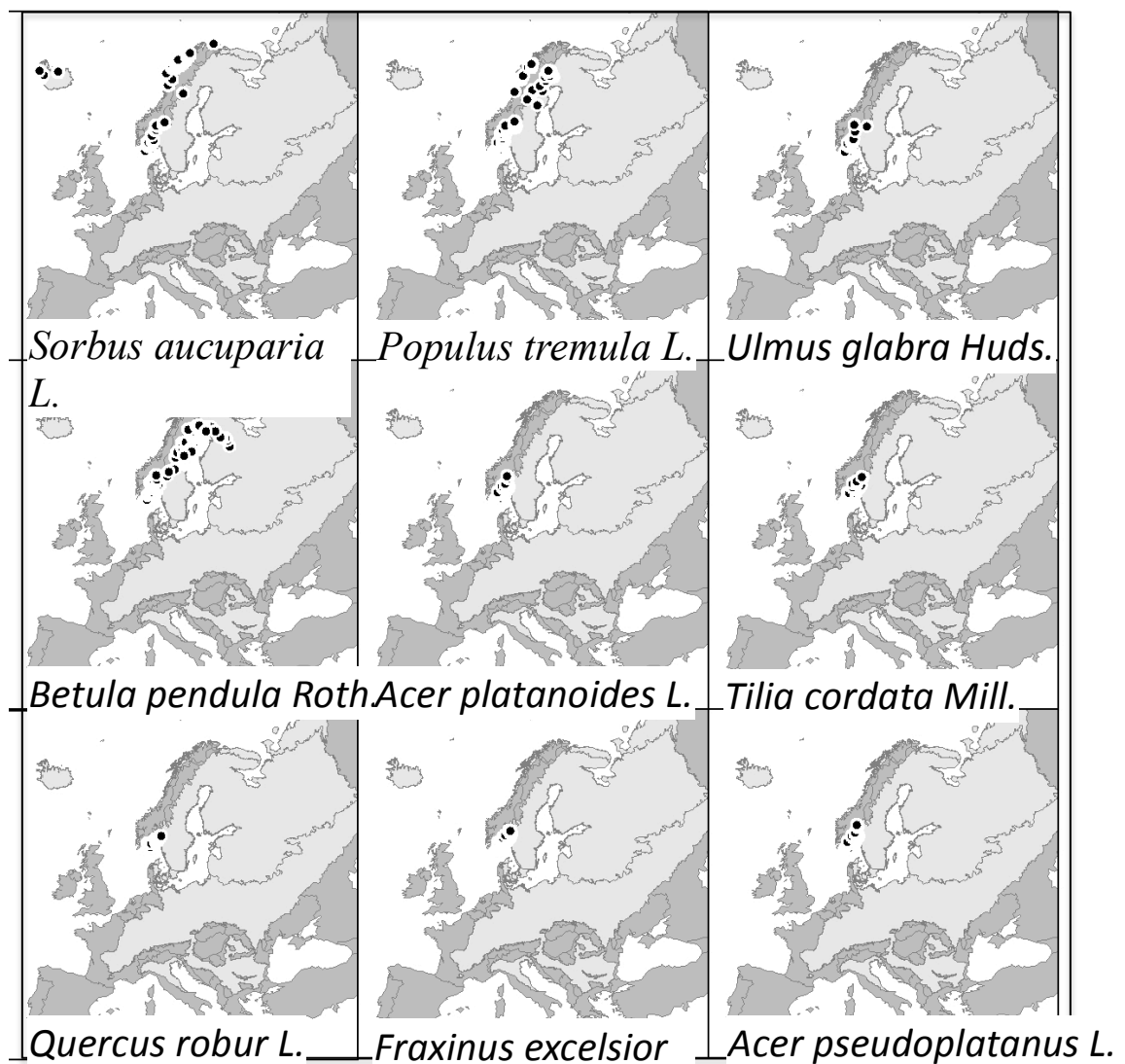
- Korhonen, J.V., Aaro, S., Skilbrei, J.R., Vaher, R., Zhdanova, L. (1998) Geophysical maps of the Fennoscandian Shield 1:1 mill. . In: *Abstracts of the SVEKALAPKO 98 work- shop* in Repino 33-34
- Körner, C. (1998) A re-assessment of high-elevation treeline positions and their explanation. *Oecologia* 115: 445-459.
- Körner, C. (2003) *Alpine Plant Life* (2nd Edition). Springer, New York.
- Körner, C. (2007a) The use of 'altitude' in ecological research. *Trends in Ecology & Evolution* 22: 569-574.
- Körner, C. (2007b) Climatic treelines: Conventions, global patterns, causes. *Erdkunde* 61: 316-324.
- Körner, C., Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* 31: 713-732.
- Körner, C., Paulsen, J., Spehn, E.M. (2011) A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alpine Botany*
- Kunstler, G., Curt, T., Lepart, J. (2004) Spatial pattern of beech (*Fagus sylvatica* L.) and oak (*Quercus pubescens* Mill.) seedlings in natural pine (*Pinus sylvestris* L.) woodlands. *European Journal of Forest Research* 123: 331-337.
- Lahti, T., Lampinen, R. (1999) From dot maps to bitmaps - Atlas Flora Europaeae goes digital. *Acta Botanica Fennica* 162
- Lechowicz, M.J. (1984) Why do temperate deciduous trees leaf out at different times? Adaptation and the ecology of forest communities. *American Naturalist* 124
- Lepais, O., Gerber, S. (2011) Reproductive patterns shape introgression dynamics and species succession within the European white oak species complex. *Evolution* 65: 156-170.
- Lorenz, M. (2010) Objectives, Strategy and Implementation of ICP Forests. Manual Part I. In: *Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests*. UNECE, ICP Forests, Hamburg.
- Magri, D., Vendramin, G.G., Comps, B., Dupanloup, I., Geburek, T., Gomory, D., Latalowa, M., Litt, T., Paule, L., Roure, J.M., Tantau, I., van der Knaap, W.O., Petit, R.J., de Beaulieu, J.L. (2006) A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytologist* 171: 199-221.
- McGlone, M.S. (1996) When history matters: scale, time, climate and tree diversity. *Global Ecology and Biogeography Letters* 5: 309-314.
- Mellert, K.H., Fensterer, V., Kuchenhoff, H., Reger, B., Kolling, C., Klemmt, H.J., Ewald, J. (2011) Hypothesis-driven species distribution models for tree species in the Bavarian Alps. *Journal of Vegetation Science* 22: 635-646.
- Meusel, H., Jäger, E., Weinert, E. (1964) Vergleichende Chorologie der zentraleuropäischen Flora – Karten, Band I. Veb Gustav Fischer Verlag, Jena.
- Ohlemüller, R., Huntley, B., Normand, S., Svenning, J.C. (2011) Potential source and sink locations for climate-driven species range shifts in Europe since the Last Glacial Maximum *Global Ecology and Biogeography* 21:152-163.
- Pigott, C.D., Huntley, J.P. (1981) Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. III. Nature and causes of seed sterility. *New Phytologist* 87: 817-839.
- R Development Core Team (2011) R 2.12.2 A language and environment.
- Rameau, J.C., Mansion, D., Dumé, G., Timbal, J., Lecointe, A., Dupont, P., Keller, R. (1989) *Flore forestière française: guide écologique illustré, 1: Plaines et collines*. Institut pour le développement forestier, Paris.
- Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters* 7: 1-15.
- Sakai, A., Weiser, C.J. (1973) Freezing resistance of trees in North-America with reference to tree regions *Ecology* 54: 118-126.
- Sakai, A., Wardle, P. (1978) Freezing resistance of New Zealand trees and shrubs. *New Zealand Journal of Ecology* 1: 51-61.
- Sakai, A., Larcher, W. (1987) *Frost survival of plants*. Responses and adaptation to freezing stress. Springer, Berlin.
- Svenning, J.-C., Skov, F. (2004) Limited filling of the potential range in European tree species. *Ecology Letters* 7: 565-573.
- Svenning, J.C., Fitzpatrick, M.C., Normand, S., Graham, C.H., Pearman, P.B., Iverson, L.R., Skov, F. (2010) Geography, topography, and history affect realized-to-potential tree species richness patterns in Europe. *Ecography* 33: 1070-1080.
- Thuiller, W., Brotons, L., Araujo, M.B., Lavorel, S. (2004) Effects of restricting environmental range of data to project current and future species distributions. *Ecography* 27: 165-172.
- Wohlgemuth, T. (1992) Die vegetationskundliche Datenbank. *Schweizerische Zeitschrift für das Forstwesen* 143: 22-35.
- Woodward, F.I. (1990) The impact of low-temperatures in controlling the geographical-distribution of plants. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 326: 585-593.
- Zimmermann, N.E., Kienast, F. (1999) Predictive mapping of alpine grasslands in Switzerland: Species versus community approach. *Journal of Vegetation Science* 10: 469-482.

Zimmermann, N.E., Yoccoz, N.G., Edwards, T.C., Meier, E.S., Thuiller, W., Guisan, A., Schmatz, D.R., Pearman, P.B. (2009) Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences of the United States of America* 106: Suppl 19723-8.

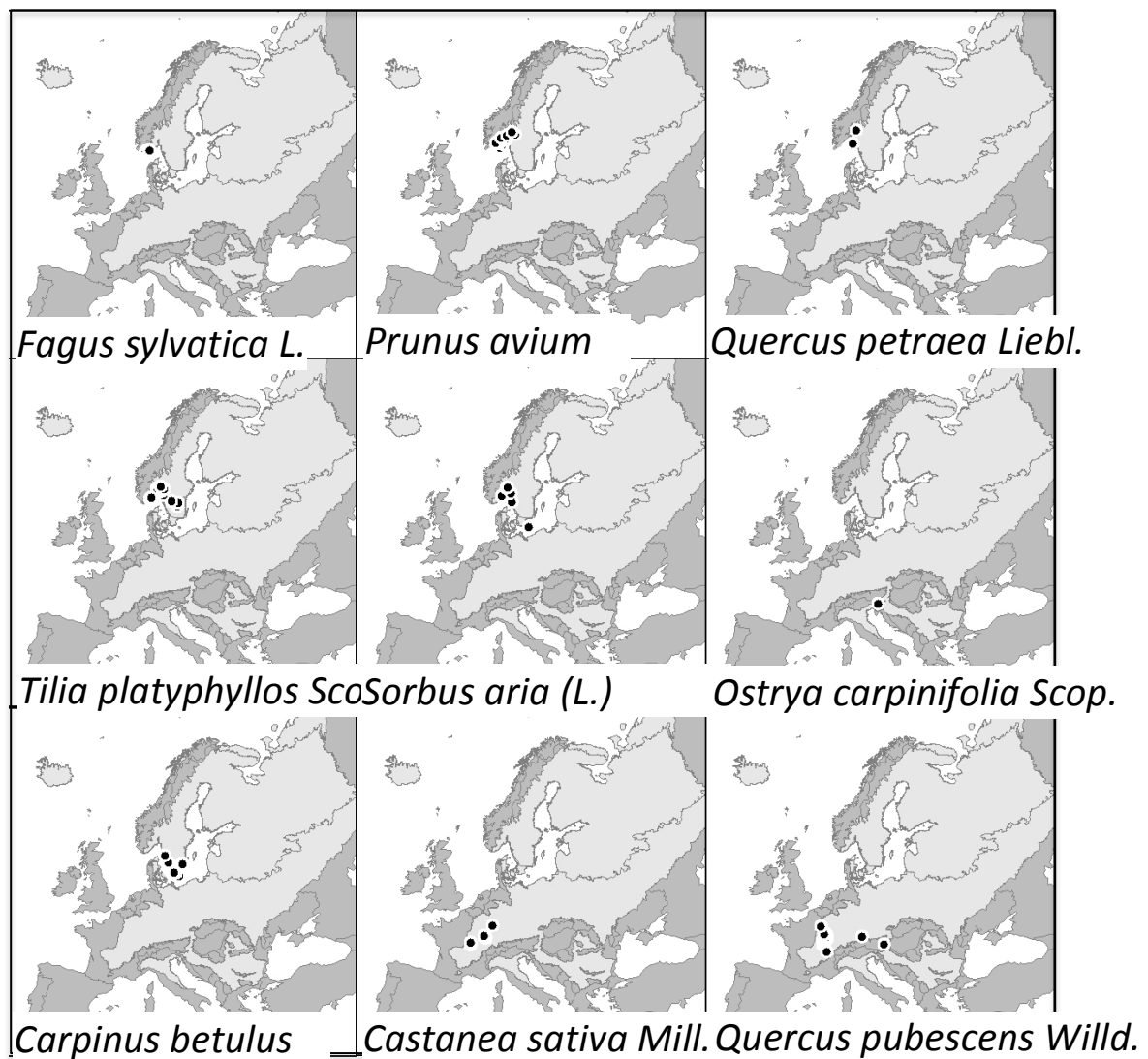
Biosketch

This study is part of the European Research Council's (ERC) TREELIM project (<http://pages.unibas.ch/botschoen/treelim/index.shtml>). Christian Körner, professor in plant ecology, is the PI of the project. Christophe Randin and Yann Vitasse are post-doctoral researchers; Chris Kollas is a PhD student. Dr. Jens Paulsen, Dr. Niklaus E. Zimmermann and Dr. Thomas Wohlgemuth are external collaborators.

Supplementary material



S1: Observation points (black dots) corresponding to the 2.5%-quantile (± 0.23 K, i.e. ± 50 m) of the thermal distance to the potential treeline. Continental, boreal and arctic biogeographic regions are represented in hell grey). Species are ranked from the smallest (*Sorbus aucuparia*) to the largest thermal distance (*Quercus pubescens*).



S1 *continued*: Observation points (black dots) corresponding to the 2.5%-quantile ($\pm 0.23 K$, i.e. $\pm 50m$) of the thermal distance to the potential treeline. Continental, boreal and arctic biogeographic regions are represented in hell grey). Species are ranked from the smallest (*Sorbus aucuparia*) to the largest thermal distance (*Quercus pubescens*).

Chapter 3

How accurate can weather stations predict temperatures at tree species limits?

Chris Kollas, Christophe F. Randin, Yann Vitasse, Christian Körner
Agricultural and Forest Meteorology, submitted

How accurate can weather stations predict temperatures at tree species limits?

Chris Kollas^{a*}, Christophe F. Randin^a, Yann Vitasse^a, Christian Körner^a

^a *Institute of Botany, University of Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland*

**Corresponding author. Tel.: +41 61 267 3506; fax: +41 61 267 2980; E-mail address: Chris.Kollas@unibas.ch*

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. The deviation between meteorological data and on-site conditions were shown to potentially exceed the extent of the worst projections of climate warming. 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 of weather station data 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 hereafter). At the time when 2-m air temperature reached its absolute monthly minimum, temperature in the top of the tree canopy was found 0.4 ± 0.1 K colder (mean \pm se, 12 sites) during growing season and 0.9 ± 0.1 K hereafter. 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.

Keywords

deciduous trees, Scandinavia, Swiss Alps, elevation gradient, temperature profile, microclimate

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 treeline (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 is 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 still 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.

First, weather stations are sparsely distributed and are often restricted to low elevation, which is critical in mountain regions. Thus, the error when predicting climate variables for higher elevation sites (e.g. where a tree species finds its upper elevational limit) is expected to increase with elevational distance. Second, due to their intrinsic structure, forests generate their own microclimate (Geiger, 2003). The structure of tree canopies affects the radiation regime and the wind profile (Van Eimern and Riedinger, 1986). The resistance of the associated aerody-

namic 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 young saplings in the understorey may experience different temperatures from both the tree canopy and standard weather station data. In addition to heat convection, radiative forcing 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).

Using a large number of temperature data loggers, we obtained data for locations where eight temperate deciduous tree species reach their upper elevational limits in the Swiss Alps (from 1165 m a.s.l to 1804 m a.s.l.) and their latitudinal limits in Sweden (from 58°18' N to 59°27' N). 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. Hence, we aim at (1) comparing the monthly mean temperature and monthly absolute minimum temperature recorded directly on trees at the species' low temperature limit with temperatures derived from weather stations; (2) at characterizing the vertical temperature profiles within forests for the same species at its elevational or latitudinal limit; and last at (3) providing correction factors for more accurate predictions of temperature from climate stations to within forest conditions.

Methods

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* L., *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 $n = 22130$ 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). Based on the

Swedish national forest inventory data (Nilsson, 2011) and explorations in the field, we identified the latitudinal limits of a subset of 4 the above mentioned species in Sweden (South Scandinavia) between Göteborg (57° 42' N, 11° 57' E) and Arvika (59° 39' N, 12° 36' E). 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 (Tab.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.

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 stem of a tall tree (d.b.h. >0.3 m) at 2 m above the ground, facing north, and hence completely shaded by the host trees canopy and stem during the growing season and by the stem only during the coldest part of the year (called hereafter on-site T_{Air}). These air temperature records were used as reference to compare with 2-m air temperature from the nearest standard weather stations. Note, in winter these forest canopies have no leaves, hence, shelter effects are small. 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 at 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

Table 1: Location and elevation of the study sites selected inside the uppermost margin of tree species distribution and coordinates of the nearest weather stations used for predictions in the three regions.

Region	Elevation (m)	Latitude	Longitude	Study site (affiliated species) / Station name
Western Swiss Alps	1374	46°8' N	7°4' E	<i>T. platyphyllos</i> , <i>Q. petraea</i>
	1460	46°11' N	6°59' E	<i>F. sylvatica</i>
	1523	46°8' N	7°4' E	<i>F. excelsior</i> , <i>P. avium</i>
	1804	46°8' N	7°4' E	<i>A. pseudoplatanus</i> , <i>S. aria</i> , <i>L. alpinum</i>
Eastern Swiss Alps	1165	46°50' N	9°35' E	<i>T. platyphyllos</i>
	1320	46°50' N	9°35' E	<i>F. excelsior</i> , <i>Q. petraea</i>
	1540	46°51' N	9°23' E	<i>F. sylvatica</i>
	1547	46°55' N	9°19' E	<i>A. pseudoplatanus</i>
South Scandinavia	159	58°21' N	12°29' E	<i>Q. petraea</i> , <i>F. sylvatica</i>
	85	58°30' N	11°57' E	<i>A. pseudoplatanus</i>
	90	58°46' N	11°48' E	<i>P. avium</i>
	83	59°1' N	12°18' E	<i>F. sylvatica</i>
Western Swiss Alps	2966	46°20' N	7°12' E	Les Diablerets
	1974	46°33' N	7°01' E	Le Moleson
	2472	45°52' N	7°10' E	Col du Grand St. Bernard
Eastern Swiss Alps	1594	46°49' N	9°51' E	Davos
	2690	46°50' N	9°48' E	Weissfluhjoch
South Scandinavia	69	59°40' N	12°38' E	Arvika
	177	59°13' N	12°4' E	Blomskog
	177	58°36' N	12°11' E	Kroppefjäll-Granán

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 or nighttime radiative cooling as such young trees are. The fourth logger was placed at the top of the tree to reflect canopy temperatures (called hereafter on-site T_{Crown}). This logger was attached to one of the uppermost lateral branches of c. 2 cm diameter, oriented south, so that this logger also could experience nighttime radiative thermal cooling but also periodic direct solar radiation. These loggers were between 6 and 14 m above ground and exposed to free atmospheric convection, laying immediately above a branch. By exposing a logger this way, we intentionally allow for violation of rules of radiation protection. In the ideal case we had tiny sensors inserted into buds or cambial tissue but this was impractical in tree tops at the geographical scale we were operating. Loggers used have similar dimensions (2,5 cm diameter), volume density (1.5 g cm⁻³) and color (grey) than the uppermost branches. Hence, we assume that by the nature of the data logger and the way we mounted it, we approximate the actual life conditions at tree tops. This assumption was tested in experiments with thin wire thermocouples and found

to conform the assumption (see Supplementary Material A). Temperature was recorded hourly from August 2009 to October 2011 in the Alps and from mid September 2010 to mid September 2011 in Scandinavia. Due to vandalism, data of 3 data logger in the Alps was available for 1 year only. Before and after this period, loggers were totally immersed in an ice-water bath for 0 °C calibration and cross-checking the sensors for identical readings. Deviations never exceeded 0.2 K, which meets the manufacturer specifications. Since we did not aim at arriving at long-term site-specific climates but rather aimed at testing correlations with nearest weather station data, the time period considered had to cover typical weather conditions of any one-year cycle. None of the sites was prone to temperature inversions.

Data analysis

Air temperature comparisons between weather station and forest climate

We first assessed the deviation between nearest weather station temperature (meteo T_{Air}) and our in situ measured 2-m air temperature (on-site T_{Air}) at all our sites. In order to demonstrate the effect of lapse rate, 3 types of lapse rates

were applied to correct weather station data for elevation: (1) the commonly used mean annual $-0.55 \text{ K } 100 \text{ m}^{-1}$ (Körner, 2007), (2) we calculated regional monthly lapse rates from weather stations at contrasting elevations for monthly mean temperature for both the Western and the Eastern Swiss Alps (linear regression model with $n = 8$ and $n = 7$ weather stations) and (3) we additionally calculated lapse rates for mean minimum temperatures by using the same data source. Notably, we found almost identical monthly lapse rates in both regions in the Alps (mean monthly sd of $\pm 0.02 \text{ K}$) when calculated with 18 years of monthly data. We therefore used the monthly mean lapse rates for both regions combined (Western and Eastern; Fig. 1) for the next step of the analysis. To underline the validity of these lapse rates for the time period used for our analysis, we also calculated short-term regional lapse rates for the years of measurements (2009-2011) using data of the same 15 weather stations.

Second, we identified the weather station that was the closest to each of our test sites (Tab. 1), excluding stations located at the bottom of the Rhône and Rhein valleys, since winter temperature inversion occurring at low elevation might bias the coherence between weather stations and our sites (Beniston and Rebetez, 1996; Bolstad et al., 1998). Next we tested the relationships between both the temperature parameters from our sites ($\text{on-site}T_{\text{Air}}$) and the corresponding nearest weather station ($\text{meteo}T_{\text{Air}}$) by calculating the coefficient of determination R^2 of the linear regression. This relationship was not used in further analysis. Instead, for every climate station used we corrected hourly temperature records by calculating the elevational difference between $\text{meteo}T_{\text{Air}}$ and $\text{on-site}T_{\text{Air}}$ and adjusting $\text{meteo}T_{\text{Air}}$ separately by (1) $-0.55 \text{ K } 100 \text{ m}^{-1}$, (2) the above mentioned mean regional monthly lapse rate and (3) the separate mean regional lapse rates for mean minimum and mean temperature for the time of measurements (09/2009-10/2011, Fig. 1). In South Scandinavia we used the regional monthly lapse rate provided by Christensen et al. (1998), although elevational differences between weather stations and sites were $<94 \text{ m}$. We did not correct weather station data for horizontal distance by latitudinal lapse

rates in South Scandinavia since weather stations were located very close to our sites (maximal horizontal distance 40 km). All adjusted weather station temperature parameters are referred hereafter as $\text{meteo}T_{\text{Air}^*}$. Third, for each site we obtained the following temperature parameter for both $\text{meteo}T_{\text{Air}^*}$ and $\text{on-site}T_{\text{Air}}$: monthly mean temperature (mean of daily means per month), monthly mean minimum temperature (mean of daily minima per month, from hourly records) and monthly absolute minimum (coldest hour of the month). Differences between altitude-corrected weather station temperature parameters and in situ measured temperature parameters ($\Delta\text{meteo}T_{\text{Air}^*-\text{on-site}T_{\text{Air}}}$, $\Delta\text{meteo}T_{\text{Air}^*-\text{on-site}T_{\text{Crown}}}$, $\Delta\text{meteo}T_{\text{Air}^*-\text{on-site}T_{\text{Ustorey}}}$) were calculated. Last, monthly values of 2 years were pooled and each temperature parameter was averaged ($n = 4$ sites) per region.

Vertical temperature profile within the forest

For each site and each month during the measurement campaign (09/2009-10/2011), we selected monthly absolute minimum temperature (coldest hour of the month) and calculated monthly mean minimum temperature (mean of daily minima per month) from $\text{on-site}T_{\text{Air}}$ (2m-air temperature within the forest) and concurrent temperatures from $\text{on-site}T_{\text{Soil}}$, $\text{on-site}T_{\text{Ustorey}}$ and $\text{on-site}T_{\text{Crown}}$. For each month and each site we then calculated the differences $\text{on-site}T_{\text{Soil}}-T_{\text{Air}}$, $\text{on-site}T_{\text{Ustorey}}-T_{\text{Air}}$ and $\text{on-site}T_{\text{Crown}}-T_{\text{Air}}$ to relate soil-, understorey- and crown-temperature to our standard 2-m air temperature. These monthly differences ($\text{on-site}\Delta T_{\text{Soil-Air}}$, $\text{on-site}\Delta T_{\text{Ustorey-Air}}$ and $\text{on-site}\Delta T_{\text{Crown-Air}}$) of 2 years were pooled and averaged for each of the three regions ($n=4$ sites per region).

To test if these differences reflect general patterns or were site specific, we explored effects of crown height, elevation, air temperature and slope exposure.

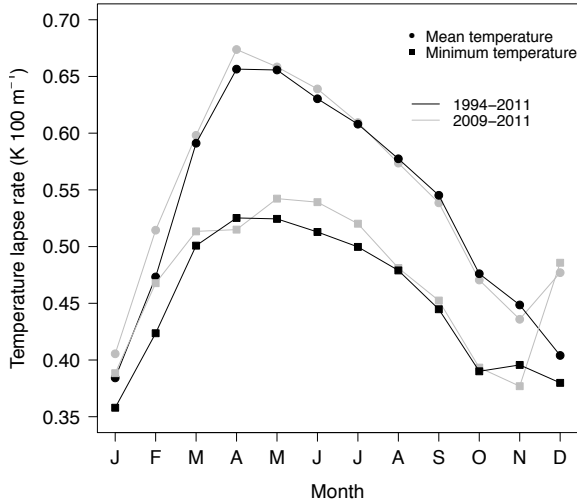


Figure 1: Seasonal variation of elevational lapse rates for mean and mean minimum temperatures, showing the long-term average (black symbols) and the study period (grey) in the Swiss Alps. Values are the mean lapse rate of both regions (Western and Eastern Swiss Alps), because data did not differ between regions ($n = 15$ weather stations).

We calculated correlations between the differences (of all 12 sites) and the site-specific parameters:

- i on-site $\Delta T_{\text{Crown-Air}}$ and crown height
- ii on-site $\Delta T_{\text{Crown-Air}}$, on-site $\Delta T_{\text{Ustorey-Air}}$, on-site $\Delta T_{\text{Soil-Air}}$ and elevation (Alps) or latitude (South Scandinavia)
- iii on-site $\Delta T_{\text{Crown-Air}}$, on-site $\Delta T_{\text{Ustorey-Air}}$, on-site $\Delta T_{\text{Soil-Air}}$ and on-site T_{Air}
- iv on-site $\Delta T_{\text{Crown-Air}}$, on-site $\Delta T_{\text{Ustorey-Air}}$, on-site $\Delta T_{\text{Soil-Air}}$ and slope exposure

The thermal growing season was defined as the period constrained by a daily mean air temperature above 5°C for more than 5 consecutive days (spring) and daily mean temperature below 5°C for more than five consecutive days (in autumn, FAO, 1978-81). This is a more constrained season compared to what might apply to evergreen conifers, and it matches a common definition applied in agriculture (Körner, 2008).

Results

Temperature lapse rates

The temperature lapse rates calculated from monthly data of 15 weather stations over 18 years showed a pronounced seasonality: rates were lowest in winter and highest in spring. Lapse rates differed widely among monthly mean and monthly mean minimum temperatures (Fig. 1), with mean temperature lapse rate having the larger seasonal amplitude. They are close to the expected moist adiabatic lapse rate ($-0.3 - -0.4 \text{ K } 100 \text{ m}^{-1}$) and comparable to those found in the Italian and Austrian Tyrol, in British Columbia and in the Appalachian Mountains (Bolstad et al., 1998; Rolland, 2003; Stahl et al., 2006). The temperature lapse rates during the study years 2009–2011 were similar to long term means as shown in Fig. 1.

Air temperature comparisons between weather station and forest climate

Over the two-year test period, we found strong linear correlations between hourly values for $\text{meteo}T_{\text{Air}}$ and $\text{on-site}T_{\text{Air}}$ for all sites, with a mean R^2 of 0.91 (range: 0.82 – 0.96). Correlations calculated separately for each month showed a minimum R^2 in January of 0.61 and a maximum value of 0.81 in November, with most values around 0.72, without any clear seasonal pattern (data not shown). Overall, we obtained higher agreement with in situ measured air temperatures within the forest when scaling $\text{meteo}T_{\text{Air}}$ by two separate month-specific lapse rates for mean and mean minimum temperature (Tab. 2). Applying these two temperature lapse rates substantially improved the predictions of most temperatures, e.g. reducing the root mean square error from 2.0 to 1.4 K in mean minima compared to applying an annual mean temperature lapse rate of $-0.55 \text{ K } 100 \text{ m}^{-1}$. However, for mean minimum temperatures, differences between $\text{meteo}T_{\text{Air}^*}$ and $\text{on-site}T_{\text{Air}}$ were slightly smaller when the annual mean lapse rate was applied (Tab. 2). Nevertheless, we used the month-specific lapse rates for mean and mean minimum temperature in all further results.

Table 2: : Results of elevation-corrections of weather station data for the Swiss Alps and South Scandinavia using 3 types of lapse rate (mean annual lapse rate, month-specific lapse rates for mean temperature and month-specific lapse rates separately for mean and mean minimum temperature). Numbers show the RMSE, Root Mean Square Error (in Kelvin) and the Bias (mean difference from actual, with direction, in Kelvin) between elevation-corrected weather station data and in situ measured forest climate (2-m air temperature) averaged over all sites in the 3 study regions (n=12 locations).

		Growing season ¹		Non-growing season		Full year	
		RMSE	Bias	RMSE	Bias	RMSE	Bias
Mean	Mean annual lapse rate	1.2	-0.9	1.1	-0.4	1.1	-0.6
	Lapse rate for mean temp. ²	0.6	-0.5	1.2	-1.0	1.0	-0.8
Mean minima	Mean annual lapse rate	1.8	-0.5	2.1	-0.1	2.0	-0.3
	Lapse rate for mean temp. ²	1.0	-0.1	1.4	-0.7	1.2	-0.4
	Lapse rate for mean minimum temp. ²	1.2	-1.1	1.5	-1.3	1.4	-1.2
Absolute minima	Mean annual lapse rate	1.9	-0.9	3.0	-1.0	2.7	-1.0
	Lapse rate for mean temp. ²	1.8	-0.4	2.9	-1.6	2.5	-1.1
	Lapse rate for mean minimum temp. ²	1.6	-1.4	2.7	-1.4	2.3	-1.4

¹Growing season refers to the months May to September

²month-specific

Minimum temperatures

In the Alps, the monthly absolute minimum temperatures (coldest hour of the month) derived from weather stations and scaled for the elevation of our test site (2 m above ground) were always colder than in situ temperatures (-1.5 to -2.5 K during the growing season, -2.5 to -4.2 K during the non-growing season; Fig. 2). Similarly, in South Scandinavia, monthly absolute minima of $\text{meteoT}_{\text{Air}^*}$ were colder than absolute minima of $\text{on-siteT}_{\text{Air}}$ (-0.5 to -2 K, except for February and December, when $\text{meteoT}_{\text{Air}^*}$ absolute minima were slightly warmer than $\text{on-siteT}_{\text{Air}}$; Fig. 2). In all regions, standard errors were smaller during the growing season (on average 0.5 K, ranging from 0.1 to 1.3 K) compared to the non-growing season (on average 0.8 K, ranging from 0.4 to 1.8 K).

Averaged across the 3 regions and all months, monthly absolute minima of $\text{meteoT}_{\text{Air}^*}$ were 1.7, 1.3 and 1.5 K colder than in situ 2-m air, crown and understory temperature, respectively, with more discrepancy in winter than during the growing season (Tab. 4). Similar to the absolute minima, monthly mean minima of $\text{meteoT}_{\text{Air}^*}$ (mean of all daily minima per month) in the Alps were colder than mean minima of $\text{on-siteT}_{\text{Air}}$ for all except one month. Although monthly mean minima show smaller deviations between $\text{meteoT}_{\text{Air}^*}$ and $\text{on-siteT}_{\text{Air}}$ than monthly absolute minima, the smaller de-

viations during the growing season were found for mean minima as well.

Mean temperatures

Differences in monthly mean temperature between $\text{meteoT}_{\text{Air}^*}$ and $\text{on-siteT}_{\text{Air}}$ were the smallest among all types of temperature measures (Fig. 2), and ranged between <2.2 K in the Alps and <1 K in South Scandinavia. As described before, smaller $\Delta\text{meteoT}_{\text{Air}^*-\text{on-siteT}_{\text{Air}}}$ was found during the growing season (Fig. 2).

In summary means and minima of weather station data scaled to on-site elevation ($\text{meteoT}_{\text{Air}^*}$) by month-specific lapse rates were almost always colder than $\text{on-siteT}_{\text{Air}}$ at 2-m height with larger differences during the non-growing season, when the deciduous tree canopy bears no foliage.

Vertical temperature profile within the forest

Temperature Profile

At both elevational and latitudinal cold limits of deciduous tree species (Alps and Scandinavia), both monthly absolute minimum and monthly mean minimum of soil temperatures were always warmer than the corresponding 2-m air

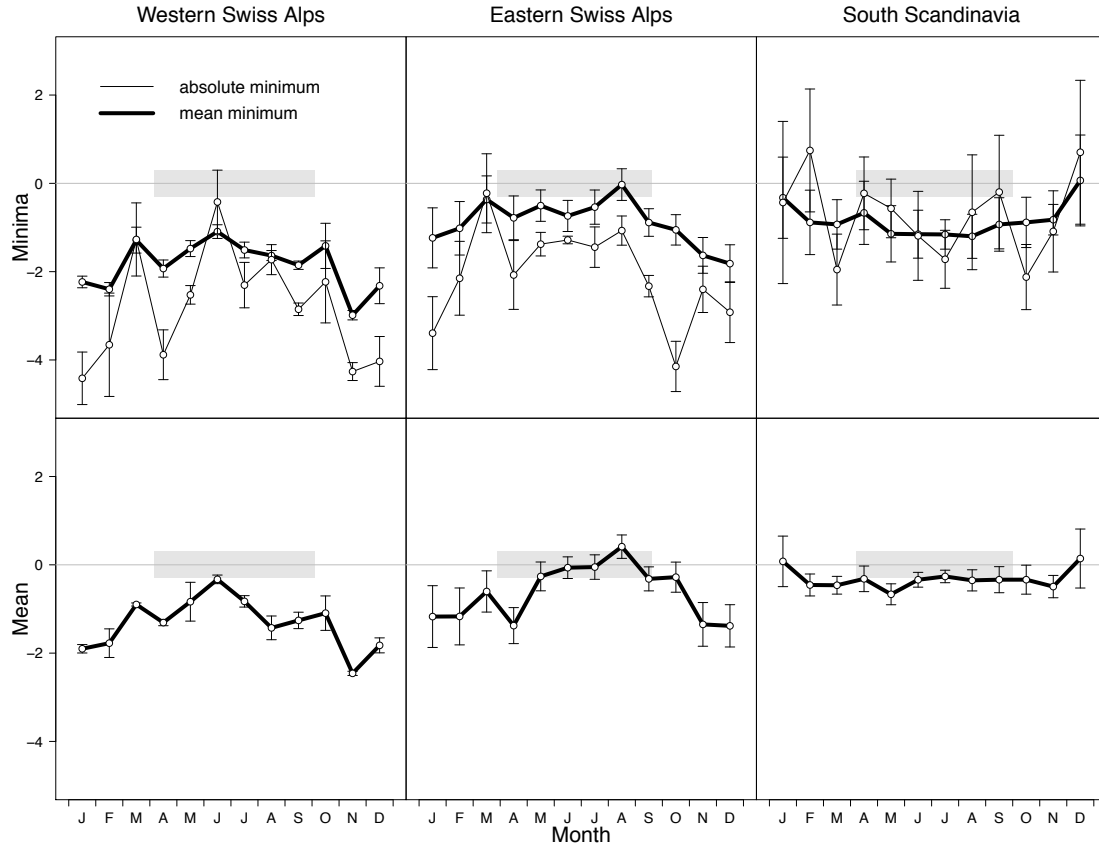


Figure 2: Seasonal variation of the deviation of in situ forest air temperature ($\text{onsite}T_{\text{Air}}$) from closest weather station data ($\text{meteo}T_{\text{Air}}$) corrected for elevational difference by month-specific lapse rates (for details see section Methods). Negative values indicate lower temperatures predicted from weather station data than those measured in situ. Error bars denote standard errors of 4 sites per region. Horizontal grey bars represent the mean duration of the thermal growing season.

temperature. They showed a seasonal pattern that reflects insulating snow cover effects in winter. Monthly absolute minima of soil temperature were on average 8.4 K (ranging from 4.2 to 15.1 K in the Alps) and 8.5 K (0 to 20.9 K in Scandinavia; Fig. 3) warmer than the corresponding 2-m air temperature.

Crown temperatures were always colder than 2-m air temperatures when these reached their monthly absolute minimum in the Alps, except in July in the Western Alps (Fig. 3), and this difference was smaller during the growing season (-0.1 to -0.6 K) than during the non-growing season, -0.6 to -1.8 K. Similarly, crown temperatures in South Scandinavia were always colder than 2-m air temperatures, when these reached their monthly absolute minimum (-0.1 to -1.7 K), with the strongest deviations occurring in spring and autumn. For all understory air temperature measurements we found that devices

had been installed above snow cover.

Surprisingly, understory minimum temperatures were also colder than 2-m air temperature, and (with few exceptions) differences showed the same seasonal pattern, but with lower amplitude than in the top canopy (Table 3). Temperatures in the understory and concurrent to 2-m air absolute minimum temperatures were closer during the growing season (+0.2 to -0.3 K) but the understory was markedly cooler during the non-growing season (0.4 to 0.6 K in the Alps). In South Scandinavia, understory temperatures were on average 0.4 K cooler than 2-m air temperatures when these reached their absolute monthly minimum.

Interestingly, in all regions, strongest negative temperature deviations in the understory occurred at the beginning and at the end of the growing period, where absolute minima are most critical for plant physiology (on average -0.7 K).

Table 3: Understorey and crown temperature deviations (on-site T_{Ustorey} , on-site T_{Crown} , in K) from 2-m air temperature (on-site T_{Air}) in the forest during the growing season, the non-growing season and the whole year. Temperature deviations are shown for monthly absolute minimum and monthly mean minimum temperatures. Numbers show the mean of data for 4 sites per region.

		Western Swiss Alps			Eastern Swiss Alps			South Scandinavia		
		Grow. season ¹	Non-grow. season	Full year	Grow. season	Non-grow. season	Full year	Grow. season	Non-grow. season	Full year
$\Delta\text{on-site}T_{\text{Crown}}-\text{on-site}T_{\text{Air}}$	Abs. min.	-0.3	-1.0	-0.7	-0.6	-1.1	-0.9	-0.3	-0.7	-0.6
	Mean min.	-0.5	-0.6	-0.6	-0.6	-0.8	-0.7	-0.1	-0.3	-0.2
$\Delta\text{on-site}T_{\text{Ustorey}}-\text{on-site}T_{\text{Air}}$	Abs. min.	0.2	-0.4	-0.2	-0.3	-0.6	-0.5	-0.2	-0.4	-0.4
	Mean min.	-0.3	-0.5	-0.4	-0.5	-0.6	-0.6	-0.4	-0.5	-0.5

¹Growing season refers to the months May to September

Effect of local topography on the vertical temperature profile

The above temperature profiles (temperature differences) were neither correlated with elevation (Alps) nor with latitude (South Scandinavia), nor had slope exposure or canopy height any influence (data not shown). Hence the patterns observed are robust across all 12 sites against local conditions as long as there was a near to closed deciduous forest stand. An exception are soil temperatures that became decoupled from atmospheric conditions under snow, an effect that increased with elevation because of increasing snow duration.

Discussion

Characterizing and predicting the position of the cold limit of tree species requires temperature data that reflects the current proximal life conditions of trees. Here we explored how to adequately infer temperature at forest sites located on mountain slopes in the Alps and in the lowlands of South Scandinavia by using weather stations and regional month-specific lapse rates. We showed that the temperature lapse rates differ consistently between means and extremes of temperature with the one calculated on mean temperatures being higher. We further showed that monthly absolute minimum air temperatures from lapse rate scaled meteorological data are systematically colder than temperatures measured 2-m above ground within the forest (-1.4 ± 0.2 K during growing season, -2.0 ± 0.2 during non-growing season; mean \pm

se). Furthermore, both top canopy and understorey monthly absolute minimum temperatures were cooler than 2-m air temperature across all sites and seasons (crown 0.4 ± 0.1 K cooler during growing season, 0.9 ± 0.1 K cooler hereafter). We largely attributed these cooler temperatures to radiative cooling occurring during clear nights.

Vertical temperature profile within the forest

In the crown and in the understorey we found monthly absolute minimum temperatures from 0.5 to 1.7 K colder than 2-m air temperatures and attributed these to radiative cooling. These rates of cooling are consistent with findings of 1-3 K radiative cooling in leaves of *Eucalyptus spp.* after sunset (Leuning and Cremer, 1988). In a beech forest, similar temperature deviations between 2-m air and understorey (0.2 m height) were found (0.5 K cooler during growing season, 2 K cooler hereafter; Van Eimern and Riedinger, 1986). Here, we attribute smaller deviations between 2-m air temperature and crown/understorey temperature during growing season compared to non-growing season to the presence of foliage that constrains radiation. Thus, when the critical role of absolute minima comes into play, the vertical position within the forest is of importance: the risk of freezing (for e.g. buds) increases from 2-m air temperature within the forest towards the understorey and crown level, and the magnitude of these differences corresponds to ca. 100-300 m of elevation or 70-250 km of latitude depending on month.

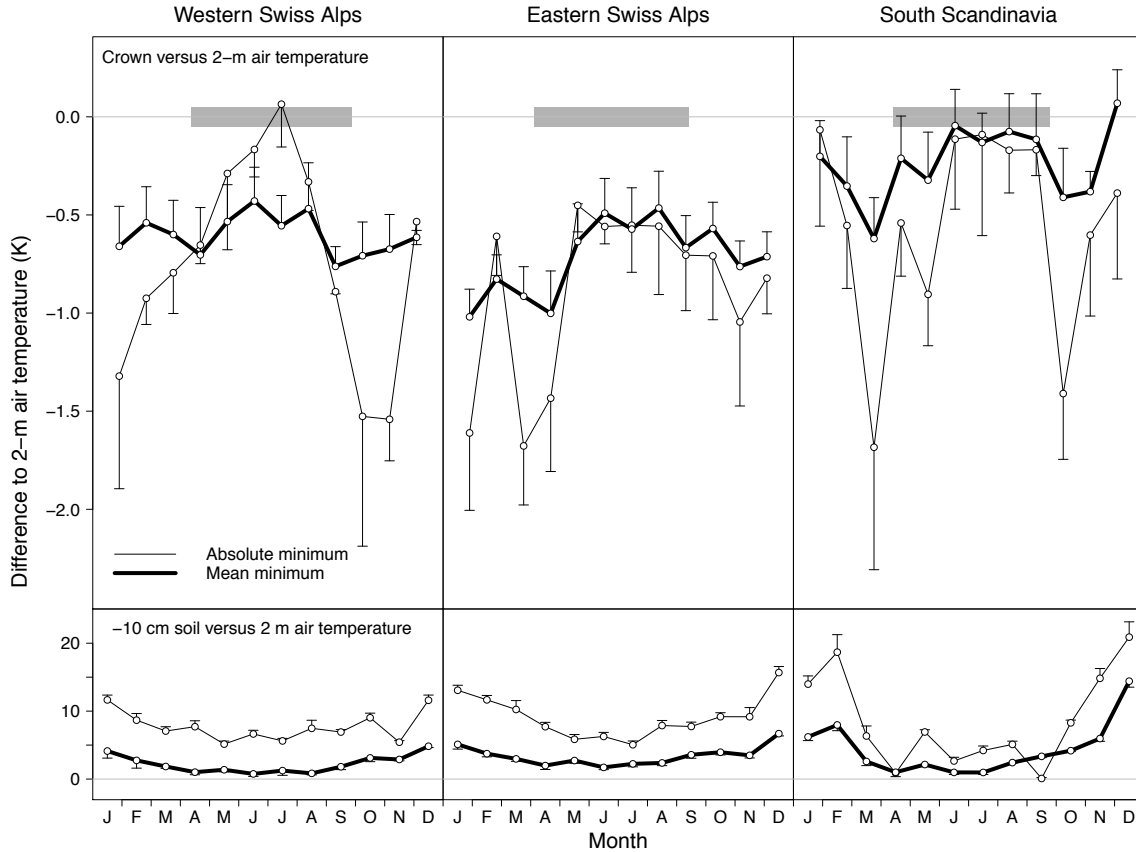


Figure 3: . In situ monthly absolute and mean minimum temperature deviations of crown and 10 cm soil temperature from air temperature at 2-m above ground. Error bars denote standard errors of 4 sites per region. Horizontal grey bars represent the mean duration of the thermal growing season. In the majority of cases crown top is cooler than the local 2-m air temperature inside the deciduous forest.

Air temperature comparisons between weather station and forest climate

The observed temperature differences between lapse rate scaled weather station data and within-forest measurements originated from two sources: (1) scaling data from a weather station across a topographically diverse landscape and (2) the forests intrinsic microclimate. Furthermore, a third and large source of deviation would arise when using geographic climatic layers instead of weather station data, as is done in many studies using correlative approaches to describe species distribution. In the following we discuss each of the three points.

Elevation-correction of weather station data

Although, elevational lapse rates of temperature are known to fluctuate seasonally, diurnally and regionally (Blandford et al., 2008; Pepin and Kidd, 2006; Richardson et al., 2004),

mean annual adiabatic lapse rates of typically -0.55 K per 100 m of elevation are still widely used for elevation-correction of weather station data. Here, we demonstrated that using a seasonal lapse rate derived from a set of regional weather stations improved the scaling from a single weather station. Subsequently, applying regional and seasonal lapse rates separately for mean temperature and mean minimum temperature improved the elevation-correction of weather station data even further. Since lapse rates built on a daily basis were shown to vary strongly within a single month (e.g. from -0.6 to $+0.8$ K 100 m $^{-1}$; Blandford et al., 2008), we suggest that a part of the remaining temperature difference between lapse rate scaled weather station data and within-forest measurements was due to the day-to-day variation of the lapse rate.

We assume that the larger temperature mismatches found during the non-growing season are explained by irregular snow cover along our test sites affecting ground albedo which could

Table 4: Deviations of monthly absolute minimum temperature (in K) measured by weather stations and corrected for elevation ($\text{meteoT}_{\text{Air}^*}$) from in situ measurements of 2-m air ($\text{on-siteT}_{\text{Air}}$), crown ($\text{on-siteT}_{\text{Crown}}$) and understorey ($\text{on-siteT}_{\text{Ustorey}}$) temperatures: Means and standard errors across all 12 sites, for the growing season, the non-growing season and the whole year. In all cases lapse rate corrected weather station temperatures are cooler than actual in situ temperatures.

	Growing season ¹	Non-growing season	Full year
$\Delta\text{meteoT}_{\text{Air}}-\text{on-siteT}_{\text{Air}}$	-1.4 ± 0.2	-2.0 ± 0.2	-1.7 ± 0.2
$\Delta\text{meteoT}_{\text{Air}}-\text{on-siteT}_{\text{Crown}}$	-1.0 ± 0.1	-1.6 ± 0.2	-1.3 ± 0.1
$\Delta\text{meteoT}_{\text{Air}}-\text{on-siteT}_{\text{Ustorey}}$	-1.1 ± 0.2	-1.8 ± 0.3	-1.5 ± 0.2

¹Growing season refers to the months May to September

bias the strict elevational temperature decrease applied in our lapse rate approach. Similarly, Rolland (2003) showed, by using a multitude of weather stations throughout the Alps, that the correlation coefficient between temperature and elevation decreases during winter months. Nevertheless, our results demonstrate that the temperature lapse rates calculated here (15 weather stations and nearly two decades of monthly data) provide a robust base for the elevation-correction of air temperature in mountainous regions, such as the Alps. Since the month-specific lapse rates for West and East Switzerland (ca. 200 km apart) were the same, the means obtained may have wider applicability. Hence, we conclude that the remaining part of the temperature mismatch between lapse rate scaled weather station data and on-site air temperature likely arose from intrinsic microclimatic effects of forests.

Forests microclimate

It is well known that forest canopies screen thermal radiative losses at night, hence daily absolute minimum temperatures inside the forest are warmer compared to open field conditions (Geiger, 2003). In deciduous forests, the moderating effect is obviously stronger during growing season. For monthly mean minima, the effect was shown to range from 0.5 to 3.2 K (Carlson and Groot, 1997; Müttrich, 1890; Renaud and Rebetez, 2009; Suggitt et al., 2011) and thus, may likely contribute to the temperature mismatch calculated here (0.1 to 2.1 K in monthly mean minima, Fig. 2).

Spatial and temporal resolution of temperature records

Averaged air temperatures have recently been employed in assessments of climate change impact on the distribution of a large number of species (e.g. Dirnbock et al., 2011; Engler et al., 2011), sometimes under the assumption that these averaged temperatures are proxies for extremes. Our data clearly show that such inferences bear a risk of substantial geographical mismatch with actual temperatures. Here two examples. First, we tested the agreement between temperature data of the WorldClim dataset (that offers a spatial resolution of 30 arc s, corresponding to ca. 1 km in temperate latitudes; Hijmans et al., 2005) with records from weather stations. Thus, we calculated differences between monthly mean temperature (1950-2000) recorded at weather stations and reported by WorldClim (where WorldClim grid cells overlay the weather station location in both study regions in the Swiss Alps, $n=8$, from 482 m to 2966 m a.s.l.). The matching of a grid cell with a weather station is not necessarily at exactly the same elevation. Notably, long-term monthly mean temperatures of WorldClim data - that is based on weather station data - were found to deviate by on average 0.5 K (mean absolute error) from weather station temperatures in the Swiss Alps, a region with a comparatively dense network of stations. At an assumed annual mean lapse rate of the altitudinal reduction of temperature of $-0.55 \text{ K } 100 \text{ m}^{-1}$ this difference corresponds to nearly $\pm 100 \text{ m}$ of elevation. Second, we explored deviations related to the temporal resolution. For each month (1981-2010) and each weather station in the two examined

regions ($n=15$, from 381 m to 2966 m a.s.l.), we calculated the following temperature differences per weather station: monthly mean temperature versus monthly absolute minimum temperature and monthly mean minimum temperature versus monthly absolute minimum temperature. In general the monthly absolute minimum was 5 to 15 K cooler than monthly mean temperature (5 % quantile from 15 to 23 K colder) and 2 to 12 K cooler than monthly mean minimum temperatures (5 % quantile from 12 to 18 K cooler, no influence of elevation). Hence, data sources of coarse spatial and/or temporal resolution contain no biologically relevant information when low temperature extremes control species ranges. Given the critical role of minimum temperatures for species range limits (Sakai and Larcher, 1987), even small temperature discrepancies could be extremely effective physiologically: The discrepancy found here between predicted and actual absolute minimum temperatures at forest canopy level was -1.9 K in spring. For *Sorbus aucuparia* growing at the timberline, such a temperature range covers locations with no to full freezing damage of expanding shoots in spring (Taschler et al. 2004; -5 to -7 °C). Thus, the use of smoothed meteorological proxy data is likely to miss physiological range limits of species to an extent similar to the warming scenarios expected for this century. Here we offer variance terms (probabilities of temperature deviations from means) that may assist in more realistic projections.

Conclusions

The use of regional, month-specific temperature lapse rates, separated for mean temperatures and mean minimum temperatures, improves scaling from weather station temperature to in situ temperatures in deciduous forests. Extreme temperatures such as monthly absolute minima measured under standard (2-m air) conditions in weather stations are on average 1.4 ± 0.2 K (mean \pm se) colder than temperatures measured within broad-leaved forests at 2-m height during growing season, despite correction for elevation (-2.0 ± 0.2 K during non-growing season). During growing season absolute minimum temperatures in the tree crowns are on average 0.4 ± 0.1 K colder than 2-m air

temperature measured inside the forest (0.9 ± 0.1 K colder during non-growing season). These deviations of tree life conditions from meteorological data correspond to >230 m of elevation or >180 km of latitude and need to be taken into account when describing species range limits on a mechanistic basis because the climatic factors decisive for shaping species limits are likely to operate on fine spatial and temporal scales.

Acknowledgements

We thank Niklaus Zimmermann and Thomas Wohlgemuth for their advice on high elevation broad-leaved tree positions in Switzerland and Dr. Jean-Pierre Randin for housing and help during the field campaigns. This work was supported by the European Research Council (advanced grant no. 233399) and was carried out as part of the TREELIM project.

References

- Beniston, M. and Rebetez, M., 1996. Regional behavior of minimum temperatures in Switzerland for the period 1979-1993. *Theoretical and Applied Climatology* 53: 231-243
- Blandford, T.R., Humes, K.S., Harshburger, B.J., Moore, B.C., Walden, V.P. and Ye, H.C., 2008. Seasonal and synoptic variations in near-surface air temperature lapse rates in a mountainous basin. *Journal of Applied Meteorology* 47: 249-261
- Bolstad, P.V., Swift, L., Collins, F. and Regniere, J., 1998. Measured and predicted air temperatures at basin to regional scales in the southern Appalachian mountains. *Agricultural and Forest Meteorology* 91: 161-176
- Carlson, D.W. and Groot, A., 1997. Microclimate of clear-cut, forest interior, and small openings in trembling aspen forest. *Agricultural and Forest Meteorology* 87:313-329
- Christensen, O.B., Christensen, J.H., Machenhauer, B. and Botzet, M., 1998. Very high-resolution regional climate simulations over Scandinavia - Present climate. *Journal of Climate* 11:3204-3229
- Dirnbock, T., Essl, F. and Rabitsch, W., 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology* 17: 990-996
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. and Mearns, L.O., 2000. Climate extremes: Observations, modeling, and impacts. *Science* 289:2068-2074.

- Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araujo, M.B., Pearman, P.B., Le Lay, G., Piedallu, C., Albert, C.H., Choler, P., Coldea, G., De Lamo, X., Dirnbock, T., Gegout, J.C., Gomez-Garcia, D., Grytnes, J.A., Heegaard, E., Hoistad, F., Nogues-Bravo, D., Normand, S., Puscas, M., Sebastia, M.T., Stanisci, A., Theurillat, J.P., Trivedi, M.R., Vittoz, P. and Guisan, A., 2011. 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology* 17:2330-2341
- FAO, 1978-81. Reports of the Agro-Ecological Zones Project. World Soil Resour. Rep., 48 Vols. 1 - Methodology and Results for Africa; 2 - South-west Asia; 3 - South and Central America; 4 - South-east Asia., Food and Agriculture Organization, Rome.
- Geiger, R., Aron, R. H., Todhunter, P., 2003. *The climate near the Ground*. Rowman & Littlefield Publishers, Inc., Maryland.
- Graae, B.J., De Frenne, P., Kolb, A., Brunet, J., Chabrierie, O., Verheyen, K., Pepin, N., Heinken, T., Zobel, M., Shevtsova, A., Nijs, I. and Milbau, A., 2012. On the use of weather data in ecological studies along altitudinal and latitudinal gradients. *Oikos* 121: 3-19
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. and Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965-1978
- Jones, H.G., 1992. *Plants and Microclimate*. Cambridge University Press, Cambridge.
- Körner, C., 2007. The use of 'altitude' in ecological research. *Trends in Ecology & Evolution* 22: 569-574
- Körner, C., 2008. Winter crop growth at low temperature may hold the answer for alpine treeline formation. *Plant Ecology & Diversity* 1: 3-11
- Körner, C., 2012. *Alpine treelines*. Springer, Basel.
- Körner, C. and Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*. 31: 713-732
- Larcher, W., 1975. *Physiological plant ecology*. Springer-Verlag.
- Leuning, R. and Cremer, K.W., 1988. Leaf Temperatures during Radiation Frost .1. Observations. *Agricultural and Forest Meteorology* 42: 121-133
- Mitchell, T., Carter, T.R., Jones, P.G. and Hulme, M., 2004. *A comprehensive set of high-resolution grids of monthly climate for Europe and the globe*, Tyndall Centre.
- Müttrich, A., 1890. Über den Einfluss des Waldes auf die periodischen Veränderungen der Lufttemperatur. *Zeitschrift für Forst- und Jagdwesen* 22:385-526
- New, M., Lister, D., Hulme, M. and Makin, I., 2002. A high-resolution data set of surface climate over global land areas. *Climate Research* 21:1-25
- Nilsson, P., Cory, N., 2011. *Forestry statistics 2011*. SLU, Umeå.
- Parmesan, C., Root, T.L. and Willig, M.R., 2000. Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society* 81:443-450
- Pepin, N. and Kidd, D., 2006. Spatial temperature variation in the Eastern Pyrenees. *Weather* 61:300-310.
- Randin, C.F., Engler, R., Normand, S., Zappa, M., Zimmermann, N.E., Pearman, P.B., Vittoz, P., Thuiller, W. and Guisan, A., 2009. Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology* 15:1557-1566
- Renaud, V. and Rebetez, M., 2009. Comparison between open-site and below-canopy climatic conditions in Switzerland during the exceptionally hot summer of 2003. *Agricultural and Forest Meteorology* 149:873-880.
- Richardson, A.D., Lee, X. and Friedland, A.J., 2004. Microclimatology of treeline spruce-fir forests in mountains of the northeastern United States. *Agricultural and Forest Meteorology* 125: 53-66.
- Rolland, C., 2003. Spatial and seasonal variations of air temperature lapse rates in Alpine regions. *Journal of Climate* 16:1032-1046
- Sakai, A. and Larcher, W., 1987. *Frost survival of plants: Responses and adaptation to freezing stress*, 62. Springer, Berlin.
- Scherrer, D., Schmid, S. and Korner, C., 2011. Elevational species shifts in a warmer climate are overestimated when based on weather station data. *International Journal of Biometeorology* 55:645-654
- Stahl, K., Moore, R.D., Floyer, J.A., Asplin, M.G. and McKendry, I.G., 2006. Comparison of approaches for spatial interpolation of daily air temperature in a large region with complex topography and highly variable station density. *Agricultural and Forest Meteorology* 139:224-236
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S. and Lima, M., 2002. Ecological effects of climate fluctuations. *Science* 297:1292-1296
- Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B. and Thomas, C.D., 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* 120:1-8
- Till, O., 1956. Über die Frosthärte von Pflanzen sommergrüner Laubwälder. *Flora - Allgemeine Botanische Zeitung* 143.
- Van Eimern, J. and Riedinger, F.P., 1986. Zur vertikalen verteilung der luft- und pflanzentemperatur in einem buchenhochwald, besonders im kronenraum. *Agricultural and Forest Meteorology* 38: 27-45
- Vitasse, Y., Hoch, G., Randin, C.F., Lenz, A., Kollas, C. and Körner, C., 2012. Tree recruitment of

European tree species at their current upper elevational limits in the Swiss Alps. *Journal of Biogeography* 1-11

Von Humboldt, A. and Bonpland, A., 1807. *Ideen zu einer Geographie der Pflanzen nebst einem Naturgemälde der Tropenländer*. Cotta, Tübingen.

Wohlgemuth, T., 1992. Die vegetationskundliche Datenbank. *Schweizerische Zeitschrift für das Forstwesen* 143:22-35

Woodward, F.I., 1987. *Climate and plant distribution*. Cambridge studies in ecology. Cambridge University Press, Cambridge.

Zimmermann, N.E., Yoccoz, N.G., Edwards, T.C., Meier, E.S., Thuiller, W., Guisan, A., Schmatz, D.R. and Pearman, P.B., 2009. Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences of the United States of America* 106:19723-19728

Role of the funding source

The funding source had no role in study design, data collection, data analysis, data interpretation, writing of the article or decision to submit the article for publication.

Supplementary material

Radiative cooling of tree branch

Background

It is well known that trees' branches, leaves and buds, as any other object, may cool below surrounding air temperature under clear-sky and calm night conditions due to radiative cooling. We conducted an experiment in order to check whether the data loggers used for understory and crown temperature in the present study approximate the temperature experienced by branches under these specific conditions.

Method

Three temperature sensors were installed as following: a thin wire thermocouple sensor was introduced into the cambium (called hereafter T_{cam}) of a freshly cropped branch of *Fagus sylvatica* (2.7 cm diameter, c. 50 cm length), a TidBit Datalogger (TidbiT v2 Temp UTBI-001, Onset Computer Corporation) was positioned on top of a second branch (T_{top}), and a third (T_{air}) was installed under a ventilated plastic screen nearby. This latter logger was used as a control (air temperature). Branches were then horizontally fixed and exposed to clear sky radiative

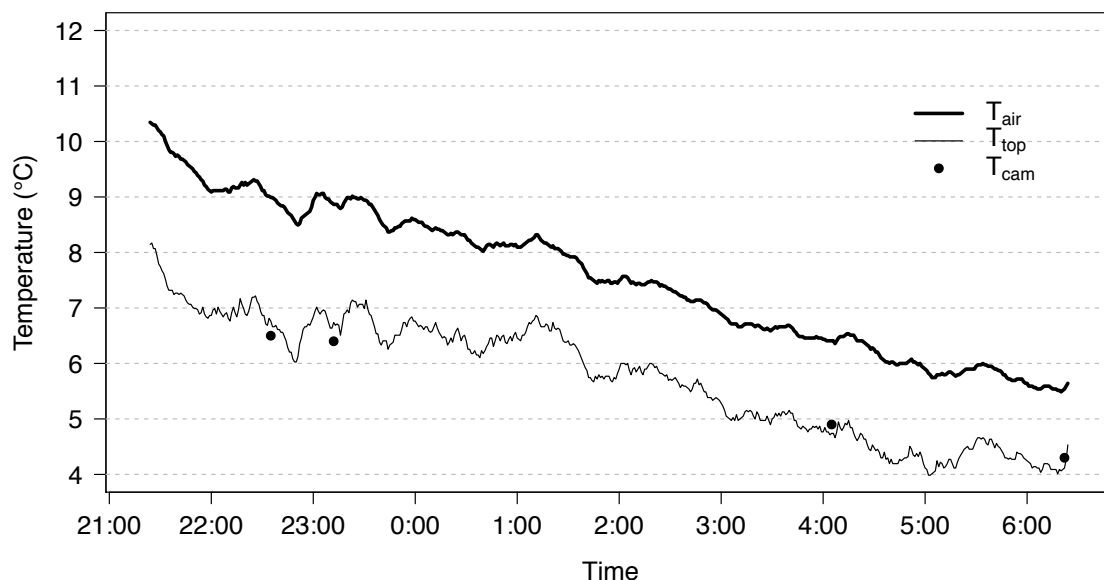
cooling for two nights in March 2012 (total 6 measurements of each of the three devices between 9:30 pm and 6:30 am, on 01.03.2012 and 16.3.2012, Basel, Switzerland). Mean and maximal temperature differences of $T_{\text{top}} - T_{\text{cam}}$, $T_{\text{cam}} - T_{\text{air}}$ and $T_{\text{top}} - T_{\text{air}}$ were calculated.

Results

T_{top} , T_{cam} and T_{air} decreased steadily during night (Fig. S1). T_{cam} and T_{top} were colder than T_{air} , due to the effect of radiative cooling (ΔT -1.3 K, Table S2) but the branch and the logger attached to it showed very similar temperatures (mean $\Delta T_{\text{top}} - T_{\text{cam}} = -0.2$ K, maximum difference $\Delta T_{\text{top}} - T_{\text{cam}} = -0.5$ K, Table S1).

S2: Differences between temperatures recorded in the air (T_{air}), in the cambium (T_{cam}) and on top of the branch (T_{top})

	Mean (K)	Maximum difference (K)
$\Delta T_{\text{top}} - T_{\text{cam}}$	-0.2	0.5
$\Delta T_{\text{cam}} - T_{\text{air}}$	-1.2	2.5
$\Delta T_{\text{top}} - T_{\text{air}}$	-1.4	2.2



S1: Temperature recorded during a clear-sky night (15.-16.03.2012) in Basel (Switzerland) for a screened position (T_{air}), for a temperature logger of ca. 2.5 cm diameter (TidBit) exposed to radiative cooling on top of a branch (T_{top}) and concurrent cambium temperature (T_{cam}) measured with thermocouples inserted into a 2.7 cm diameter piece of branch.

Chapter 4

Critical temperatures determining the elevational and latitudinal range limits of European broad-leaved trees

Chris Kollas, Christophe F. Randin, Christian Körner,
Journal of Biogeography, submitted

Critical temperatures determining the elevational and latitudinal range limits of European broad-leaved trees

Chris Kollas^{*1}, Christian Körner¹, Christophe F. Randin¹

**Corresponding author, Tel.: +41 61 267 3506; fax: +41 61 267 2980; E-mail address: Chris.Kollas@unibas.ch*

¹Institute of Botany, University of Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland

Summary

Aim The aim of this study was to test which facet of temperature is most closely associated with the cold elevational and latitudinal limits of seven European broad-leaved tree species. We compared three temperature-related potential constraints across three study regions: (1) absolute minimum temperature within 100 years, (2) lowest temperatures during the period of bud-break and (3) length and temperature of the growing season.

Location Western and Eastern Swiss Alps (1165-2160 m a.s.l.) and Southern Sweden (57°N – 59°N)

Methods *In situ* temperature was recorded at the cold elevational and latitudinal limits of seven broad-leaved tree species and correlated with temperatures at the nearest weather stations, to reconstruct the past 50 years' temperature regime. Applying generalized extreme value distribution theory, we estimated the return periods of absolute minimum temperature within 100 years.

Results At their high elevation limits, five out of seven examined tree species experienced winter minimum temperatures considerably warmer than their known maximum freezing resistance in winter. In four species (for which phenological data was available) we found potentially deleterious temperatures at both limits in late spring during the period of bud-break. Three out of five species showed similar length of growing season at their elevational and latitudinal limits. The mean temperature during the growing season was always warmer at species latitudinal limits compared to their elevational limits.

Main conclusions Low temperature extremes in spring occurring during bud break are the most likely candidates controlling broad-leaved trees species' elevational and latitudinal limits. Absolute minimum temperature in winter and the mean temperature during the growing season are unlikely constraining species cold limits. Thus, the results call for the use of high-resolution (hourly) temperature data during key phenological stages when using correlative approaches (such as species distribution models) to infer range shifts of broad-leaved trees.

Keywords absolute minimum temperature, bud-break, deciduous trees, freezing resistance, growing season, leading edge, LT50, Sweden, Swiss Alps

Introduction

For predicting species potential range shifts in response to a warmer climate, it will be decisive to know which particular facet of temperature constrains the current cold species limits and to abandon the assumption that mean annual temperature relates to species limits. In a recent review, Austin & Van Niel (2011) pointed at the inconsistent relationship between species distribution and the commonly-used parameters that are supposed to control range limits in species distribution modeling (hereafter SDM). So far, numerous SDM studies on plant species have relied on long-term averaged climate variables to define range limits although it has been shown that using extremes improves predictions for tree species (Zimmermann et al. 2009). There is thus, an urgent need to identify the effective facet of temperature that constrains range limits of plant species.

Both the upper elevational and northern latitudinal limit of broad-leaved tree species that do not reach the treeline are likely controlled by temperature-related drivers (Sakai & Larcher, 1987; Woodward, 1987). However, the mechanisms controlling these tree species limits are not exactly known. While the response of tree growth to changes in temperature is well understood (Tranquillini, 1979; Way & Oren, 2010), it still remains uncertain which expression of temperature at which phenological stage controls the species-specific cold limits.

All tree species of temperate and boreal regions modify their organ-specific resistance to freezing temperatures according to the seasonal course of temperature. Exceptionally low temperature extremes can, however, severely damage plant tissue. Mid-winter hardiness may shape the northern distributional limits (Sakai & Weiser, 1973; Woodward, 1987) when absolute minima of temperature are injuring buds or dormant meristems in adults or eradicate young cohorts at the expanding edge of marginal populations. A more likely scenario are damages while plants acclimate and de-acclimate to/from cold temperature (Sakai & Weiser, 1973; Sakai & Wardle, 1978), that is during the transition periods from a dormant to an active stage (at bud-break) and from an active to a dormant stage (at leaf-fall). Temperatures of only 3 ± 1 °C were shown to kill leaves and flowers of most

European broad-leaved tree species shortly after bud-break when leaves flush and are not yet fully developed (Till, 1956). A restricted length of the growing season may exert another constraint for trees at their cold limits. Short seasons may cause failure of seed maturation (Pigott & Huntley, 1981; Chuine, 2010) seedling establishment (Jump et al., 2007), or late wood formation and in general may prevent maturation.

All these potential low-temperature thresholds call for rather specific measures of temperature such as absolute minima or means for certain critical developmental stages. Annual or monthly mean temperature could have little or even no predictive value, except where such temperatures are auto-correlated with more specific threshold-temperatures by coincidence. SDMs commonly rely on geographic climatic layers (e.g. Sykes et al., 1996; Montoya et al., 2009; Meier et al., 2010). These layers (e.g. WorldClim; Hijmans et al., 2005) are (1) based on long-term averages and are (2) provided in coarse spatial resolution, that both can diverge massively from the life conditions experienced by plants (Randin et al., 2009; Scherrer & Körner, 2010; Kollas et al., submitted).

In this study, we aimed at identifying critical temperature attributes associated with the low temperature range limit of seven European broad-leaved tree species. More specifically, we focused on three facets of temperature: (1) absolute minimum temperature, (2) lowest temperatures during the time period of bud-break and (3) the length and mean temperature of the growing season.

For this, we linked *in situ* measured temperatures to weather stations to reconstruct temperature parameters over the last 50 years and to predict absolute minimum temperatures by applying generalized extreme value distribution theory. We then compared the three potential limiting facets of temperature (1) across species' elevational and latitudinal limits and (2) with literature-derived frost resistance data.

Methods

Study area, study species and in situ measurements

We first selected seven widely distributed deciduous tree species: *Acer pseudoplatanus* L., *Fa-*

gus sylvatica L., *Fraxinus excelsior* L., *Prunus avium*, *Quercus petraea* (Matt.) Liebl., *Tilia platyphyllos* Scop. and *Sorbus aucuparia* L. We then extracted occurrences of these species from the Swiss National Forest Inventory (NFI, two inventory periods: 1983–1985 and 1995–1997, regular 1-km and 1.4-km grid, respectively). Additional tree occurrences in Switzerland were derived from a forest plots database from Wohlgenuth (1992). This database allowed us to identify the highest elevation reached for each study species. All nine taxa reached their highest elevation either in one or both of the following two regions in Switzerland: one in the Western Alps (West) near Martigny ($46^{\circ} 6' \text{ N}$, $7^{\circ} 4' \text{ E}$) and the other in the Eastern Alps (East) near Chur ($46^{\circ} 51' \text{ N}$, $9^{\circ} 32' \text{ E}$; Fig. 1). Based on the Swedish national forest inventory data (Nilsson, 2011) and our own explorations in the field, we identified the latitudinal limits of a subset of five species in Sweden (North) between Göteborg ($57^{\circ} 42' \text{ N}$, $11^{\circ} 57' \text{ E}$) and Arvika ($59^{\circ} 39' \text{ N}$, $12^{\circ} 36' \text{ E}$). For each species, we selected one adult tree within the regional uppermost (Alps) or northernmost (Sweden) margin of distribution, within closed forest stands and within several reproductive individuals of the given species. By doing so, we avoided selecting (i) a single highest individual such as outposts reflecting peculiar microclimatic conditions and (ii) individuals belonging to non-reproductive sink populations. 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 temperature measurements related to these species. This resulted in five measurement sites in each of the three regions (West, East and North; Tab.1, Fig. 1). At each site monitored, we placed one temperature logger (TidbiT v2 Temp UTBI-001, Onset Computer Corporation) at two metres above the ground, on the north facing side of a tall tree in a way that it remained completely shaded by the host trees canopy and stem during the growing season and by the stem only during the coldest part of the year. Temperature was recorded hourly from August 2009 to October 2011 in the Alps and from mid September 2010 to mid September 2011 in Scandinavia. In total we employed 15 datalogging sites.

Temperature data analysis

For each site, we first calibrated three linear models by relating the first year (08/2009 – 07/2010) of in situ measured temperatures (T_{Log}) to the corresponding temperatures of the closest weather station (T_{Met}) for daily mean, daily absolute minimum and daily absolute maximum temperatures. Like the sites monitored, the selected weather stations in Switzerland were all above the elevational position of the temperature inversion occurring during the winter period in the Rhone (West) and Rhine (East) valleys (Fig. 1).

To test the quality of the resulted linear regression, we reconstructed temperatures corresponding to the second year of measurements (08/2010 – 07/2011) for sites, where two years of *in situ* measurements were available (Appendix S1). Thus, we applied the linear models to the corresponding weather station temperatures of the second year. The temperatures reconstructed from weather stations were then correlated with the *in situ* measurements of the second year and the root mean square error (RMSE) and Spearman's rho (r) were calculated. This represents an independent 2-fold cross-validation. The predictive power of the linear models was high when tested on the second year (2011) of in situ data. Spearman's coefficient of correlation (rho) ranged between 0.96 and 1.00 and RMSE between 0.7 and 2.4 K (Appendix S2).

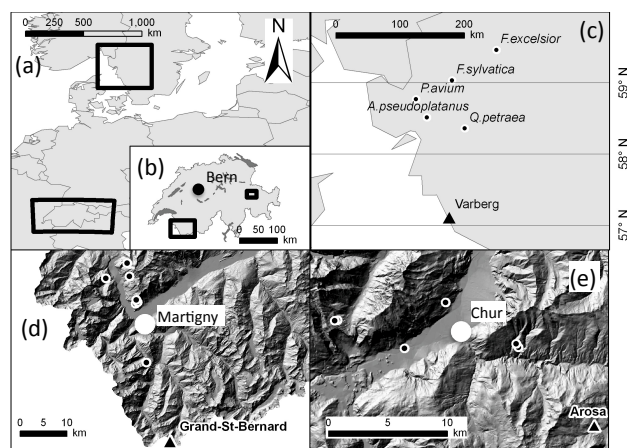


Figure 1: Locations of the selected study sites (white circle around black dots) and weather stations (black triangle) in South Sweden (c), in the Western Alps (d) and Eastern Alps (e) within Switzerland (b) and Europe (a).

Table 1: : Location and elevation of the study sites at the elevational and latitudinal range limits of deciduous tree species and coordinates of the nearest weather stations used for temperature reconstructions in the three test regions.

Region	Elevation (m)	Latitude	Longitude	Study site (affiliated species) / Station name
West	1374	46°8' N	7°4' E	<i>T. platyphyllos</i> , <i>Q. petraea</i>
	1460	46°11' N	6°59' E	<i>F. sylvatica</i>
	1523	46°8' N	7°4' E	<i>F. excelsior</i> , <i>P. avium</i>
	1804	46°8' N	7°4' E	<i>A. pseudoplatanus</i>
	2160	46°1' N	7°6' E	<i>S. aucuparia</i>
East	1165	46°50' N	9°35' E	<i>T. platyphyllos</i>
	1320	46°50' N	9°35' E	<i>F. excelsior</i> , <i>Q. petraea</i>
	1540	46°51' N	9°23' E	<i>F. sylvatica</i>
	1547	46°55' N	9°19' E	<i>A. pseudoplatanus</i>
	2020	46°47' N	9°39' E	<i>S. aucuparia</i>
North	159	58°21' N	12°29' E	<i>Q. petraea</i>
	85	58°30' N	11°57' E	<i>A. pseudoplatanus</i>
	90	58°46' N	11°48' E	<i>P. avium</i>
	83	59°1' N	12°18' E	<i>F. sylvatica</i>
	52	59°27' N	12°56' E	<i>F. excelsior</i>
West	2966	46°20' N	7°12' E	Les Diablerets
	1974	46°33' N	7°01' E	Le Moleson
	2472	45°52' N	7°10' E	Col du Grand St. Bernard
East	1594	46°49' N	9°51' E	Davos
	2690	46°50' N	9°48' E	Weissfluhjoch
North	69	59°40' N	12°38' E	Arvika
	177	59°13' N	12°4' E	Blomskog
	177	58°36' N	12°11' E	Kroppefjäll-Granán

We then reconstructed 50 years (1961-2010) of daily mean, daily absolute minimum and daily absolute maximum temperatures (needed for the calculation of daily means, see below) at the temperature logging sites by applying the linear model for each site (intercept and lapse rate). Reconstructed temperatures were later used for calculating growing-degree days, growing season length and obtaining extreme value distributions (see below). We lost two loggers due to vandalism at the cold limits of *F. excelsior* and *P. avium* in the Western Swiss Alps (Tab. 1). Since two other loggers were installed on the same slope located below and above the elevation position of the missing devices (0.5 km from the missing device), we used these two loggers to gap-fill temperature records for these species at this location using daily regressions.

Return period of absolute minimum temperatures

Generalized extreme value distributions (GEV) have been extensively used to estimate rare events. For this, within a given period (e.g.

100 years) every year's/month's/week's minimum or maximum of a given parameter are extracted. An appropriate GEV distribution (Fréchet, Weibull or Gumbel distribution) is then fitted to the observed frequency distribution of the study parameter. The shape of the tail of the predicted distribution describes the likely occurrences of very rare events and allows extrapolations outside the observed temporal range of calibration.

As budburst occurs at the scale of weeks, we selected weekly absolute minimum temperatures for the analysis. The distribution of weekly absolute minimum temperatures meets the assumptions of extreme value theory (Coles, 2001) and thus belongs to the generalized extreme value distributions (GEV):

$$G(z) = \exp\left\{-\left[1 + \xi \frac{(z-\mu)}{\sigma}\right]^{-\frac{1}{\xi}}\right\} \quad \text{Eq. 1}$$

with μ, σ, ξ representing the location, scale and shape parameter of the model, respectively. Prior to this analysis we transformed all minimum temperatures to their absolute values because the GEVs are restricted to positive numbers (Guttorp & Xu, 2011). We back-transformed the results into their negative val-

ues after the analysis. Hence, for each site we obtained the absolute minimum temperature per week from the reconstructed 50-years datasets. That data was found to be non-stationary, due to climate change. The approximate increase of annual absolute minima of 0.3 K per decade (during the years 1961-2010) is consistent with findings of 0.32 K decadal temperature increase in monthly absolute minimum temperatures in December, January and February at Neuchatel (Rebetez & Reinhard, 2008). Thus, separately for each week of the year, we fitted two models to the minimum temperatures as follows: One model included a linear trend in the location parameter (to account for the warming trend) and one without (using maximum likelihood, library `extRemes` of R software; Gilleland et al., 2009). We found no significant improvement of the models that include the long-term warming trend compared to the model without that trend (likelihood ratio test). Hence, we kept the models without trend and, by inverting Eq. 1., we calculated separately for each week of the year the return periods of low temperature extremes ranging from 0 °C to -40 °C for a 100 year period. The -40 °C low temperature limit was chosen because the weather stations (used for temperature reconstruction) were always situated higher than our test sites and none of them ever recorded temperatures below -40 °C during the last 50 years. Return periods longer than 100 years were not considered, since for the species studied the reproductive cycle is accomplished by that time. We applied the parametric bootstrap procedure to assess the uncertainty of low temperature return periods. Namely, the 5th and 95th percentiles of the resulting 100 bootstrapped samples were used as lower and upper confidence boundaries (the range of recurrence) for the return period considered.

Reconstructed temperature conditions during growing season

The thermal growing season was calculated for each site and each year. Here, we used the growing season defined as the period constrained by a daily mean air temperature above 5 °C for more than five consecutive days (spring) and daily mean temperature below 5 °C for more than five consecutive days (autumn, FAO, 1978-

81). Further, monthly mean temperature and monthly mean minimum (mean of the absolute minima of all days per month) temperature across the 50-year reconstruction were calculated for each site. Growing degree days within the thermal growing season were calculated for each site and each year using:

$$GDD = \frac{(T_{\max} + T_{\min})}{2} - T_{\text{base}} \quad \text{Eq. 2}$$

(Womach, 2005), with T_{\max} = daily absolute maximum temperature, T_{\min} = daily absolute minimum temperature and T_{base} set to 5 °C. Daily minimum temperatures lower than T_{base} were set to T_{base} for that purpose. In order to determine a proper estimate of how long broad-leave trees are exposed to low temperature, we extracted leaf unfolding dates for the four species (*S. aucuparia*, *A. pseudoplatanus*, *F. sylvatica* and *P. avium*) available at the MeteoSwiss phenological database (<https://gate.meteoswiss.ch/idaweb/>) and at the Pan European Phenological database (PEP725, 2012). On average, six observation sites per species (within an elevational belt of ± 150 m of our sites) and 22 years of observation were available. The first and last date of leaf unfolding were selected and rounded to the week of the year.

Results

Absolute minimum temperature

The lowest temperatures predicted to occur within ≤ 100 years were -25 °C (Western Alps) and -28 °C (Eastern Alps) at the uppermost elevational limit in our survey (i.e. at the upper limits of *S. aucuparia*; Tab. 2). At the lower end of the elevational ranking of the species (i.e. in *Q. petraea*), the lowest predicted temperatures were -19 °C (Western Alps) and -23 °C (Eastern Alps). Notably, there was an important variation of predicted temperature between the three test regions: the coldest temperature experienced was found in Sweden for all species. Lowest temperatures at the same species limit in the Eastern Alps were 4-14 K warmer than in Sweden and in the Western Alps 9-17 K warmer than in Sweden (Tab. 2, Fig. 2). In other words, the absolute minima were far from being consistent across sites.

Absolute minimum temperature in spring

For each species at its respective upper elevational limit, weekly lowest temperatures were very similar between the Western and Eastern Swiss Alps regions in defined, critical spring periods (Tab. 3, Fig. 2). Also, at the northern latitudinal species limits in Sweden lowest temperatures per week match well with temperatures in the Alps during spring from ca. week 17 (April 23rd – 29th) onwards, e.g. lowest temperatures of -6, -7 and -6 °C for *Prunus avium* in Western Alps, Eastern Alps and Sweden, respectively. Across the three test regions, temperatures below the freezing point (0 °C) can occur until the end of May for species having the lowest elevational limits (*Q. petraea*, *T. platyphyllos*, *P. avium* and *F. excelsior*, Tab. 3). For the same species, leaf-killing temperatures of 3 ± 1 °C (Till, 1956; Liepe, 1993), were predicted to occur until the second week of May. In all three test regions, a second group of species (*F. sylvatica* and *S. aria*) may experience 0 °C until the beginning of June and 3 ± 1 °C until the 3rd week of May. At the species limit of *S. aucuparia* and *A. pseudoplatanus* freezing temperatures (0 °C) can occur almost all year long, whereas 3 ± 1 °C were predicted to occur until the first week of June across the three test regions.

Temperature conditions during the growing season

In the Alps, the reconstructed mean length of the growing season for 1961-2010 was the longest at the range limit of *Q. petraea* (West: 23 ± 35 , East: 214 ± 30 and North: 207 ± 27 days, mean \pm SD; Tab. 3) and the shortest for the limits of *S. aucuparia* (124 ± 26 and 135 ± 28 days, with the shortest growing season of 59 days within 50 years). For each species, growing season length was very similar across study regions West, East and North. Excluding *A. pseudoplatanus*, the mean difference within a given species ranged from 11 to 31 days among the three regions. Among species, the sequence of decreasing growing season length (as well as growing degree-days) reflected well the elevational ranking of species cold limits in the Alps provided by Randin et al. (in press): *Q. petraea* > *T. platyphyllos* > *P. avium* > *F. excelsior* > *F. sylvatica* > *A. pseudoplatanus* > *S. aucuparia*. At the cold, high latitude limits of *F. excelsior*, *F. sylvatica* and *A. pseudoplatanus* in Sweden the reconstructed growing degree-days during the growing season were always higher (i.e. warmer) compared to corresponding elevational limits in the Western and Eastern Swiss Alps. The reconstructed mean temperature during the growing season (as well as the mean temperature during the two warmest months) was the highest for *Q. petraea* (West: 10.9 °C, East: 10.8 °C and North: 12.1 °C, Tab. 3) and the coldest for *S. aucuparia* (West and East: 8.9 °C). Notably, among all five species for which a replicate in South Sweden was available, mean temperature during the growing season was warmest in Sweden. All reconstructed monthly mean temperatures were warmest for *Q. petraea* and the coldest for *S. aucuparia* (Appendix S3). Finally, monthly mean temperatures in winter (i.e. defined here as from December to February) at the species limits in South Sweden were always colder and mean temperatures for summer months (i.e. defined here as from June to September) were always warmer compared to the corresponding tree species limits in the Swiss Alps. However, continentality in South Scandinavia and in the Alps was approximately the same (Continental index calculated from Ivanov, 1959).

Finally, paired Wilcoxon signed-rank tests showed no significant differences for the mean values of the reconstructed season length, growing degree days and the minimum temperature in April and May when the two regions of the Swiss Alps were compared together (N=7 species; all P-values > 0.05), and when the two regions of the Swiss Alps were compared with South Sweden (N=5 species; all P-values > 0.05). However, significant and marginally significant differences in annual absolute minimum temperature were found between the two regions of the Swiss Alps (N=5 species; P-values = 0.0222) and between the two regions of the Swiss Alps compared to South Sweden (N=5 species; two P-values = 0.0625). In addition, marginally significant differences were found for the mean temperature of the growing season and the two warmest months when the two regions of the Swiss Alps were compared to Sweden (warmer in Sweden, N=5 species; two P-values = 0.0625).

Table 2: Different measures of the temperature regime at the elevational and latitudinal range limit of seven broad-leaved tree species in the Western Alps, Eastern Alps and South Sweden. Length of growing season LGS, in brackets the minimum length in 50 years, growing degree days GDD, mean temperature during the growing season MST and during the two warmest months TWM (mean±sd) derived from a 50-years dataset (scaled to actual site conditions using own microclimate data). Predicted absolute minimum temperature AMT within 100 years, range of recurrence rates (RR) and freezing resistance (LT50).

Species	Region	Reconstructed					Predicted			Measured LT50* Till (1956) °C
		LGS (d)	GDD >5 °C	MST °C	TWM °C	AMT °C	Range of RR years			
<i>S. aucuparia</i>	West	124 ± 26 (59)	553 ± 115	8.9 ± 0.8	10.0 ± 1.0	-25	74-104	-43 ⁻¹		
	East	135 ± 28 (61)	622 ± 160	8.8 ± 0.9	10.2 ± 1.2	-28	71-99			
<i>A. pseudoplatanus</i>	West	170 ± 31 (106)	1026 ± 139	10.4 ± 0.8	12.6 ± 1.0	-22	62-91	-21/-40 ⁻¹		
	East	150 ± 34 (76)	742 ± 172	9.3 ± 1.0	10.9 ± 1.2	-27	57-78			
	North	204 ± 21 (165)	1589 ± 133	12.5 ± 0.7	16.2 ± 1.2	-31	48-75			
<i>F. sylvatica</i>	West	206 ± 34 (147)	1283 ± 121	10.8 ± 1.1	14.0 ± 1.0	-20	50-79	-22		
	East	159 ± 33 (88)	803 ± 173	9.9 ± 0.9	11.7 ± 1.2	-26	62-90			
	North	196 ± 22 (143)	1529 ± 134	12.6 ± 0.8	16.3 ± 1.3	-37	57-81			
<i>F. excelsior</i>	West	201 ± 32 (146)	1250 ± 117	10.9 ± 0.9	13.8 ± 1.0	-20	44-69	-27		
	East	214 ± 30 (142)	1403 ± 192	11.2 ± 0.9	14.3 ± 1.2	-23	73-100			
	North	192 ± 22 (140)	1614 ± 133	13.0 ± 1.1	16.6 ± 1.3	-37	42-67			
<i>P. avium</i>	West	201 ± 32 (146)	1250 ± 117	10.9 ± 0.9	13.8 ± 1.0	-20	44-69	-29 ⁻¹		
	East	214 ± 30 (142)	1403 ± 192	11.2 ± 0.9	14.3 ± 1.2	-23	73-100			
	North	195 ± 22 (143)	1370 ± 120	12.0 ± 0.8	15.3 ± 1.2	-32	70-98			
<i>T. platyphyllos</i>	West	231 ± 35 (176)	1552 ± 121	11.1 ± 1.7	15.3 ± 1.0	-19	40-67	-34		
	East	214 ± 30 (142)	1420 ± 195	11.1 ± 0.9	14.2 ± 1.1	-23	79-106			
<i>Q. petraea</i>	West	231 ± 35 (176)	1552 ± 121	11.1 ± 1.7	15.3 ± 1.0	-19	40-67	-24		
	East	214 ± 30 (142)	1403 ± 192	11.2 ± 0.9	14.3 ± 1.2	-23	73-100			
	North	207 ± 27 (165)	1544 ± 130	12.3 ± 0.7	16.0 ± 1.2	-28	54-77			

* frost resistance of buds in winter
⁻¹ from A. Lenz et. al. in prep.

Table 3: The absolute minimum temperatures per week during spring predicted for the past 100 years at broad-leaved tree species limits in three regions (Western Swiss Alps, Eastern Swiss Alps, South Sweden).

Species	Region	Week of the year													
		12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>S. aucuparia</i>	West	-14	-13	-14	-13	-11	-10	-10	-8	-6	-6	-4	-2	-2	-2
	East	-13	-14	-14	-13	-10	-11	-10	-7	-6	-5	-4	-4	-3	0
<i>A. pseudoplatanus</i>	West	-12	-11	-11	-10	-8	-8	-8	-5	-4	-3	-4	-1	0	0
	East	-13	-14	-14	-12	-10	-11	-9	-7	-6	-5	-4	-3	0	0
	North	-19	-11	-11	-9	-8	-4	-3	-3	-2	0	-	-	-	-
<i>F. sylvatica</i>	West	-10	-9	-9	-8	-6	-6	-6	-4	-2	-1	-2	0	-	-
	East	-11	-13	-12	-11	-9	-10	-8	-6	-4	-4	-2	-1	-	-
	North	-24	-16	-15	-13	-12	-8	-5	-3	-3	-3	-2	0	-	-
<i>F. excelsior</i>	West	-10	-9	-9	-9	-7	-6	-6	-4	-2	-2	-2	0	-	-
	East	-8	-10	-9	-8	-6	-7	-5	-3	-2	-1	-1	0	-	-
	North	-25	-16	-15	-13	-12	-9	-5	-5	-4	-3	-2	0	0	-
<i>P. avium</i>	West	-10	-9	-9	-9	-7	-6	-6	-4	-2	-2	-2	0	-	-
	East	-8	-10	-9	-8	-6	-7	-5	-3	-2	-1	-1	0	-	-
	North	-20	-13	-12	-10	-9	-6	-3	-3	-2	-2	0	-	-	-
<i>T. platyphyllos</i>	West	-9	-8	-9	-8	-6	-5	-5	-3	-1	-1	-1	-	-	-
	East	-9	-10	-10	-8	-6	-7	-5	-3	-2	-1	-1	0	-	-
<i>Q. petraea</i>	West	-9	-8	-9	-8	-6	-5	-5	-3	-1	-1	-1	-	-	-
	East	-8	-10	-9	-8	-6	-7	-5	-3	-2	-1	-1	0	-	-
	North	-16	-10	-9	-7	-7	-3	-2	-2	-1	0	-	-	-	-

Numbers in bold print indicate periods of bud break and flushing for those species and regions for which phenological data were available from the Swiss Meteorological service (MeteoSchweiz) and from the Pan European Phenological Database (PEP725). All temperatures were predicted to occur within a range of 41 to 100 years.

Discussion

At the upper elevational and latitudinal limits of five broad-leaved tree species (i.e. *A. pseudoplatanus*, *F. sylvatica*, *P. avium*, *F. excelsior* and *Q. petraea*), the mean temperature during the growing season as well as the absolute minimum temperatures (within past 100 years) revealed strong differences across test regions and thus, these expressions of temperatures are unlikely explaining biogeographical limits. In contrast, similar recurring minimum temperatures during the regional, site-specific period of bud-break were found at both elevational and latitudinal limits (temperatures below a critical threshold of -3 ± 1 °C). This suggests that freezing events during the sensitive phenological stages in spring exert a significant influence on species limits.

Absolute minimum temperatures

The lowest minimum temperature (i.e. the absolute minimum) during the period of maximum hardening in winter, has often been considered a critical factor shaping the global distribution of large groups of taxa or plant functional types (Sakai & Larcher, 1987; Woodward, 1987). However, within our group of temperate deciduous tree taxa, all seven species examined tolerate low temperatures between -22 and -43 °C in winter (Tab. 2), temperatures that five out of seven species never even closely experienced according to our analysis. Surprisingly, for all species in the Swiss Alps, except *F. sylvatica* and *Q. petraea*, the lowest annual temperature predicted to occur within a 100-year period was 4–18 K warmer than the known thresholds for freezing damage of fully hardened buds in winter (Tab. 2, Till, 1956; Tranquillini & Plank, 1989). Interestingly, in South Sweden, all studied species experienced temperatures consider-

ably colder than the tolerance thresholds, determined in the Alps (Tirol, Tranquillini & Plank, 1989) and in German lowlands (Göttingen, Till, 1956). Presumably, the northern populations acquired greater freezing tolerance in the dormant state, as was shown for *Picea spp* from Central Alaska and Ontario or *Pinus sylvestris* in Scandinavia (review in Parker, 1963; Sakai & Okada, 1971; Savolainen et al., 2011). However, the species-specific absolute minimum temperatures experienced at the Swedish range limit were still 3 to 8 K warmer than the same species specific site minima calculated from climatic envelopes for western Eurasia (Manthey & Box, 2007). Hence, there seems to be a substantial evolutionary potential for regional differentiation in maximum freezing resistance in winter (ecotypes).

Because we lack freezing resistance data from the latitudinal limits of temperate tree species, it remains unclear whether such ecotypic differentiation with regard to absolute minimum temperatures has taken place. We need to assume it has.

Temperature conditions during the growing season

Global comparisons have evidenced that the high elevation limit of the life form “tree” (the treeline) is related to a common mean temperature of the growing season (Körner & Paulsen, 2004, Körner, 2012). A similar correlation has been proposed for temperate deciduous taxa by Chuine (2010), regarding constraints for reproduction. For the Alps we can exclude reproductive limitations at the range limit (Kollas et al., 2012; Vitasse et al., 2012). In all five species for which a replicate in South Sweden was available (i.e. *A. pseudoplatanus*, *F. sylvatica*, *Q. petraea*,

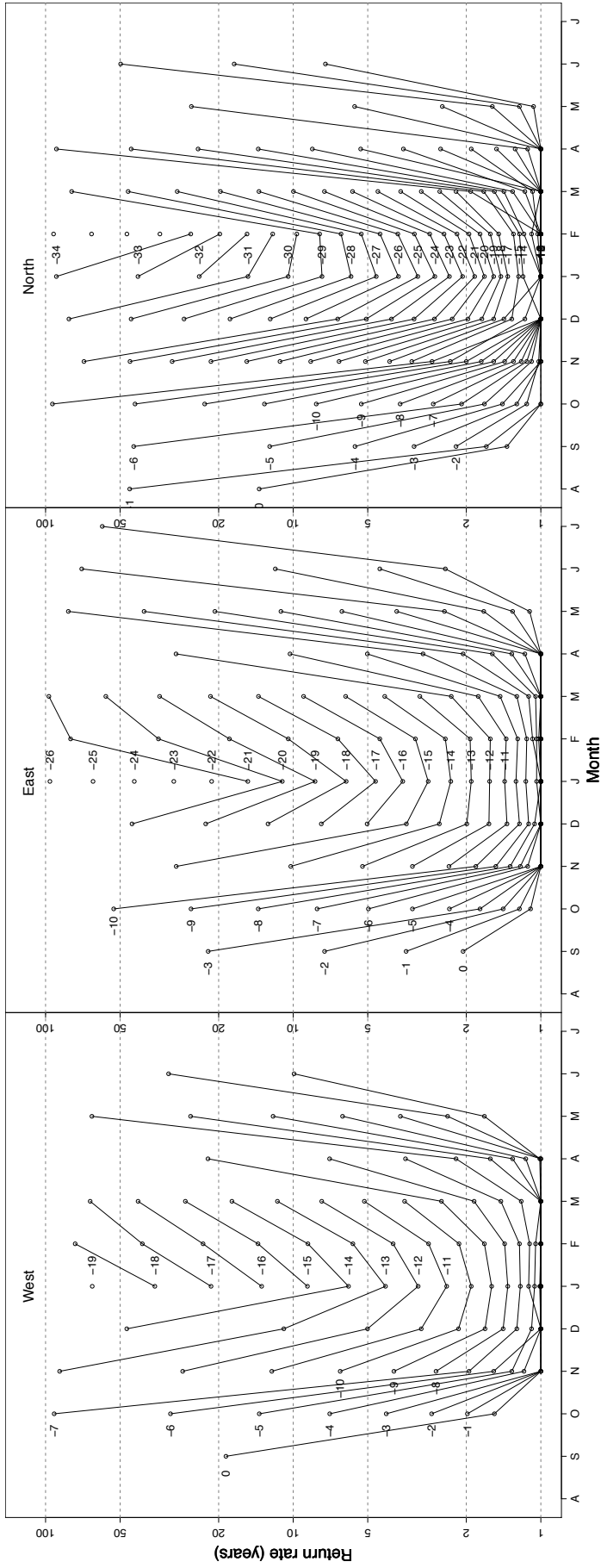


Figure 2: Predicted Return periods of temperature thresholds for species limits of *F. sylvatica* in the Western and Eastern Swiss Alps (West, East) and in Sweden (North). Note the log-scaled y-axis.

P. avium and *F. excelsior*), the mean temperatures during the growing season and the mean temperatures during the two warmest months were much warmer at their latitudinal limit in Sweden compared to their elevational limit in the Alps. Similarly, three out of five species show higher growing degree days at their latitudinal limit compared to their elevational limit. These results suggests that either these species are not limited by temperature during the Swedish growing season or that such expressions of temperature are not bearing predictive value for a comparison of altitudinal and latitudinal range limits of such deciduous taxa.

In contrast, the species site-specific length of the growing season offered more consistent values for all species at both the elevational and latitudinal limits. For four out of five species (*P. avium*, *Q. petraea*, *F. sylvatica* and *F. excelsior*) the length of the growing season did not show significant variation between the elevational and the latitudinal limit. In the remaining species (*A. pseudoplatanus*, longer growing season at the latitudinal limit compared to limits in the Alps) the current position may not be in equilibrium and thus, has not yet reached its northern cold limit (as shown by Randin et. al in press).

Absolute minimum temperatures in spring

During the period of de-hardening and bud-break in spring there is a risk of late freezing events and tissue damage (Sakai & Larcher, 1987). At this time, active tissue of broad-leaved tree species is damaged at 3 ± 1 °C (Till, 1956; for *S. aucuparia*: -7 °C; Taschler, 2004) In this study, deleterious freezing temperatures during the period of bud-break (and several weeks after) were predicted to occur consistently at the upper elevational and latitudinal limits of the four study species for which phenological data was available (i.e. *S. aucuparia*, *A. pseudoplatanus*, *F. sylvatica* and *P. avium*).

Freezing damage in buds, delayed de-hardening and flushing (Liepe 1993), a reduction of radial growth by up to 90 % (Dittmar 2006), reproductive failure and reduced final canopy density (Augspurger 2009), but also resprouting from secondary buds (Liepe 1993) make late frosts highly relevant for the species range limit

question. On the positive side, such extreme events may affect herbivore pressure (Innouye 2001). In the long-term, the cost to produce replacement foliage is high and thus, tree fitness may become reduced. The very close operation of phenology and freezing tolerance at the actual, critical temperature regime at all sites in all species suggest that late spring freezing is a decisive factor for the species range limits. Since there is a similarity of growing season length across range limit sites, low spring temperatures and seasonality may be auto-correlated or act interactively. The timing of bud break (phenology control) is most critical because species hardly differ in freezing tolerance during that developmental phase at the local climatic conditions. Although we attribute a critical role to late spring freezing, the associated selective adjustment of phenology is constraining the length of the growing season, and with it the time available to complete seasonal development and tissue maturation.

Conclusion

We conclude, that the risk of tissue damage by late spring freezing events at a 41-100 year return rate, and associated with it, spring phenology, are the most likely candidates controlling the low temperate range limits of the studied deciduous tree taxa. We cannot exclude a critical decisive tradeoff between the resultant season length constrains and the escaping from freezing damage in spring. Our data do not suggest a critical role of absolute minimum temperature in winter and the mean temperature during the growing season, although the latter may be confounded with season length effects.

Implications for correlative distribution models

Our findings have important implications for projections of climate change impacts on tree species distribution when using correlative approaches such as species distribution models (SDM). Our results call for the use of absolute minimum temperatures during key phenological stages and thus, for a high (hourly) resolution of temperature data instead of long-term averaged monthly or annual temperatures. Given

the significance of spring phenology, process-based rather than correlative phenological models need to be employed in order to better determine the interactions between development, tissue sensitivity to freezing and the actual temperature regime at species specific range limits.

Acknowledgements

We are grateful to Niklaus Zimmermann and Thomas Wohlgemuth for their advice on high elevation broad-leaved tree positions in Switzerland. We wish to thank Dr. Jean-Pierre Randin for housing and help during the field work, Yann Vitasse for valuable advice on the manuscript and Armando Lenz for unpublished data on freezing events. Phenological data were provided by the members of the PEP725 project. Meteorological data for Sweden was obtained from the Swedish Meteorological and Hydrological Institute. The research leading to these results has been funded by the European Research Council (ERC) grant 233399 (project TREE-LIM).

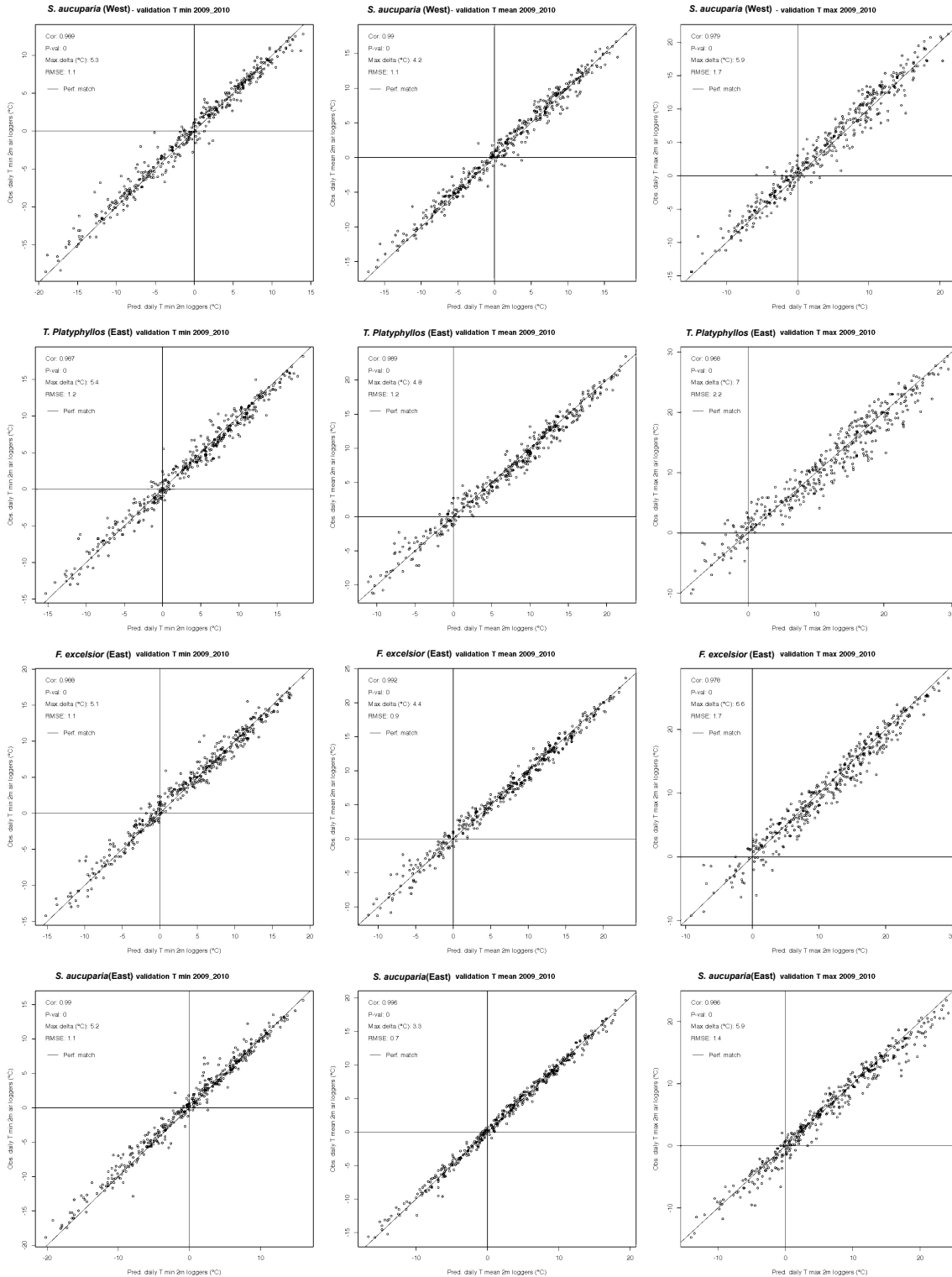
References

- Austin, M.P., Van Niel, K.P. (2011) Improving species distribution models for climate change studies: variable selection and scale. *Journal of Biogeography* 38: 1-8.
- Chuine, I. (2010) Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B-Biological Sciences* 365: 3149-3160.
- Coles, S. (2001) *An Introduction to Statistical Modeling of Extreme Values*. Springer.
- FAO (1978-81) Reports of the Agro-Ecological Zones Project. *World Soil Resour. Rep.*, 48. Vols. 1 - Methodology and Results for Africa; 2 - Southwest Asia; 3 - South and Central America; 4 - South-east Asia. Food and Agriculture Organization, Rome.
- Gilleland, E., Katz, R., Young, G. (2009) *extRemes: extreme value toolkit*. R package version 1.60.
- Guttorp, P., Xu, J. (2011) Climate change, trends in extremes, and model assessment for a long temperature time series from Sweden. *Environmetrics* 22: 456-463.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965-1978.
- Ivanov, N. (1959) Belts of Continentality on the Globe. *Izvestiia Vsesoivznoe Geografiia Obschestvo* 91: 410-423.
- Jump, A.S., Hunt, J.M., Penuelas, J. (2007) Climate relationships of growth and establishment across the altitudinal range of *Fagus sylvatica* in the Montseny Mountains, northeast Spain. *Ecology* 88: 507-518.
- Kollas, C., Randin, C., Vitasse, Y., Körner, C. (submitted) How accurate can weather stations predict temperatures at tree species limits? *Agricultural and Forest Meteorology*.
- Kollas, C., Vitasse, Y., Randin, C.F., Hoch, G., Körner, C. (2012) Unrestricted quality of seeds in European broad-leaved tree species growing at the cold boundary of their distribution. *Annals of Botany* 109: 473-480.
- Körner, C. (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115: 445-459.
- Körner, C. & Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* 31: 713-732
- Körner, C. (2012) *Alpine treelines*. Springer, Basel.
- Liepe, K. (1993) Growth-Chamber Trial on Frost Hardiness and Field Trial on Flushing of Sessile Oak (*Quercus petraea* Liebl). *Annales Des Sciences Forestieres* 50: Supplement 1.
- Manthey, M. & Box, E.O. (2007) Realized climatic niches of deciduous trees: comparing western Eurasia and eastern North America. *Journal of Biogeography* 34: 1028-1040.
- Meier, E.S., Kienast, F., Pearman, P.B., Svenning, J.C., Thuiller, W., Araujo, M.B., Guisan, A., Zimmermann, N.E. (2010) Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography* 33: 1038-1048.
- Montoya, D., Purves, D.W., Urbieto, I.R., Zavala, M.A. (2009) Do species distribution models explain spatial structure within tree species ranges? *Global Ecology and Biogeography* 18: 662-673.
- Nilsson, P., Cory, N. (2011) *Forestry statistics 2011* SLU, Umeå.
- Parker, J. (1963) Cold Resistance in Woody Plants. *Botanical Review* 29: 123-201.
- PEP725, m.o.t. (2012) PEP725 Pan European Phenology Data.
- Pigott, C.D., Huntley, J.P. (1981) Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. III. Nature and causes of seed sterility. *New Phytologist* 87: 817-839.
- Randin, C., Paulsen, J., Vitasse, Y., Kollas, C., Wohlgemut, T., Zimmerman, N.E., Körner, C. (in press) Do elevational limits of deciduous tree species match with their thermal latitudinal limits? *Global Ecology and Biogeography*
- Randin, C.F., Vuissoz, G., Liston, G.E., Vittoz, P., Guisan, A. (2009) Introduction of Snow and Geomorphic Disturbance Variables into Predictive Models of Alpine Plant Distribution in the Western Swiss Alps. *Arctic Antarctic and Alpine Research* 41: 347-361.

- Rebetez, M., Reinhard, M. (2008) Monthly air temperature trends in Switzerland 1901-2000 and 1975-2004. *Theoretical and Applied Climatology* 91: 27-34.
- Sakai, A., Okada, S. (1971) Freezing resistance of conifers. *Silvae Genetica* 20: 91-97.
- Sakai, A., Weiser, C.J. (1973) Freezing Resistance of Trees in North-America with Reference to Tree Regions. *Ecology* 54: 118-126.
- Sakai, A., Wardle, P. (1978) Freezing resistance of New Zealand trees and shrubs. *New Zealand Journal of Ecology* 1: 51-61.
- Sakai, A., Larcher, W. (1987) *Frost survival of plants: Responses and adaptation to freezing stress*. Springer, Berlin.
- Savolainen, O., Kujala, S.T., Sokol, C., Pyhajarvi, T., Avia, K., Knurr, T., Karkkainen, K., Hicks, S. (2011) Adaptive Potential of Northernmost Tree Populations to Climate Change, with Emphasis on Scots Pine (*Pinus sylvestris* L.). *Journal of Heredity* 102: 526-536.
- Scherrer, D., Körner, C. (2010) Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology* 16: 2602-2613.
- Sykes, M.T., Prentice, I.C., Cramer, W. (1996) A bi-climatic model for the potential distributions of north European tree species under present and future climates. *Journal of Biogeography* 23: 203-233.
- Taschler, D., Neuner, G. (2004) Summer frost resistance and freezing patterns measured in situ in leaves of major alpine plant growth forms in relation to their upper distribution boundary. *Plant Cell and Environment* 27: 737-746.
- Till, O. (1956) Über die Frosthärte von Pflanzen sommergrüner Laubwälder. *Flora - Allgemeine Botanische Zeitung* 143: 34-542
- Tranquillini, W. (1979) *Physiological ecology of the alpine timberline : tree existence at high altitudes with special reference to the European alps*. Springer, Berlin.
- Tranquillini, W., Plank, A. (1989) Ökophysiologische Untersuchungen an Rotbuchen (*Fagus sylvatica* L.) in verschiedenen Höhenlagen Nord- und Südtirols. *Centralblatt für das gesamte Forstwesen* 106: 225-246.
- Way, D.A., Oren, R. (2010) Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology* 30: 669-688.
- Wohlgemuth, T. (1992) Die vegetationskundliche Datenbank. *Schweizerische Zeitschrift für das Forstwesen* 143: 22-35.
- Womach, J. (2005) *Agriculture: A Glossary of Terms, Programs, and Laws*, 2005 Edition. In: CRS Report for Congress. The Library of Congress
- Woodward, F.I. (1987) *Climate and plant distribution*. Cambridge University Press, Cambridge.
- Woodward, F.I. (1990) The Impact of Low-Temperatures in Controlling the Geographical-Distribution of Plants. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 326: 585-593.

Supplementary material

Appendix S1 Validation of linear models on the second year of measurement in the Western and Eastern Swiss Alps



Appendix S2: Correlations (r and associated P-values P) and root mean square errors between predicted temperature by linear models based on first year data and measured *in situ* temperature during the second year used for validation.

	T_{min}			T_{mean}			T_{max}		
	r	P	RMSE (K)	r	P	RMSE (K)	r	P	RMSE (K)
<i>S. aucuparia</i> (West)	0.989	< 0.001	1.1	0.99	< 0.001	1.1	0.979	< 0.001	1.7
<i>T. platyphyllos</i> (East)	0.987	< 0.001	1.2	0.989	< 0.001	1.2	0.968	< 0.001	2.2
<i>F. excelsior</i> (East)	0.988	< 0.001	1.1	0.992	< 0.001	0.9	0.978	< 0.001	1.7
<i>A. pseudoplatanus</i> (East)	0.973	< 0.001	1.7	0.976	< 0.001	1.7	0.963	< 0.001	2.4
<i>S. aucuparia</i> (East)	0.990	< 0.001	1.1	0.996	< 0.001	0.7	0.986	< 0.001	1.4

Appendix S3: Monthly mean minimum temperatures and monthly mean temperatures at broad-leaved tree species limits in three regions (Western Swiss Alps, Eastern Swiss Alps, Sweden). Numbers represent means across 50 years (1961-2010).

Species	Region	Jan		Feb		Mar		Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec		
		min*/ mean	min/ mean	min*/ mean	min/ mean	min*/ mean	min/ mean	min*/ mean	min/ mean	min*/ mean	min/ mean	min*/ mean	min/ mean	min*/ mean	min/ mean	min*/ mean	min/ mean	min*/ mean	min/ mean	min*/ mean	min/ mean	min*/ mean	min/ mean	min*/ mean	min/ mean	
<i>S. aucuparia</i>	West	-6.9/-4.8	-7.1/-5	-5.7/-3.5	-3.2/-1.1	1.2/3.5	4.6/7.3	7/10.1	7.2/10	4.7/7.1	1.6/3.6	-3.4/-1.5	2/4.2	1.6/3.6	-6/-3.9											
	East	-6.7/-4.5	-7/-4.5	-5.1/-2.5	-2.2/0.3	2/4.8	5.1/8	7.4/10.3	7.4/10	4.9/7.3	2/4.2	-3.1/-1.1	2/4.2	4.9/7.3	-5.9/-3.8											
<i>A. pseudoplatanus</i>	West	-4.5/-1.9	-4.7/-2.1	-3.3/-0.6	-0.8/1.8	3.5/6.2	6.8/9.9	9.2/12.7	9.3/12.6	6.9/9.7	3.8/6.3	-1.1/1.4	3.8/6.3	-3.6/-1												
	East	-6.7/-4.1	-6.9/-4.1	-5.1/-2.1	-2.3/0.8	1.9/5.4	4.9/8.7	7.1/11.1	7.1/10.8	4.7/7.9	1.8/4.7	-3.1/-0.6	1.8/4.7	-5.9/-3.4												
	North	-4.5/-2	-5.1/-2.3	-2.7/0.5	1/4.9	5.9/10.3	10.1/14.6	12.2/16.6	11.9/15.8	8.4/11.9	4.8/7.5	0.5/2.8	4.8/7.5	-3.1/-0.6												
<i>F. sylvatica</i>	West	-2.8/-0.5	-3/-0.8	-1.6/0.7	0.9/3.1	5.1/7.6	8.5/11.3	10.9/14	11/13.9	8.6/11.1	5.5/7.7	0.6/2.7	5.5/7.7	-1.9/0.4												
	East	-5.3/-3.3	-5.5/-3.3	-3.7/-1.3	-0.9/1.6	3.3/6.1	6.4/9.5	8.6/11.8	8.6/11.5	6.1/8.7	3.3/5.5	-1.7/0.2	3.3/5.5	-4.5/-2.5												
	North	-7.2/-3.5	-7.8/-3.5	-4.8/-0.1	-0.6/4.9	4.3/10.8	8.8/15	10.9/16.8	10.4/15.8	6.8/11.3	3.1/6.6	-1.7/1.5	3.1/6.6	-6/-2.2												
<i>F. excelsior</i>	West	-3/-0.7	-3.2/-0.9	-1.8/0.6	0.7/3	4.9/7.4	8.3/11.1	10.7/13.9	10.8/13.8	8.4/11	5.3/7.5	0.4/2.6	5.3/7.5	-2.1/0.2												
	East	-2.6/-0.2	-2.8/-0.2	-1/1.7	1.7/4.5	5.8/8.9	8.7/12.2	10.9/14.4	10.9/14.1	8.5/11.4	5.7/8.3	0.9/3.2	5.7/8.3	-1.9/0.5												
	North	-7.7/-4.4	-8.3/-4.3	-5.3/-0.7	-1.1/4.5	3.8/10.8	8.2/15.2	10.4/17.2	9.9/16.1	6.2/11.4	2.5/6.4	-2.2/1	2.5/6.4	-6.4/-3												
<i>P. avium</i>	West	-3/-0.7	-3.2/-0.9	-1.8/0.6	0.7/3	4.9/7.4	8.3/11.1	10.7/13.9	10.8/13.8	8.4/11	5.3/7.5	0.4/2.6	5.3/7.5	-2.1/0.2												
	East	-2.6/-0.2	-2.8/-0.2	-1/1.7	1.7/4.5	5.8/8.9	8.7/12.2	10.9/14.4	10.9/14.1	8.5/11.4	5.7/8.3	0.9/3.2	5.7/8.3	-1.9/0.5												
	North	-5.3/-3	-5.8/-2.9	-3.1/0.2	0.6/4.7	4.9/10.2	8.9/14.1	10.8/15.7	10.4/14.8	7.1/10.7	3.8/6.4	-0.4/1.7	3.8/6.4	-4.2/-1.8												
<i>T. platyphyllos</i>	West	-2.1/0.5	-2.3/0.2	-0.9/1.8	1.5/4.2	5.8/8.8	9.1/12.6	11.5/15.4	11.6/15.3	9.2/12.4	6.1/8.9	1.3/3.8	6.1/8.9	-1.2/1.4												
	East	-2.8/-0.2	-3.1/-0.2	-1.3/1.7	1.4/4.5	5.4/8.9	8.3/12.1	10.4/14.3	10.4/14	8.1/11.3	5.3/8.3	0.6/3.1	5.3/8.3	-2.1/0.5												
<i>Q. petraea</i>	West	-2.1/0.5	-2.3/0.2	-0.9/1.8	1.5/4.2	5.8/8.8	9.1/12.6	11.5/15.4	11.6/15.3	9.2/12.4	6.1/8.9	1.3/3.8	6.1/8.9	-1.2/1.4												
	East	-2.6/-0.2	-2.8/-0.2	-1/1.7	1.7/4.5	5.8/8.9	8.7/12.2	10.9/14.4	10.9/14.1	8.5/11.4	5.7/8.3	0.9/3.2	5.7/8.3	-1.9/0.5												
	North	-3.7/-1.6	-4.2/-1.9	-2/0.7	1.3/5	5.8/10.3	9.7/14.4	11.5/16.3	11.3/15.6	8.1/11.8	4.8/7.5	0.9/3	4.8/7.5	-2.4/-0.3												

*mean of daily minima

Chapter 5

Unrestricted quality of seeds in European broad-leaved tree species growing at the cold boundary of their distribution

Chris Kollas, Yann Vitasse, Christophe F. Randin, Günter Hoch, Christian Körner
Annals of Botany, (2012) 109:473-480

Unrestricted quality of seeds in European broad-leaved tree species growing at the cold boundary of their distribution

C. Kollas*, Y. Vitasse, C. F. Randin, G. Hoch and C. Körner

Institute of Botany, University of Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland

*For correspondence. E-mail chris.kollas@unibas.ch

Received: 14 July 2011 Returned for revision: 21 September 2011 Accepted: 31 October 2011

• **Background and Aims** The low-temperature range limit of tree species may be determined by their ability to produce and disperse viable seeds. Biological processes such as flowering, pollen transfer, pollen tube growth, fertilization, embryogenesis and seed maturation are expected to be affected by cold temperatures. The aim of this study was to assess the quality of seeds of nine broad-leaved tree species close to their elevational limit.

• **Methods** We studied nine, mostly widely distributed, European broad-leaved tree species in the genera *Acer*, *Fagus*, *Fraxinus*, *Ilex*, *Laburnum*, *Quercus*, *Sorbus* and *Tilia*. For each species, seeds were collected from stands close to optimal growth conditions (low elevation) and from marginal stands (highest elevation), replicated in two regions in the Swiss Alps. Measurements included seed weight, seed size, storage tissue quality, seed viability and germination success.

• **Key Results** All species examined produced a lot of viable seeds at their current high-elevation range limit during a summer ranked 'normal' by long-term temperature records. Low- and high-elevation seed sources showed hardly any trait differences. The concentration of non-structural carbohydrates tended to be higher at high elevation. Additionally, in one species, *Sorbus aucuparia*, all measured traits showed significantly higher seed quality in high-elevation seed sources.

• **Conclusions** For the broad-leaved tree taxa studied, the results are not in agreement with the hypothesis of reduced quality of seeds in trees at their high-elevation range limits. Under the current climatic conditions, seed quality does not constitute a serious constraint in the reproduction of these broad-leaved tree species at their high-elevation limit.

Key words: Rosaceae, Fagaceae, Aceraceae, Oleaceae, Tiliaceae, Aquifoliaceae, Fabaceae, seed morphology, elevation, germination, carbohydrates, Alps.

INTRODUCTION

Niche boundaries of species are often controlled by adverse environmental effects (Austin and Smith, 1989; Guisan and Zimmermann, 2000). Such range limits can be identified in the landscape by searching for 'outpost' individuals or using archive data (Jalas and Suominen, 1988). However, when using such range limits for predictive purposes, it is essential that individuals found at the periphery of a species range reproduce successfully, rather than reflecting historical long-distance seed dispersal events only, as was shown for *Tilia cordata* at the northern species limit in the United Kingdom (Pigott and Huntley, 1978).

Broad-leaved tree taxa such as *Fagus*, *Quercus*, *Fraxinus*, *Sorbus*, *Acer*, *Tilia*, *Ilex* and *Laburnum* reach their upper elevational limits between 1100 and 2200 m in the Swiss Alps (Aeschimann *et al.*, 2004). Among those species, only *Sorbus aucuparia* is able to grow at the tree-line (a life-form limit) at around 2200 m. While the worldwide tree-line phenomenon is comparatively well understood (Körner, 2007; Hoch and Körner, 2011), the species-specific range limits for non-tree-line-forming taxa still need functional explanations. Among many other decisive factors for the current range limit, the ability to produce viable seed is crucial for tree populations to remain viable or even to expand the range limit.

Many factors can constrain the production of viable seeds in cold environments such as the upper-elevational limits. These include successful flowering and pollen transfer (Kudo, 1996), pollen tube growth (Pigott and Huntley, 1981), fertilization, embryogenesis and seed maturation into a viable propagule (for details of predispersal hazards, see Fenner, 1985). Even if trees succeed in producing seeds in such cold environments, the quality of the mature seeds may still be inferior compared with those produced in warmer conditions. In particular, the length of the growing season might be too short to achieve seed maturation (Grenier and Sirois, 2009). Important seed traits encompass seed size, seed weight, quality of seed storage tissue (endosperm or storage cotyledons), viability and germination success. The quality of storage tissue is reflected in the concentration of nitrogen (protein) and non-structural carbohydrates (NSC) or lipids.

Seed mass tends to increase with increasing elevation in herbaceous taxa (Körner, 2003; Pluess *et al.*, 2005), but no general pattern has been detected for trees. For example, seed mass had been reported to decline with elevation in *Sorbus aucuparia*, *Pinus sylvestris* and *Picea abies* (Engler, 1913; Barclay and Crawford, 1984; Oleksyn *et al.*, 1998), whereas the opposite was found for *Betula pubescens* (Holm, 1994).

A sufficient supply of C- and N-reserves is a prerequisite for successful seedling establishment (e.g. Naegle *et al.*, 2005). Tissue concentrations of NSC and nitrogen may either be adaptive or be the result of accumulation due to restricted structural growth as was reported for plants growing at high elevation (e.g. Körner, 1989; Hoch and Körner, 2011). To our knowledge, the present study is the first to investigate the influence of elevation on storage carbohydrates in seeds of deciduous tree species.

Once well supplied with reserves, seeds may be viable but may still show restricted germination. Both viability and germination capacity have been reported to decline with increasing elevation/latitude of the seed source, e.g. for *Pinus* (Engler, 1913), *Picea* (Sirois, 2000), *Nothofagus* (Cuevas, 2000) and *Betula* (Holm, 1994; Sveinbjörnsson *et al.*, 1996). An exception to this pattern is the (sub-) tropical woody species *Polylepis australis*, which has been shown to increase germination capacity with elevation of seed source (Marcora *et al.*, 2008).

So far, no comparative study focusing on tree seed response to elevation has included a wider range of tree taxa. Here we explored seed traits in a suite of major European broad-leaved tree species at their current high-elevation limit in the Alps. We quantified the quality of their seeds by the above criteria at high and low elevation in two regions in the Swiss Alps.

We predicted that due to the lower temperatures and shorter growing season there would be a decline in regenerative performance, as seeds from the high-elevation limit for tree species would (1) show reduced quality and (2) exhibit reduced germination success as compared with lower-elevation seed sources.

MATERIALS AND METHODS

Species and seed sources studied

We selected nine broad-leaved tree species with a wide distributional range in Europe: *Acer pseudoplatanus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Ilex aquifolium*, *Laburnum alpinum*, *Quercus petraea*, *Sorbus aria*, *Sorbus aucuparia* and *Tilia platyphyllos*.

To identify the uppermost elevational limit of the nine selected species in the Swiss Alps, species occurrence data were extracted from a spatial-temporal, multi-species vegetation database of Switzerland based on the Second Swiss National Forest Inventory (Brändli, 2010) and the forest plots database (Wohlgemuth, 1992). Considering the 10% highest occurrences of these species in Switzerland, two distinct regions were identified: near Martigny (46°6'N, 7°4'E) in the western part of the Swiss Alps (called hereafter West, covering about 750 km²) and the Upper Rhine region near Chur (46°51'N, 9°32'E) in the eastern part (called hereafter East, covering an area of about 650 km²; see Fig. 1). For each species high- and low-elevation mother trees were selected in these two regions (West and East). Hereafter, the term provenance refers to seeds sampled in one region and one elevation. The West and East areas were considered as replicates. Seed sources of two species deviate from that design: seeds of *L. alpinum* were obtained in the western region only (West High and West Low) because this species does not occur in the eastern region. Furthermore seeds of *I. aquifolium* were collected in between these two former regions (where it is absent) at Niederhorn (Kanton Bern),

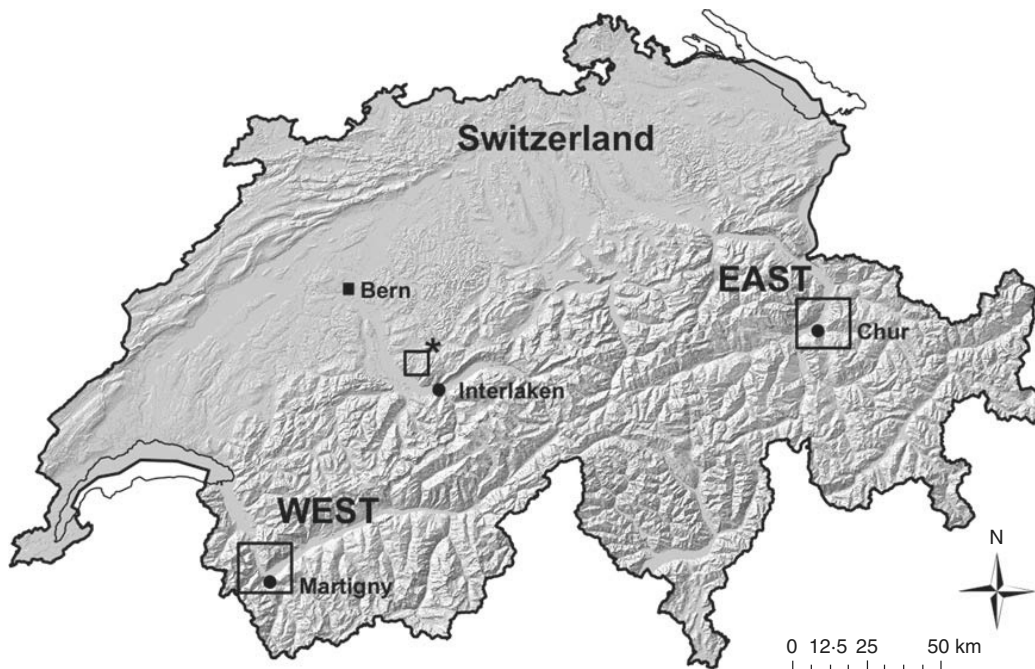


FIG. 1. Locations of the two areas (West and East) selected as seed sources of eight broad-leaved tree species. * Sampling area of *Ilex aquifolium*.

TABLE 1. Mean elevations (with difference in brackets) for the four sampled provenances (West Low, West High, East Low, East High) for each selected species, with type (cold, warm, unstratified) and length (in months) of seed stratification

Species	West Low–High (m)	East Low–High (m)	Type of stratification/length (months)
<i>A. pseudoplatanus</i>	400–1760 (1360)	590–1430 (840)	Cold/2
<i>F. sylvatica</i>	540–1240 (700)	610–1280 (670)	Cold/2
<i>F. excelsior</i>	420–1440 (1020)	570–1230 (660)	Warm, cold/4,4
<i>I. aquifolium</i>	630–1120 (490)	–	Cold/4
<i>L. alpinum</i>	690–1770 (1080)	–	Unstratified
<i>Q. petraea</i>	550–1080 (530)	580–1130 (550)	Unstratified
<i>S. aria</i>	570–1750 (1180)	620–1290 (670)	Cold/5
<i>S. aucuparia</i>	950–2060 (1110)	930–1870 (930)	Cold/5
<i>T. platyphyllos</i>	440–1190 (750)	600–1200 (600)	Cold/6

TABLE 2. Location, long-term temperature/precipitation records and records of the seed sampling year of the two regions (seed sources)

Region	Co-ordinates	Elevation (m a.s.l.)	Temperature _{6–8} [*] (°C) [min–max]	Precipitation _{6–8} [†] (mm a ⁻¹) [min–max]
West	46°19'N 6°58'E	381	19.4 [17.7–21.4]	266 [212–575]
	46°7'N 7°30'E	1825	12.4 [10.7–15.1]	152 [152–447]
East	46°51'N 9°32'E	556	19.2 [17.2–21.9]	280 [223–484]
	46°47'N 9°41'E	1840	11.5 [10.0–14.5]	391 [348–637]

Lowest and highest seasonal means of temperature and precipitation sums during the period 1991–2010 are shown in square brackets.

* Temperature_{6–8}, mean summer temperature from June to August 2009.

† Precipitation_{6–8}, sum of precipitation from June to August 2009.

where this species reaches the highest elevation in Switzerland (see Fig. 1 and Table 1).

Seeds were collected in 2009 from June to November, first at low and later at high elevation, according to their maturation stage. Over the last 20 years, 2009 was a normal year in terms of temperature and slightly drier than average (Table 2). Due to snowmelt, seasons commonly start with high soil moisture and critical water shortage becomes effective only late in the season if at all. For each selected provenance and species, about 500 seeds were collected from each of five trees randomly sampled with a minimal distance of 50 m from each other and within 50 m of elevation. Since seed traits have been shown to be variable even within an individual tree crown (Salisbury, 1976), samples were taken from as many branches and positions within the tree as possible and were pooled per tree. Immediately after collection, seeds were cleaned and aborted, predated or malformed seeds were removed. Seeds from fleshy fruits were separated from the fruit pulp by rinsing squashed fruits with tap water over a sieve. All cleaned seeds were allowed to after-ripen and dry at room temperature (approx. +22 °C). Here and subsequently, the term 'seed' refers to an embryo plus endosperm and seed coat, whereas the seed plus dispersal appendages and pericarp is termed 'diaspore'.

Morphological and physiological seed traits

Prior to measurements, the following parts were removed from the diaspores: wings and pericarp in *F. excelsior*, *A. pseudoplatanus* and *T. platyphyllos*, the pod in *L. alpinum* and the pericarp in *Q. petraea* and *F. sylvatica*. A subsample

of 20 healthy seeds of each individual was analysed for the following morphological traits. Seed dry mass (± 0.01 mg) was obtained after drying at 80 °C for 48 h. The size of dry seed was determined by scanning (300 dpi) and calculating the projected area (software WinSEEDLE Version 2001a). Seed viability was tested applying the tetrazolium test (The International Seed Testing Association, 2006) on a different subsample of 20 seeds per tree and evaluating stained living tissue visually.

NSC (low molecular weight sugars, such as glucose, fructose and sucrose, plus starch) were analysed using the method of Wong (1990) as described in detail in Hoch *et al.* (2002). All NSC concentrations are given on a percentage dry matter basis. Total nitrogen concentration was determined in dry and powdered samples with a CHN elemental analyser (Vario EL III; Elementar Analysensysteme, Hanau, Germany).

Germination trials

Each species was represented by 20 mother trees, ten from each region (East and West), five from high elevation and five from low elevation. For the germination experiment, seeds were stratified by species-specific treatments according to Burkart (2000) (see Table 1). According to these recommendations seeds were mixed with a moist substrate (50 % turf, 50 % sand) in perforated plastic bags. The bags were then stored either outdoors in closed plastic boxes (cold stratification) under roofed (shaded, weather-proof) conditions or indoors in the office (warm stratification; Basel, 47°33'N, 7°36'E). Mean temperature in the cold stratified boxes was 2.8 °C during the stratification period (December 2009 to

TABLE 3. Differences in seed traits between low and high populations of nine broad-leaved tree species in the Swiss Alps

	Seed size	Seed weight	NSC	Nitrogen	Viability	Germination capacity	Germination rate
<i>A. pseudoplatanus</i>	0.193	0.160	< 0.001 / +	0.053 / +	0.689	0.003 / +	0.552
<i>F. sylvatica</i>	0.068	0.066	< 0.001 / +	0.458	0.470	/	/
<i>F. excelsior</i>	0.525	0.116	0.619	0.912	0.036	0.033 /–	0.098
<i>I. aquifolium</i>	0.560	0.840	0.192	0.011 /–	0.763	/	/
<i>L. alpinum</i>	0.906	0.026 / +	0.075	0.439	0.272	0.152	0.035 / +
<i>Q. petraea</i>	0.162	0.093	0.390	0.016 / +	/	/	/
<i>S. aria</i>	0.160	0.179	0.332	< 0.001 /–	0.051	0.050 /–	0.162
<i>S. aucuparia</i>	0.002 / +	< 0.001 / +	< 0.001 / +	< 0.001 /–	0.039 / +	/	/
<i>T. platyphyllos</i>	0.697	0.048 /–	0.008 /–	0.014 /–	0.342	/	/
Overall*	0.266	0.098	< 0.001	0.050	0.294	0.795	0.777

P-values of the factor elevation in the generalized linear model ($P < 0.05$ in bold) are given along with the direction of influence: +, higher trait value at high elevation; –, lower trait value at high elevation; /, no data (low germination or unsuitability of tetrazolium test).

**P*-values obtained from generalized linear mixed effects model across all species (species stated as random effect; see Materials and Methods for details).

March 2010; absolute minimum -6.3 °C). The substrate in the bags was checked regularly to be moist. Seeds of *Q. petraea* were sown in pots and placed outside (unroofed) 1 week after seed collection (Burkart, 2000).

Seeds of *S. aucuparia*, *S. aria*, *A. pseudoplatanus* and *F. sylvatica* were transferred to an unheated, open-window greenhouse and sown on 1 March 2010. Seeds of *F. excelsior*, *T. platyphyllos*, *I. aquifolium* and *L. alpinum* were transferred to the greenhouse and sown on 1 April to account for their known longer dormancy. One hundred ripe seeds per mother tree were randomly chosen and evenly spaced (3×4 cm) in gridded germination trays. They were covered with a layer of substrate corresponding to the diameter of the seed. The substrate was a mix of 30 % pumice stone, 20 % bark compost, 20 % quartz sand, 16 % cocofibre, 10 % turf and 4 % clay. Trays were put on tables and watered regularly with tap water. Every 2 weeks all trays were randomized within the greenhouse to avoid position effects. Daily mean temperatures at seedbed level varied between 9 and 15 °C in March and April and between 10 and 22 °C in May. Daily mean soil temperatures at seed depth oscillated between 10 and 20 °C over the whole germination experiment. The greenhouse was moderately heated overnight during the first two weeks of March.

All seed trays were checked for germinating seeds every 2–3 d. Germination was defined as the first emergence of cotyledons. Germination capacity was defined as the final percentage of germinated seeds, and germination rate (t_{50}) was defined as the time in days required to reach 50 % of final germination percentage.

Data analysis

We assessed general trends in seed traits across species using generalized linear mixed models. We considered region and elevation nested in region as fixed effects, species as random effect and mother tree as the replicated unit [function `lme` in package `nlme` (Pinheiro *et al.*, 2011) within the R statistical software (R Development Core Team, 2011)].

In a second step, the effect of elevation on seed traits was analysed species by species. The corresponding generalized linear models used region and elevation nested in region as linear predictors and Gaussian error distributions. For all

traits and analysis, residuals conformed to the assumptions of normality and homoscedasticity, except for seed-weight and seed-size data which were therefore log-transformed prior to analyses.

Pearson's correlation coefficients were calculated between all traits within species. Furthermore species were ranked by their mean NSC and nitrogen concentrations to evaluate whether these traits are related to species ecological indices (e.g. dispersal type, shade tolerance) as listed by Brzeziecki and Kienast (1994).

RESULTS

Seed size and seed weight

Adult individuals growing at the upper elevational limit of a given species all produced plentiful seeds of good quality (see below). Across the species studied, neither seed size nor seed weight varied consistently between low- and high-elevation provenances (Table 3). For example, seed size of *S. aucuparia* from the low-elevation provenances was significantly smaller than from high-elevation provenances. None of the other species showed significant differences in seed size, but the seed weight of both *L. alpinum* and *S. aucuparia* was heavier at high elevation, whereas the seed weight of *T. platyphyllos* was lighter at high elevation. The other five species investigated did not show significant differences in seed weight between high and low provenances.

Seed carbon-reserves and total nitrogen concentrations

Elevation effects on NSC and nitrogen were inconsistent: in three species (*A. pseudoplatanus*, *F. sylvatica* and *S. aucuparia*) NSC concentrations increased with elevation, in *T. platyphyllos* concentrations decreased and no difference was detected in the other species (Table 3). Both of the *Sorbus* species and *T. platyphyllos* and *I. aquifolium* showed lower seed nitrogen concentrations at higher elevation, whereas in *A. pseudoplatanus* and *Q. petraea* nitrogen concentrations increased with elevation. Neither NSC nor nitrogen concentration was found to correlate with other seed traits, hence there was no relationship between concentrations of NSC or nitrogen and seed viability. NSC and nitrogen

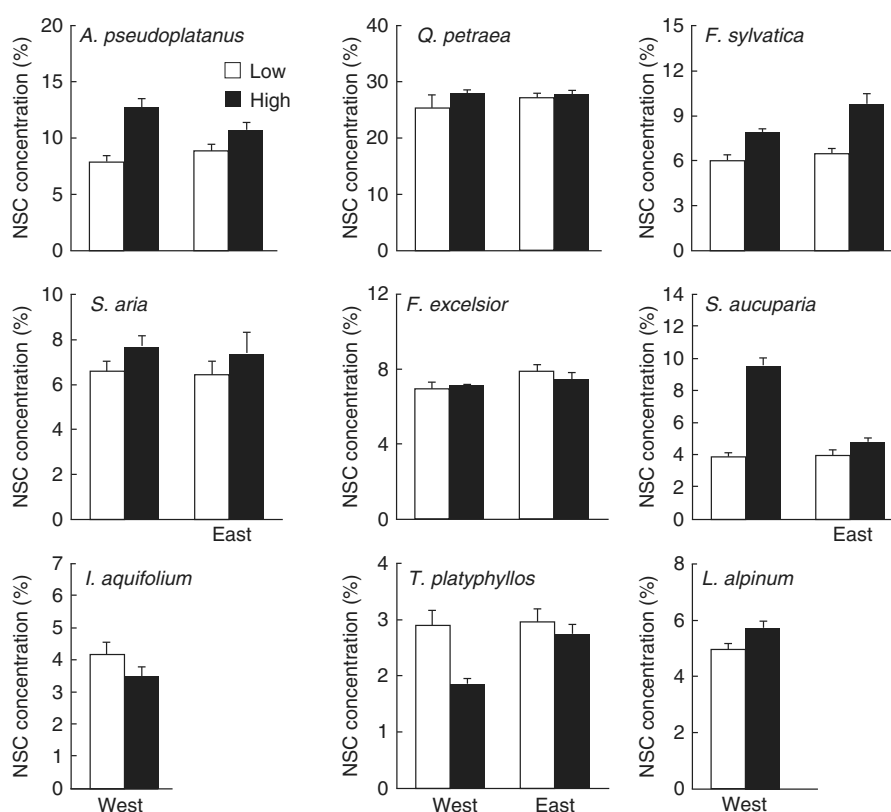


FIG. 2. NSC concentration in seeds of nine broad-leaved tree species from low and high elevation in both selected regions (West Low, West High, East Low, East High). Means and standard errors are shown ($n = 5$ trees per elevation, region and species, with 20 seeds per tree; for statistics see Table 3). Note the different scales for each species.

concentration did not correlate with any of the species ecological indices such as species dispersal type, shade tolerance, frequency of seed crop, temperature index, frost resistance, drought resistance and nitrate index as defined by Brzeziecki and Kienast (1994).

Viability and germination

Seed from high-elevation provenances showed high viability and germination success. The tetrazolium test revealed no effect of elevation on seed viability for seven of the tested species, while for seeds of *Q. petraea* the test was unsuitable (The International Seed Testing Association, 2006). *Sorbus aucuparia* turned out to be the only species in which the fraction of viable seeds was significantly higher in high-elevation seed sources (Table 3).

Despite the positive viability tests, five species (*T. platyphyllos*, both Fagaceae species, *S. aucuparia* and *I. aquifolium*) showed very poor germination irrespective of source elevation. Hence, no statistics for germination can be provided for these species. For the remaining four species, both germination traits (capacity and rate) showed no consistent elevation effect (Table 3). In seeds of *A. pseudoplatanus* germination capacity was significantly higher for high-elevation sources, whereas seeds of *S. aria* and *F. excelsior* showed the

opposite trend and *L. alpinum* showed no trend with elevation. Seeds of *L. alpinum* obtained from high elevations germinated significantly slower than seeds of low-elevation provenances.

In summary, all seed traits studied did not show consistent differences between low and high seed provenances in each of the nine investigated species, except for *Sorbus aucuparia* with seed from high elevation exhibiting an overall higher quality (seed weight, seed size, NSC, viability; Table 3 and Fig. 3). For concentrations of NSC we found a trend for higher concentrations in high elevation seed sources (Table 3 and Fig. 2).

DISCUSSION

At their uppermost elevational limit, the reproductive success of trees may strongly depend on seed quality. Tests of seed quality and germination of seeds from low- and high-elevation provenances of nine broad-leaved tree species revealed no indication that adult trees from high elevations of any of the tested species have difficulties producing viable seed. Elevational differences in traits across species were inconsistent. The seed-failure hypothesis for trees at their upper elevational limit can therefore be rejected for the set of species explored here under the current climatic conditions.

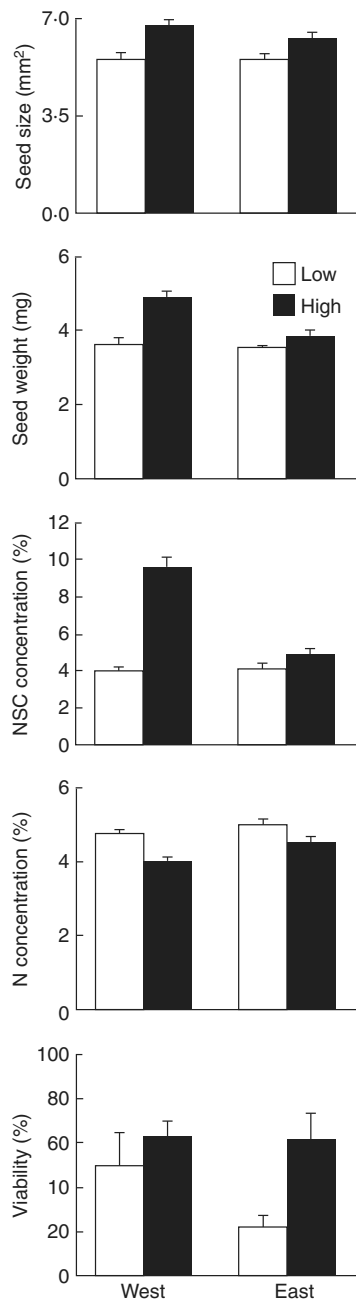


FIG. 3. Differences in seed size, seed weight, nitrogen concentration, NSC concentration and seed viability between low and high provenances of *S. aucuparia* in the two selected regions (West Low, West High, East Low, East High). Means and standard errors are shown ($n = 5$ trees per elevation and region, with 20 seeds per tree; for statistics see Table 3).

Summer temperatures during the year of seed collection (2009) were 12.4/11.5 °C (June to August, West/East) at 1825/1840 m a.s.l., indicating that this year was not out of the temperature range for the last 20 years for both regions (Table 2). The slightly reduced precipitation during June to

August is unlikely to have affected trees in this mountainous terrain, but it is possible that trees at the lowest elevation were affected by the drier conditions during the final part of seed maturation.

Seed size and seed weight

Since the growing season and the period available for seed maturation get shorter the higher the elevation, we expected lower seed weights at the tree species' limits. Surprisingly, seed weight did not show significant differences between high- and low-elevation provenances in six out of nine of the species studied, and the three remaining species showed opposite trends (two increasing, one decreasing). The existing literature is similarly inconsistent in this respect. Some studies showed no change in seed mass with elevation or latitude, e.g. for *Sorbus torminalis* in Croatia (Orsanic, 2009) and for *Nothofagus* spp. in New Zealand (Ledgard and Cath, 1973), while seed weight in *Betula pubescens* was reported to increase with elevation (Holm, 1994). A strong decrease of seed weight in *S. aucuparia* along an elevational gradient from 0 to 600 m a.s.l. in Scotland found by Barclay and Crawford (1984) contrasts with our observations. However, this may reflect a collection bias because the Scottish *Sorbus* seeds were collected on the same day; hence the decrease in seed weight with elevation might reflect incomplete maturation at high elevation. Overall, our data support the notion that seed weight is a conservative trait (Fenner, 1985). It is well known that species retain seed size irrespective of plant size (homeostasis effect) over a wide range of life conditions (Harper *et al.*, 1970), with strong theoretical support (Smith and Fretwell, 1974). Plants vary the number rather than the size of their seeds. Based on the optimization theory, the mother plant should invest in fewer seeds if reserves for reproduction are scarce. Hence we would expect high-elevation trees to produce fewer seeds than trees at low elevation if there were resource limitations. This is hard to assess for isolated tall trees in closed mountain forest, but from our experience during the seed harvesting campaign, there was no obvious decline in seed numbers with elevation in the deciduous species. The seed quality traits (NSC, nitrogen), however, did not indicate any resource limitation at the upper distribution limits. The data for *S. aucuparia* may reflect the smaller stature of this species, causing the lower-elevation individuals to be suppressed by tall trees in the montane forest, whereas the individuals at the tree-line profited from full sun exposure and hence tended to produce larger, heavier, more viable seeds with higher NSC and lower nitrogen concentration.

Seed carbon-reserves and total nitrogen concentrations

The majority of the investigated species exhibited high concentrations of NSC and nitrogen in seeds from the uppermost trees and revealed no indication of carbon shortage or nutrient starvation. In fact, most of the species even tended to have higher NSC concentrations in seeds from high elevation (Fig. 2), matching general trends of mobile carbon charging in high elevation-tree tissues (e.g. Hoch *et al.*, 2003; Shi *et al.*, 2008). In the case of seeds, we cannot exclude ecotypic differentiation for higher quality of seed near the upper tree

species limit, although the isolation of these outpost trees and the presumed gene-flow from lower elevation make this unlikely. These trends may equally well reflect the consequences of retarded growth rate of trees at otherwise hardly constrained CO₂ uptake, with the inevitable consequence of high abundance of non-structural carbon compounds (growth-limitation hypothesis; Körner, 1998, 2003). It remains open whether seedlings take advantage from that trend of higher NSC reserves at our high-elevation sites. The fact that seed size and weight do not decline with elevation in most of the nine species studied indicates that seed growth is not constrained at the current tree-species limit, perhaps because it is confined to the warmest part of the season. We attribute the missing correlation between germination rate and NSC concentrations (in otherwise viable seeds) to developmental constraints (seed dormancy). Unlike NSC, nitrogen did not show a consistent trend with elevation across species. Hence, if there were elevational reductions in tree nutrient supply, these are not reflected in seeds' nitrogen concentrations, which was also found in leaves (Körner, 1989; Birman and Körner, 2009).

Viability and germination

As with our first hypothesis of lower seed quality at high elevations, our second hypothesis predicting lower germination success in seeds sourced from the upper range limit, is not supported by the current study. However, five of the species studied germinated poorly (across all provenances) and could thus not be taken into account for the germination analyses. Fungal infections (in *Q. petraea* and *S. aucuparia*) and insufficient time to complete the needed seed coat decay (in *I. aquifolium*) were likely explanations for the very low germination success, while we have no explanation for the low germination success in *F. sylvatica*. For *T. platyphyllos* it is known from nurseries that it is generally hard to raise plants from seed.

As seen in our results, trends in germination capacity have been previously reported to be species dependent. An increase of germination capacity with increasing latitude was found in *Betula papyrifera* (Bevington, 1986), whereas a decreasing capacity with elevation or latitude was found in *Abies guatemalensis*, *Pinus sylvestris*, *Picea mariana*, *Nothofagus pumilio* and *Betula* spp. (Engler, 1913; Holm, 1994; Sveinbjörnsson *et al.*, 1996; Cuevas, 2000; Sirois, 2000; Strandby Andersen *et al.*, 2008). The lack of an overall decline in germination capacity with increased elevation observed here, might relate to the monotone life conditions far below the tree-line. Like the overall germination success, the rate (speed) of germination (analysed as the date by which 50% of the final germination was reached) did not show a consistent elevational trend across the four species that germinated well. Only one species (*L. alpinum*) showed significantly slower germination in seeds from higher elevation. Since all germination trials were conducted under 'common garden' conditions at low elevation, *in situ* germination behaviour remains to be explored, yet the observed seedling success of high-elevation provenances (Y. Vitasse *et al.*, unpubl. res.) suggests that the seed traits observed here scale to reproductive fitness.

Conclusions

In summary the present study revealed two major outcomes.

(1) High-elevation seed sources exhibit high quality, similar to those produced by trees growing under close-to-optimal conditions (lower elevation). In addition, seeds of high-elevation provenances of *S. aucuparia* (at the tree-line) exhibit an even higher quality than their lower-elevation counterparts, indicating that life conditions at the cold boundary of deciduous tree growth do not constrain seed development.

(2) Consequently, as the seed traits were largely unchanged from the optimum stands to the low-temperature limits of the tree species investigated, the notion is supported that reproduction at the upper-elevation species limit is not limited by seed quality. Since proper seed formation and germination success constitute only one chapter of the demographic novel (Moles and Westoby, 2006), extended studies of population dynamics are needed to complement the current results (Lenoir *et al.*, 2009). Based on our ongoing work (Y. Vitasse *et al.*, unpubl. res.) and the data presented here, there is successful tree recruitment above the current deciduous species limits in Switzerland. These results are consistent with the general rise in elevation of species-abundance peaks in trees (Lenoir *et al.*, 2009).

ACKNOWLEDGEMENTS

We thank Niklaus Zimmermann and Thomas Wohlgemuth for their advice on high-elevation broad-leaved tree positions in Switzerland and Anton Burkart for his advice on seed treatments. We also thank Pascale Flury and Lea Steinle for field assistance and the Technologiezentrum Witterswil for providing their large greenhouse for the germination trials. This work was supported by the European Research Council (233399) and carried out as part of the TREELIM project.

LITERATURE CITED

- Aeschimann D, Lauber K, Moser DM, Theurillat JP. 2004. *Flora alpina*. Paris: Belin.
- Austin MP, Smith TM. 1989. A new model for the continuum concept. *Vegetatio* 83: 35–47.
- Barclay AM, Crawford RMM. 1984. Seedling emergence in the rowan (*Sorbus aucuparia*) from an altitudinal gradient. *Journal of Ecology* 72: 627–636.
- Bevington J. 1986. Geographic differences in the seed germination of paper birch (*Betula papyrifera*). *American Journal of Botany* 73: 564–573.
- Birmann K, Körner C. 2009. Nitrogen status of conifer needles at the alpine tree-line. *Plant Ecology & Diversity* 2: 233–241.
- Brändli U-B. 2010. *Swiss National Forest Inventory – results of the third inventory 2004–2006*. Bern: Paul Haupt.
- Brzeziecki B, Kienast F. 1994. Classifying the life-history strategies of trees on the basis of the Grimian model. *Forest Ecology and Management* 69: 167–187.
- Burkart A. 2000. *Kulturbücher. Angaben zur Samenernte, Klengung, Samenlagerung, Samenausbeute und zur Anzucht von Baum- und Straucharten*. Birmensdorf: Swiss Federal Institute for Forest, Snow and Landscape Research, WSL.
- Cuevas JG. 2000. Tree recruitment at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego, Chile. *Journal of Ecology* 88: 840–855.
- Engler A. 1913. Einfluss der Provenienz des Samens auf die Eigenschaften der forstlichen Holzgewächse. *Mitteilungen der Schweizerischen Centralanstalt für das forstliche Versuchswesen* 10: 189–386.
- Fenner M. 1985. *Seed ecology*. London: Chapman and Hall.

- Grenier M, Sirois L. 2009.** Reproductive development and seed ripening in *Betula papyrifera* along an altitudinal thermal gradient in eastern Appalachia (Canada). *Botany* **87**: 492–500.
- Guisan A, Zimmermann NE. 2000.** Predictive habitat distribution models in ecology. *Ecological Modelling* **135**: 147–186.
- Harper JL, Lovell PH, Moore KG. 1970.** The shapes and sizes of seeds. *Annual Review of Ecology, Evolution, and Systematics* **1**: 327–356.
- Hoch G, Körner C. 2011.** Global patterns of mobile carbon stores in trees at the high-elevation tree line. *Global Ecology and Biogeography*, in press. <http://dx.doi.org/10.1111/j.1466-8238.2011.00731.x>.
- Hoch G, Popp M, Körner C. 2002.** Altitudinal increase of mobile carbon pools in *Pinus cembra* suggests sink limitation of growth at the Swiss tree-line. *Oikos* **98**: 361–374.
- Hoch G, Richter A, Körner C. 2003.** Non-structural carbon compounds in temperate forest trees. *Plant, Cell & Environment* **26**: 1067–1081.
- Holm SO. 1994.** Reproductive patterns of *Betula pendula* and *B. pubescens* Coll. along a regional altitudinal gradient in northern Sweden. *Ecography* **17**: 60–72.
- Jalas J, Suominen J. 1988.** *Atlas florae Europaeae: distribution of vascular plants in Europe*. Cambridge: Cambridge University Press.
- Körner C. 1989.** The nutritional status of plants from high altitudes – a world-wide comparison. *Oecologia* **81**: 379–391.
- Körner C. 1998.** A re-assessment of high-elevation tree-line positions and their explanation. *Oecologia* **115**: 445–459.
- Körner C. 2003.** *Alpine plant life*. Berlin: Springer.
- Körner C. 2007.** Climatic tree-lines: conventions, global patterns, causes. *Erdkunde* **61**: 316–324.
- Kudo G. 1996.** Effects of snowmelt timing on reproductive phenology and pollination process of alpine plants. *Memoirs of National Institute of Polar Research Special Issue* **51**: 71–82.
- Ledgard NJ, Cath PW. 1973.** Seed of New Zealand *Nothofagus* species: studies of seed weight, viability, shape and the effect of varying stratification periods. *New Zealand Journal of Forestry* **28**: 150–162.
- Lenoir J, Gégout J-C, Pierrat J-C, Bontemps J-D, Dhôte J-F. 2009.** Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). *Ecography* **32**: 765–777.
- Marcora P, Hensen I, Renison D, Seltmann P, Wesche K. 2008.** The performance of *Polylepis australis* trees along their entire altitudinal range: implications of climate change for their conservation. *Diversity and Distributions* **14**: 630–636.
- Moles AT, Westoby M. 2006.** Seed size and plant strategy across the whole life cycle. *Oikos* **113**: 91–105.
- Naegle ER, Burton JW, Carter TE, Ruffy TW. 2005.** Influence of seed nitrogen content on seedling growth and recovery from nitrogen stress. *Plant and Soil* **271**: 329–340.
- Oleksyn J, Modrzynski J, Tjoelker MG, Zytkowski R, Reich PB, Karolewski P. 1998.** Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. *Functional Ecology* **12**: 573–590.
- Orsanic M. 2009.** Variability of morphological and biological characteristics of wild service tree (*Sorbus torminalis* (L.) Crantz) fruits and seeds from different altitudes. *Periodicum Biologorum* **111**: 495–504.
- Pigott CD, Huntley JP. 1978.** Factors controlling distribution of *Tilia cordata* at northern limits of its geographical range. 1. Distribution in northwest England. *New Phytologist* **81**: 429–441.
- Pigott CD, Huntley JP. 1981.** Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. 3. Nature and causes of seed sterility. *New Phytologist* **87**: 817–839.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team. 2011.** nlme: linear and nonlinear mixed effects models. R package version 3-1-102.
- Pluess AR, Schutz W, Stöcklin J. 2005.** Seed weight increases with altitude in the Swiss Alps between related species but not among populations of individual species. *Oecologia* **144**: 55–61.
- R Development Core Team. 2011.** *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Salisbury E. 1976.** Exceptional fruitfulness and its biological significance. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **193**: 455–460.
- Shi P, Körner C, Hoch G. 2008.** A test of the growth-limitation theory for alpine tree line formation in evergreen and deciduous taxa of the eastern Himalayas. *Functional Ecology* **22**: 213–220.
- Sirois L. 2000.** Spatiotemporal variation in black spruce cone and seed crops along a boreal forest-tree line transect. *Canadian Journal of Forest Research* **30**: 900–909.
- Smith CC, Fretwell SD. 1974.** The optimal balance between size and number of offspring. *The American Naturalist* **108**: 499–506.
- Strandby Andersen U, Prado Cordova JP, Bräuner Nielsen U, Kollmann J. 2008.** Provenance variation in germination and seedling growth of *Abies guatemalensis* Rehder. *Forest Ecology and Management* **255**: 1831–1840.
- Sveinbjörnsson B, Kauhanen H, Nordell O. 1996.** Tree-line ecology of mountain birch in the Torneträsk Area. *Ecological Bulletins* **45**: 65–70.
- The International Seed Testing Association. 2006.** *International rules for seed testing*. Bassersdorf: The International Seed Testing Association (ISTA).
- Wohlgemuth T. 1992.** Die vegetationskundliche Datenbank. *Schweizerische Zeitschrift für das Forstwesen* **143**: 22–36.
- Wong SC. 1990.** Elevated atmospheric partial-pressure of CO₂ and plant growth. 2. Non-structural carbohydrate content in cotton plants and its effect on growth parameters. *Photosynthesis Research* **23**: 171–180.

Chapter 6

Tree recruitment of European tree species at their current upper elevational limits in the Swiss Alps

Yann Vitasse, Günter Hoch, Christophe F. Randin, Armando Lenz, Chris Kollas and Christian Körner

Journal of Biogeography, (2012) 39:1439-1449

ORIGINAL
ARTICLE

Tree recruitment of European tree species at their current upper elevational limits in the Swiss Alps

Yann Vitasse*, Günter Hoch, Christophe F. Randin, Armando Lenz,
Chris Kollas and Christian Körner

*Institute of Botany, University of Basel,
4056 Basel, Switzerland*

ABSTRACT

Aim The physical and physiological mechanisms that determine tree-line position are reasonably well understood, but explanations for tree species-specific upper elevational limits below the tree line are still lacking. In addition, once these uppermost positions have been identified, questions arise over whether they reflect past expansion events or active ongoing recruitment or even upslope migration. The aims of this study were: (1) to assess current tree recruitment near the cold-temperature limit of 10 major European tree species in the Swiss Alps, and (2) to rank species by the extent that their seedlings and saplings exceed the elevational limit of adult trees, possibly reflecting effects of the recent climate warming.

Location Western and eastern Alps of Switzerland.

Methods For each species, occurrences were recorded along six elevational transects according to three size classes from seedlings to adult trees in 25-m-elevation steps above and below their regional upper elevational limit. Two methods were used to compare upper elevational limits between seedlings, saplings and adults within species. First, we focused on the uppermost occurrence observed in each life stage for a given species within each studied region; and second, we predicted their upper distribution range using polynomial models fitted to presence/absence data.

Results Species exhibited a clear ranking in their elevational limit. Regional differences in species limits (western versus eastern Swiss Alps) could largely be attributed to regional differences in temperature. Observed and predicted limits of each life stage showed that all species were represented by young individuals in the vicinity of the limit of adult trees. Moreover, tree recruitment of both seedlings and saplings was detected and predicted significantly beyond adult tree limits in most of the species. Across regions, seedlings and saplings were on average found at elevations 73 m higher than adult trees.

Main conclusions Under current conditions, neither seed dispersal nor seedling establishment constitutes a serious limitation of recruitment at the upper elevational limits of major European trees. The recruits found beyond the adult limits demonstrate the potential for an upward migration of trees in the Alps in response to ongoing climate warming.

Keywords

Alps, climate change, elevational gradient, low temperature, seedlings, Switzerland, tree recruitment, upper elevational limit.

*Correspondence: Yann Vitasse, Institute of Botany, University of Basel, 4056 Basel, Switzerland.
E-mail: yann.vitasse@unibas.ch

INTRODUCTION

When assessing the population dynamics of tree species at the 'leading edge' of their distribution area, most studies have

focused on changes occurring at the tree-line ecotone (the zone between closed forest and uppermost tree establishment irrespective of species). A number of these studies have suggested that tree-line elevation is likely to increase in

response to climatic change in many locations (Harsch *et al.*, 2009). However, an upward shift of the tree line does not necessarily mean that other species-specific limits below the tree line will move upslope as well, although the position of the abundance peak of tree species has been shown to have shifted upslope in recent years (Lenoir *et al.*, 2008; Akatov, 2009). While the close association of tree line with temperature (Körner & Paulsen, 2004) and the mechanisms controlling tree line are reasonably well explained (Körner, 2007a), the species-specific controls of the upper limits of broad-leaved taxa are poorly understood. There are very few studies focusing on the upper elevational limits of broad-leaved species that include their various tree life stages (but see Lenoir *et al.*, 2009; Mellert *et al.*, 2011). Elevational ranges of tree species exhibit large differences, with some species restricted to low elevations, others ranging to mid-montane conditions, and a few able to advance to the regional tree line (Ohsawa, 1995; Körner *et al.*, 2005). For non-tree-line tree species, an accurate assessment of the upper elevational limits is still missing for many species, especially at a regional scale. Temperature is assumed to be the primary factor determining such below-tree-line species limits (Woodward, 1990; Pither, 2003), with the physiological mechanisms involved mostly unknown. For the tree-line ecotone, local influences, such as competitive exclusion, herbivory, and geomorphic and anthropogenic disturbance, potentially may modify the current upper limits of tree species at local and regional scales (Cairns & Moen, 2004; Gehrig-Fasel *et al.*, 2007; Moen *et al.*, 2008), but the global nature of the tree-line phenomenon suggests the possibility of a uniform overarching climatic control (Körner, 2007a). On a regional or a global scale, there are many ways in which temperature may be related to such limits, with a distinction to be made between the gradual influence of temperature, which might directly affect growth rates, and extreme events such as late spring frosts, which could affect survival (Körner, 2007a,b). Among the main possible temperature constraints on tree performance at their leading edge of distribution are the ability of tissue to form (structural growth), successful reproduction and germination, seedling establishment and seedling survival, as well as the ability to survive freezing temperature (Sakai & Weiser, 1973; Woodward & Williams, 1987; Woodward, 1990; Morin *et al.*, 2007; Körner, 2012). So far, there is no satisfactory explanation for the different low-temperature limits of different species.

A species' seedling limit is defined here as the uppermost location of tree seedlings of a given species within the montane forest belt (Lenoir *et al.*, 2009). For non-tree-line species, the elevational limit of seedlings may be of particular significance when assessing the potential future response of the species' distribution range to climatic warming. Unlike the situation beyond the tree line, such recruits continue to profit from forest shelter, and thus have a good chance of becoming adults. However, sensitivity to climate may differ between adult and young trees (Grubb, 1977), and the transition from seed to seedling is known to be a major bottleneck in tree recruitment (Stohlgren *et al.*, 1998; Clark *et al.*, 2007). Thus, it is crucial to know the recruitment status to understand why a species' local

upper margins advance, retreat, or stand still (Clark *et al.*, 2007). The absence of young trees close to adult tree limits may reflect the effects of recent extreme events, which might have killed younger cohorts that are less resistant than adults (Jump *et al.*, 2009). However, trees may also be much less exposed to such events during their early developmental stages, because of snow-cover protection or other shelter effects in the forest. For instance, the presence of evergreen conifers around the upper elevational limit of a given broad-leaved species may facilitate its development during its early life stages. An absence of young trees may also arise either from the inability of adult trees to produce viable seeds or/and from a limitation of upward dispersal from lower-elevation seed sources. Conversely, the presence of seedlings and saplings beyond the adult life stage margins would suggest that seedling establishment is possible at these elevations, irrespective of where the seeds came from. Climate warming may enhance the expansion of species beyond their current range limits (Kullman, 2002; Lenoir *et al.*, 2009). While the uppermost position of adult trees along an elevational gradient indicates that those trees have been able to cope with local conditions for several decades, their presence alone does not tell us whether this adult limit represents a 'dynamic' front. In relation to ongoing climate warming, we would expect a higher upper elevational limit of seedlings than of adults of the same species.

Based on a presence/absence survey we aim to assess the presence of seedlings, saplings and adults of 10 major European tree species below, at and above their regional upper elevational limits within the Swiss Alps. More specifically, we address the two following questions. (1) Do the elevational limits of juvenile trees match with the limits of the adult trees? (2) Which species have the greatest potential for extending their distribution limit in the future?

MATERIALS AND METHODS

Study area and climate

A preliminary exploration of dominant broad-leaved tree species distributions using databases in Switzerland revealed two well-delimited regions in the Alps where a large number of species reach their maximum elevational limits (Brändli, 2010). These two areas were selected, and a demographic survey conducted along six elevational transects. The first area is located around Martigny (western Swiss Alps, 46°08' N–46°11' N; 07°02' E–07°04' E) and the second one around Chur (eastern Alps of Switzerland, 46°50' N–46°56' N; 09°30' E–09°37' E; Table 1). The linear distance between these two selected regions is about 200 km.

They are characterized by a temperate continental climate. However, the eastern region is colder and slightly drier than the western region. From 1961 to 1990, the mean annual precipitation was 1209 mm and 1472 mm, and the mean summer temperature (from June to August) was 11.2 °C and 12.5 °C at 1500 m a.s.l. in the eastern and western transects, respectively.

Table 1 Location, elevational range and slope aspect of the transects in the western and eastern Alps of Switzerland.

Area	Transect	Elevational range (m a.s.l.)	Latitude*	Longitude*	Slope aspect	Rainfall* (mm)	T_{6-8}^* (°C)
West	W1	1100–2200	46°11' N	07°02' E	SW	1501	12.6
	W2	1060–2200	46°09' N	07°03' E	SW	1464	12.4
	W3	1100–2200	46°08' N	07°04' E	S	1451	12.4
East	E1	975–1800	46°50' N	09°37' E	SW	1088	11.6
	E2	600–1775	46°53' N	09°30' E	E	1219	11.1
	E3	850–1800	46°56' N	09°30' E	E	1321	10.8

*Latitude and longitude points refer to those recorded at 1500 m a.s.l. for each transect, with the corresponding annual rainfall and summer temperature. T_{6-8} , mean daily temperature from 1 June to 31 August during the period 1961–1990.

We calculated monthly linear lapse rates from long-term monthly mean temperature data (1961–1990) from 115 climate stations taken from the national meteorological network of Switzerland. Next, we normalized the monthly values to sea level (0 m a.s.l.), using the regression lapse rates, and interpolated the sea-level data to the whole surface of both study areas at 25-m resolution using thin-plate SPLINE functions (Franke, 1982; Mitas & Mitasova, 1988). The spatially interpolated values (representing locally adjusted regression intercepts) were reprojected to actual elevations using the 25-m DEM (Digital Elevation Model) of Switzerland (DHM25; <http://www.swiss topo.admin.ch/internet/swisstopo/en/home/products/height/dhm25.html>) and the regression lapse rates. This procedure in essence follows the approach developed by Zimmermann & Kienast (1999). Summer temperature (from June to August) was used as a proxy to characterize the temperature during the growing season. Lastly, a linear lapse rate of summer temperature was recalculated for each transect and the elevational position of the highest adult tree of each species within a given region was converted to temperature using the lapse rate equation of the corresponding transect. Over the six studied transects, the lapse rate during summer ranged between 0.50 and 0.59 K 100 m⁻¹ with a mean of 0.55 K 100 m⁻¹.

Study species

The study focuses on the main tree species and tall shrubs (e.g. *Corylus avellana*, *Laburnum alpinum*) occurring in the Swiss Alps. However, we disregarded some species, either because their numbers were too low ($n < 50$ per region across all three transects) or because their upper limits exceeded our survey elevational range (typically for species forming the tree line such as *Pinus cembra* or *Larix decidua*). Consequently, we focused on 10 species belonging to seven plant families. These species exhibit contrasting seed dispersal strategies, namely (1) wind dispersal (anemochory) for *Acer pseudoplatanus* L., *Fraxinus excelsior* L. and *Abies alba* Mill.; (2) unassisted dispersal (barochory) with only secondary animal dispersal for *Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl., *Corylus avellana* L. and *Laburnum alpinum* (Mill.) Bercht. & J. Presl; and (3) bird dispersal (zoochory) for *Prunus avium* L., *Sorbus aria* L. and *Sorbus aucuparia* L.

Survey method

Surveys were conducted along forested elevational transects replicated three times in each of the two regions. The maximum linear distance between any two transects within an area was about 8 km for the western transects and 17 km for the eastern transects. Transects started from 600 m a.s.l. in the eastern region and from 1100 m in the western region and were extended upslope until none of the studied species were found (up to 2200 m in the western area; Table 1). The western transects were located on south- or south-west-facing slopes, whereas one of the eastern transects was located on a south-facing slope and the two others on east-facing slopes. Along each transect, the presence of seedlings, saplings and adults of all tree species was recorded every 25 m of elevation increase following the fall line of the slope. Signs of browsing damage for each size class were also recorded. At every 25-m step, an area of about 500 m² was surveyed on both the left and the right side of the virtual line of the transect. Trees were classified into three age/size categories: (1) seedling for height < 0.5 m, (2) sapling for height 0.5–4 m or for height > 4 m but with a diameter at breast height (d.b.h.) < 0.15 m, and (3) adult for height > 4 m and d.b.h. > 0.15 m (Table 2). However, small adult tree species and transitory shrubby species that can exhibit multi-stem architecture (i.e. *C. avellana*, *L. alpinum*, *S. aria* and *S. aucuparia*) were considered as saplings between 0.5 and 2 m height and as adults above 2 m irrespective of their d.b.h. (Table 2). We did not rank 'adults' by actual reproduction, given that reproduction is too irregular, but those individuals ranked as adults have a size at which reproducing individuals were seen during the survey.

Table 2 Characteristics of the various age size classes of trees used in the demographic survey.

Life stage	Criterion
Seedlings	Height 0.00–0.50 m
Saplings*	Height 0.50–4 m or height > 4 m and d.b.h. < 0.15 m
Adult trees*	Height > 4 m and d.b.h. ≥ 0.15 m

**Corylus avellana*, *Sorbus aucuparia*, *S. aria* and *Laburnum alpinum* were considered as saplings for height 0.50–2 m and as adults for height > 2 m, irrespective of their d.b.h. (diameter at breast height).

In most cases the surveyed transects followed the slope, but they were shifted sideways to avoid natural barriers (e.g. rocks or cliffs) and obvious human disturbances.

Presence/absence records analysis

For each species, and each region, we considered the upper elevational limit of adults observed (OL_{Adult}) as the uppermost occurrence of an individual belonging to the adult size class. In a similar way, we defined the observed upper elevational limits of seedlings ($OL_{Seedling}$) and saplings ($OL_{Sapling}$). The species limits were not defined per transect but rather per region, because the surveyed transects were very close to each other in a given region and shared similar climatic conditions.

For each selected species, a generalized linear model (GLM; McCullagh & Nelder, 1989) with a binomial probability distribution and a logit link function was fitted using presence/absence data against elevation for each of the three classes within each study region. Second-order polynomials (linear and quadratic terms) were allowed for elevation as the response variable using the polynomial function of the Design library (Azola & Harrell, 2006) in R software (R Development Core Team, 2011). This type of response curve was appropriate to allow easy comparisons between elevational limits of the three life stage categories focusing on the leading edge of the distribution (but see Austin & Gaywood, 1994 for a discussion on the shape of response curves). The model fit was estimated with the adjusted geometric mean squared improvement R^2 (Cox & Snell, 1989; Nagelkerke, 1991). This R^2 is rescaled for a maximum of 1 and adjusted for the numbers of both observations and predictors in the model. The predictive power of the GLM was evaluated by running a 10-fold cross-validation (Van Houwelingen & Le Cessie, 1990) on the training data set. During the cross-validation procedure of the GLM, the original prevalence of the species presences and absences in the data set was maintained in each fold. Based on the predictions emerging from the cross-validation, the area under the curve (AUC) of a receiver operating characteristic plot (ROC; Fielding & Bell, 1997) was calculated for each model. AUC takes values between 0 and 1, where 0.5 means no agreement, 0 an inverse relationship (errors better predicted), and 1 perfect agreement. The probability of occurrence for each species was predicted along elevation within the range of the observations for each of the three life stage categories. The predicted upper elevational limits of seedlings ($PL_{Seedling}$), saplings ($PL_{Sapling}$) and adults (PL_{Adult}) calculated from the GLMs were defined as the elevation corresponding to the 10% probability of occurrence. We decided to use the 10% probability values in the graphs and analyses because they are more conservative and closer to the majority of observed limits than absolute maxima. The transect E1 was removed from GLMs for *Abies alba* and *Fagus sylvatica* because these two species were almost absent from the transect (fewer than five occurrences). Irrespective of the size class (seedlings, saplings and adults), the AUC values of the GLMs ranged between 0.56 and 0.83 with most being higher than 0.65, and

R^2 values ranged between 0.08 and 0.44 with most being higher than 0.20 (see Appendix S1 in the Supporting Information). Our models allowed us to compare the upper elevational limits by taking into account the whole distribution of a given species along elevational gradients within the studied region. In contrast, when using field data, we compared the uppermost limits of each class of a given species using only the uppermost observed occurrence. Hence, models were used to support the idea that the difference found among the three life stages is not only attributable to the uppermost individual.

The differences of observed and predicted upper elevational limits between seedlings, saplings and adult trees among the 10 studied species were analysed for significance within and across regions using Student's paired-sample *t*-test. The survey data were examined before analysis and found to conform to a normal distribution. Correlations between OL_{Adult} and summer temperature at OL_{Adult} found in the two studied regions were assessed by Pearson's correlation coefficient. All statistical analyses were performed using R software 2.12.2 (R Development Core Team, 2011).

RESULTS

Ranking species upper elevational limits and comparisons among study areas

The upper elevational limits of the studied adult trees (OL_{Adult}) differed among species but revealed a consistent pattern of similar relative positions of species between regions (Pearson correlation coefficient $r = 0.93$, $P < 0.001$, Fig. 1). *Fraxinus excelsior* had the lowest position (1460 m, mean of the two regions) and *S. aucuparia* the highest (1975 m), with the other species ranked in between (Fig. 1). However, OL_{Adult} significantly differed between the two regions and was always higher for the western transects (paired *t*-test: $t = 7.23$, $P < 0.001$). This mean absolute difference was 261 m, with the smallest contrast found in *Fraxinus excelsior* ($\Delta OL_{Adult} = 75$ m) and the largest in the three highest species: *Abies alba*, *S. aria* and *S. aucuparia* ($\Delta OL_{Adult} \geq 350$ m, Fig. 1). Interestingly, when replacing elevation by the corresponding interpolated mean temperature during the growing season for the three transects per region, no significant difference was observed between the two regions' tree species limits ($t = 0.55$, $P = 0.60$). On average, the mean absolute difference was 0.55 K (Fig. 1), which corresponds to an elevational difference of 100 m. Thus, temperature explained most of the discrepancy in elevation found between the two regions. Furthermore, the differences in species-specific limits between the two regions were smaller than 0.5 K for five out of eight species common to both regions, with the largest differences found in the two highest species, *S. aucuparia* and *S. aria* (1.3 K and 0.8 K, respectively; Fig. 1).

Seedling/sapling tree limits versus adult tree limits

Across regions, the upper elevational limits of both seedlings ($OL_{Seedling}$) and saplings ($OL_{Sapling}$) were significantly higher

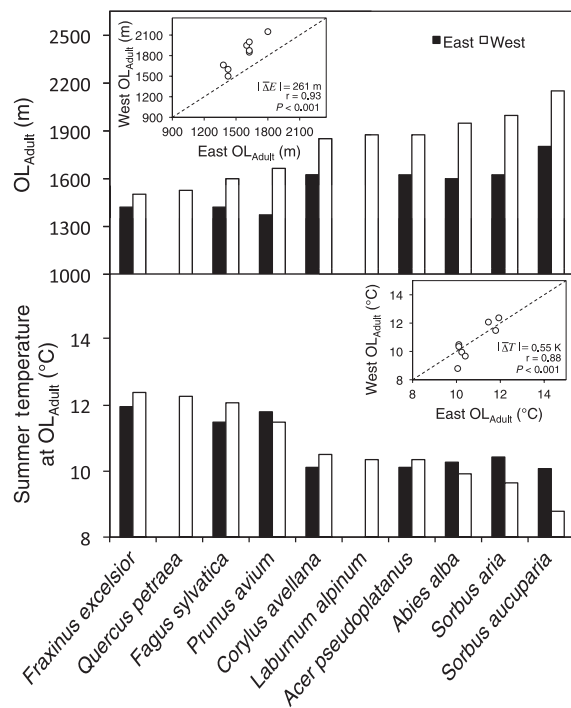


Figure 1 Elevation (upper graphs) and summer temperature (bottom graphs) of the uppermost adult tree for each of 10 species observed in both study areas, namely western and eastern Switzerland. Each bar corresponds to the elevation or summer temperature of the highest adult individual found within the three transects examined in the western part of Switzerland (white bars) and in the eastern part (black bars). Summer temperature corresponds to the mean of daily temperature from 1 June to 31 August from 1961 to 1990. OL_{Adult} , upper elevational limits observed for adult class; $|\Delta E|$, mean absolute difference of elevation between OL_{Adult} of the two studied regions; $|\Delta T|$, mean absolute difference of summer temperature between OL_{Adult} of the two studied regions. Note that the discrepancy between regions disappears when temperature rather than elevation is considered (the two inset diagrams).

than OL_{Adult} among the 10 studied species: about $69 \text{ m} \pm 19 \text{ m}$ (mean difference $\pm 1 \text{ SD}$, $t = 3.67$, $P = 0.002$) and $76 \text{ m} \pm 24 \text{ m}$ ($t = 3.19$, $P = 0.005$), respectively (paired

Table 3 Differences in elevation (m) between observed or predicted seedling and sapling limits and the adult tree limits in both study regions (western and eastern Switzerland).

	West (n = 10)	P	East (n = 8)	P	Overall (n = 18)	P
$OL_{Seedling} - OL_{Adult}$	67.5 (± 25.0)	0.025	70 (± 30.0)	0.052	68.6 (± 18.7)	0.002
$OL_{Sapling} - OL_{Adult}$	72.5 (± 34.8)	0.067	79.4 (± 33.4)	0.049	75.6 (± 23.7)	0.005
$OL_{Sapling} - OL_{Seedling}$	5.0 (± 28.5)	0.864	-9.4 (± 31.7)	0.776	-6.94 (± 20.5)	0.739
$PL_{Seedling} - PL_{Adult}$	81.4 (± 29.9)	0.024	61.6 (± 49.2)	0.250	72.6 (± 26.7)	0.015
$PL_{Sapling} - PL_{Adult}$	76.5 (± 37.1)	0.069	85.5 (± 50.2)	0.133	80.5 (± 29.5)	0.014
$PL_{Sapling} - PL_{Seedling}$	4.9 (± 26.2)	0.856	-23.9 (± 43.0)	0.596	-7.9 (± 23.5)	0.741

$OL_{Seedling}$, $OL_{Sapling}$, OL_{Adult} , upper elevational limits observed for seedling, sapling and adult classes, respectively; $PL_{Seedling}$, $PL_{Sapling}$, PL_{Adult} , predicted limits from generalized linear models with probability of occurrence of 10% for seedling, sapling and adult classes, respectively.

P represents probability values from Student's paired-sample *t*-tests ($P < 0.10$ in bold font). Standard errors of the mean are provided in parentheses.

t-test, Table 3). $OL_{Seedling}$ and $OL_{Sapling}$ were observed at slightly lower elevations than OL_{Adult} in both regions for *S. aucuparia* only. $OL_{Seedling}$ was found to be lower than OL_{Adult} in the eastern region for *S. aria* and the sub-canopy species *C. avellana*. $OL_{Sapling}$ was observed at lower elevations than OL_{Adult} for *S. aria* and *C. avellana* in the western and the eastern region, respectively (Fig. 2). Finally, $OL_{Seedling}$ and $OL_{Sapling}$ were found at the same elevation as OL_{Adult} for the other sub-canopy species *L. alpinum*. In all the other species, $OL_{Seedling}$ and $OL_{Sapling}$ were found at higher elevations than OL_{Adult} (Fig. 2). The highest discrepancy between juvenile trees and OL_{Adult} was found for *Quercus petraea* and *Fagus sylvatica*, where seedlings and saplings were observed at 100 m to 200 m higher elevation than adults (Figs 2 & 3). Observed limits of seedlings and saplings do not differ significantly from each other within and across the two regions (Table 3).

The upper elevational ranges of seedling, sapling and adult occurrences predicted by the models are consistent with the observed limits based on the uppermost occurrence solely (Pearson correlation coefficient $r > 0.88$, $P < 0.001$). In most of the species, upper limits of seedlings and saplings were predicted above adult trees (Fig. 4). Overall, the models predicted $PL_{Seedling}$ and $PL_{Sapling}$ to be $73 \pm 27 \text{ m}$ ($t = 2.72$, $P = 0.008$) and $81 \pm 30 \text{ m}$ ($t = 2.73$, $P = 0.016$) higher than PL_{Adult} , respectively (paired *t*-test, Table 3). These results indicate successful seedling establishment in the immediate surrounding of adult tree limits. $PL_{Sapling}$ significantly exceeded PL_{Adult} by 70 m for 6 out of 10 species (Fig. 3). As for observed limits, no difference was found between predicted limits of seedlings and saplings within and across the two regions (Table 3).

Interestingly, the eastern transects revealed a negative linear relationship between the distance separating $OL_{Sapling}$ from OL_{Adult} and the elevational limit of the adult trees, meaning that the species-specific limits between saplings and adult trees differed more for species having lower elevational limits (data not shown, $r^2 = 0.67$, $P = 0.013$). The same trend was found for the distance separating $OL_{Seedling}$ from OL_{Adult} and the elevational limit of the adult trees in the western transects (data not shown, $r^2 = 0.33$, $P = 0.085$). Furthermore, in the eastern region two of the highest-growing species, *Abies alba* and *S. aucuparia*, exhibited more browsing damage than the other species: this could have potentially restricted the

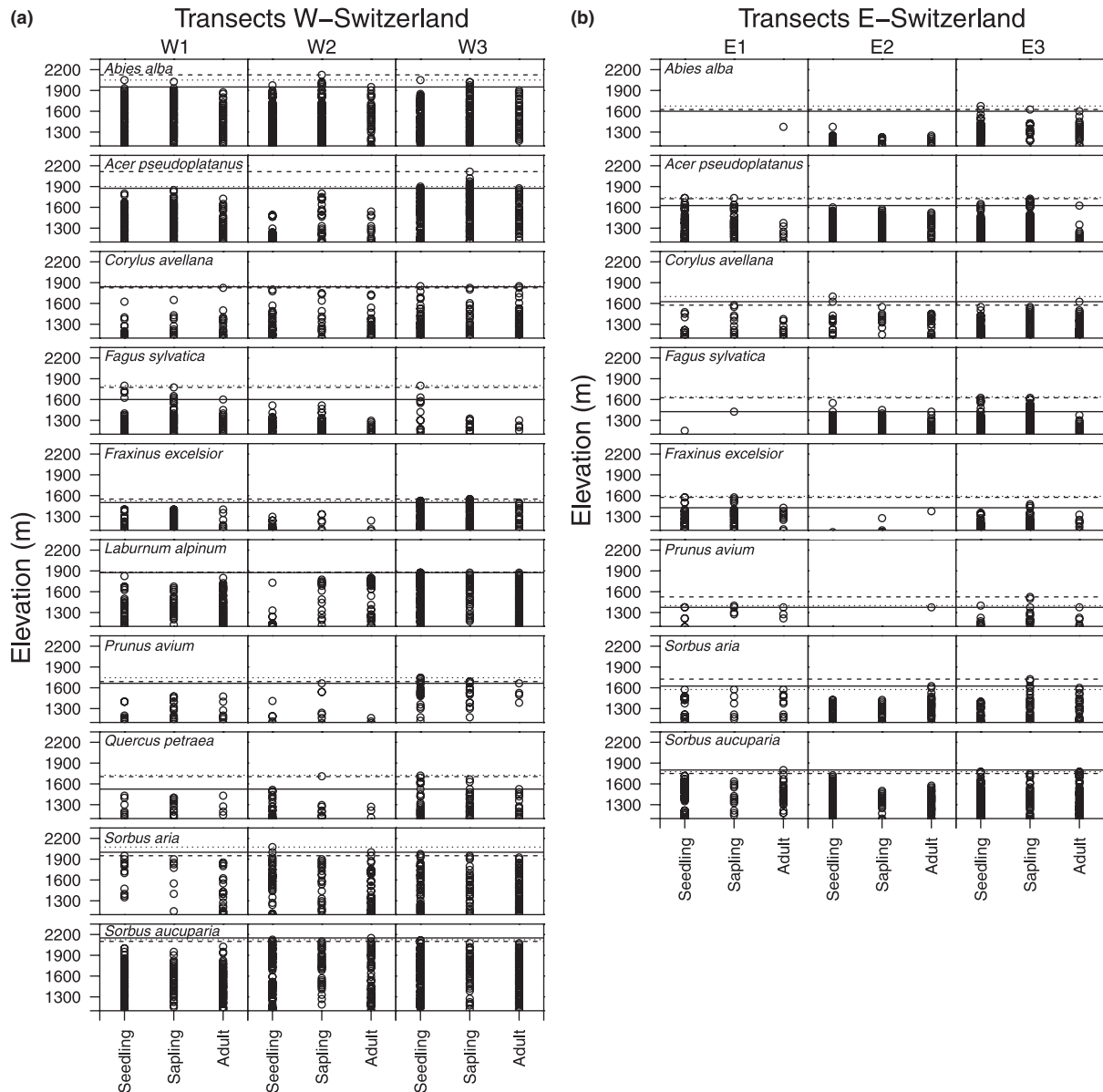


Figure 2 Occurrence data for 10 tree species recorded along three elevational transects and classified into three life stages, namely seedling, sapling and adult classes in (a) the western part (W1–3) of Switzerland, and (b) the eastern part (E1–3) of Switzerland. For each species and life stage, the horizontal lines indicate the highest individual observed within all three transects as follows: solid line, upper elevational limits observed for adult class (OL_{Adult}); dashed line, upper elevational limits observed for sapling class ($OL_{Sapling}$); dotted line, upper elevational limits observed for seedling class ($OL_{Seedling}$).

establishment of their seedlings. However, no significant relationship was found between the percentage of damage observed around the species limit and the discrepancy between seedling/sapling tree limits and adult tree limits (data not shown).

DISCUSSION

In agreement with our initial expectations, this study demonstrates seedling and sapling establishment above the current

elevational limits of adults for the majority of the studied species. The elevational discrepancy between adult and young tree limits varied among species. However, this variation was not related to seed dispersal strategy, but rather reflected the overall elevational position of a species: the mismatch between upper elevational limits of juveniles and adults tends to be higher for species inhabiting lower elevations, such as *Quercus petraea* or *Fagus sylvatica*. Furthermore, because both seedlings and saplings were represented around the adult limit, this study implies that neither limitation in reproduction (seed

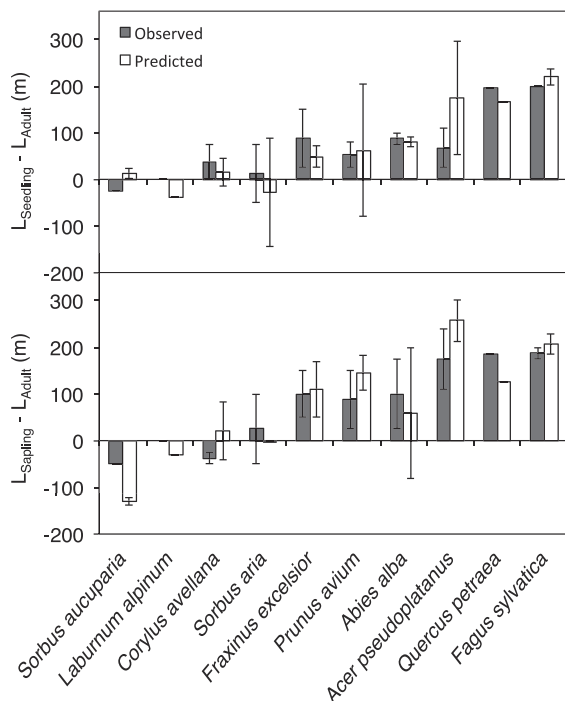


Figure 3 Difference in elevation (m) between observed or predicted seedling and sapling limits and the adult tree limits. The observed limits correspond to the highest individual observed for each life stage within all three transects of each region. The predicted limits were derived for each life stage from generalized linear models with a probability of occurrence of 10%. Error bars show the standard deviation between the eastern and western regions of Switzerland.

availability, germination) nor seedling establishment constitutes a serious limitation to the upward extension of tree limits under current climatic conditions. The abundant presence of young life stages above the adult tree limit suggests a response to recent climatic warming, matching the trend of rising abundance maxima found in various mountain areas in France (Lenoir *et al.*, 2009). However, we do not yet know if the observed seedlings and saplings above the adult tree limits will survive site conditions in older life stages and therefore increase a species' elevational limit in the near future. Indeed, the niche requirements may change during the life of individuals (Grubb, 1977; Auffret *et al.*, 2010). Nevertheless, the recruits include specimens of respectable size and age, suggesting no dramatic constraints to their growth and development in the recent past.

Elevational limits of tree taxa are tightly temperature-associated

Our survey relied on the assumption that the upper tree species limits reflect climate drivers rather than human influence or biotic interactions. The present survey was focused on the highest elevation at which species were present

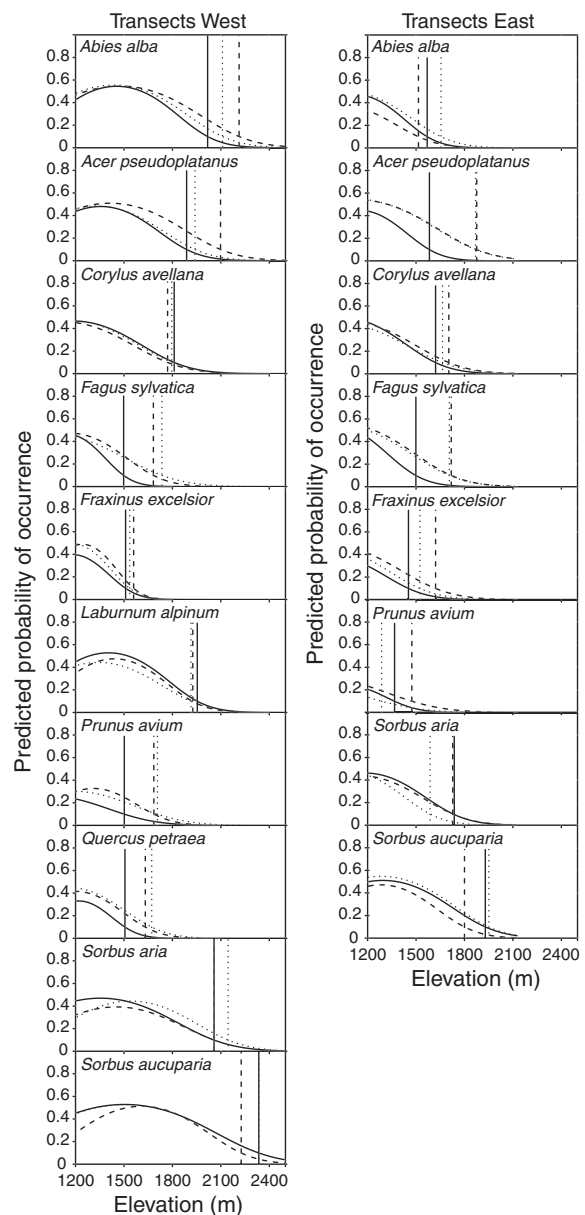


Figure 4 Predictions of the probability of occurrence of each life stage of 10 tree species in the two study regions (eastern and western Switzerland) obtained using generalized linear models fitted to presence/absence data. The vertical lines correspond to predictions of 10% probability of occurrence for each life stage as follows: solid line, predicted limit of adult class (PL_{Adult}); dashed line, predicted limit of sapling class (PL_{Sapling}); dotted line, predicted limit of seedling class (PL_{Seedling}).

(rather than on abundance), with data collected in steep and remote terrain without indication of any logging activities in order to minimize human influence, even though land use can never be excluded completely anywhere in Europe (Garbarino *et al.*, 2009). In addition, we used independent spatial replication to increase the likelihood of detecting the natural limits

of species. Finally, by pooling the three transects per region we aimed to attribute more importance to the presence of a species than to its absence in a specific transect. It is highly unlikely that either human influence or herbivory pressure was similar across the three transects investigated per region and across the widely separated test regions. Human disturbance, browsing or species competition may influence the abundance (density) of individuals per species in certain locations, but not necessarily their presence at a specific site (Austin, 2002; Randin *et al.*, 2009; Kuijper *et al.*, 2010), and, if so, these factors are unlikely to act in the very same way across transects and regions. The data show that the upper limit varied little across transects and regions, and hence neither human disturbance nor browsing pressure seemed to have seriously affected the presence of most of the studied species. Such effects may, however, have influenced the uppermost position of *Abies alba*, *S. aria* and *S. aucuparia* in the eastern transect, where these species limits were significantly lower than in the western transect. *Abies* and *Sorbus* species are the most browsing-affected taxa, and their recruitment is near to impossible when deer populations are high, a situation well known to local foresters (Motta, 2003). As foreseen, we found the highest degree of browsing signs in these taxa in the eastern transects.

Our results do not reveal any competitive exclusion, given that target species are found intermixed with different dominant tree species according to the studied region, while tree species limits are still similar. When accounting for actual summer temperature, species limits between the two studied regions are very similar within each species. This is consistent with the assumption that seedlings as well as adult trees are determined mainly by influences associated with summer warmth (Jump *et al.*, 2007; Kuijper *et al.*, 2010). Our data clearly highlight the dominant role of temperature in explaining the elevational limits of these taxa in the Swiss Alps, although it remains to be resolved which facet of the temperature regime is crucial.

Young trees are able to grow at or above the upper elevational limit of adult trees

Temperature can control the elevational limits of species in many ways and at all life stages. It has been suggested that low temperatures first constrain reproduction (seed quality and seed production) or seedling establishment (Woodward & Williams, 1987; Giesecke *et al.*, 2010). In contrast, this study indicates that seed availability at the upper elevational limits of tree species does not pose a serious constraint for tree recruitment in any of those studied species under current climatic conditions. Recruits were detected at and above the adult tree limits for all species, irrespective of their seed dispersal mode. Saplings were represented to the same extent as seedlings beyond adult tree limits, indicating that it was not just a few good years in the very recent past that contributed to tree establishment. While Woodward & Williams (1987) stated that cool summer temperatures might be too low at species

elevational limits for successful regeneration, the results of this study do not suggest a recruitment limitation under current climatic conditions. This study is in line with an experiment conducted in the same area that showed that seed quality is currently not limited in broad-leaved tree species at their upper elevational limits (Kollas *et al.*, 2012).

While it is old wisdom that plenty of seedlings can be found above the tree line (Kullman, 2002; Hofgaard *et al.*, 2009; Battlori *et al.*, 2010), these seedlings are commonly confined to favourable microsites among taller ground vegetation or among rocks and never become trees, but remain constrained to the grass/shrub layer. The situation is quite different for the tree species that find their upper limit within the closed montane forest. Here the recruits found in our survey all occurred within the montane forest (except for *S. aucuparia*, which can grow near to the tree-line ecotone) and were quite tall and, thus, fully coupled to ambient air conditions and not confined to peculiar microhabitats. The current higher elevational position of young trees could be the result of the warmer climate in recent decades, and several studies have also highlighted young trees well above the adult limit (Wardle & Coleman, 1992; Lenoir *et al.*, 2009). In the regions surveyed here, summer temperatures (June to August) were 1.3 K warmer during the period 1990–2006 than during the period from 1960 to 1989 (Fig. 5). Assuming a lapse rate of 0.55 K 100 m⁻¹, this temperature increase corresponds to an elevation shift of about 240 m, roughly corresponding to the distance found here between the uppermost young trees (seedlings or saplings) and adult trees for several of our species confined to below-tree-line elevations.

The species showing the greatest advancement of seedling- or sapling-sized recruits beyond their adult tree limit include

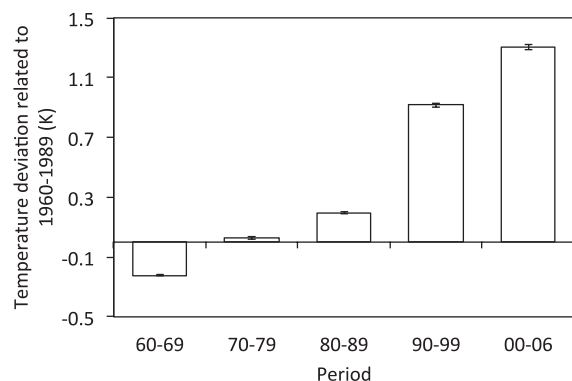


Figure 5 Temperature deviation of the last five decades relative to the period 1961–1990 in the survey area in Switzerland (including both western and eastern transects). Minimum summer temperature (June to September) based on the difference (10-year average) – (1961–90 average) generated in each relevé where the exact coordinates were recorded ($n = 78$). The temperature data set was extracted from 115 climate stations taken from the national meteorological network of Switzerland (see Materials and Methods for further details). The error bars represent the standard errors calculated over these 78 locations.

Fraxinus excelsior, *Abies alba*, *P. avium*, *Acer pseudoplatanus*, *Q. petraea* and *Fagus sylvatica*, all species that have comparatively low elevational limits. Conversely, in the remaining four species (*C. avellana*, *L. alpinum*, *S. aria* and *S. aucuparia*) sapling and adult limits differ little, and these are all species of smaller stature that exhibit quite high elevational limits. Following from the close association of current tree species limits with temperature in all species, the first group of tall-stature forest tree species is most likely to show an upward shift, also in the adult stage, in the near future as a result of ongoing climate warming. Our study could serve as a basis for long-term monitoring and the regions studied should be resurveyed in the future in order to examine the potential shifts of the upper elevational limits of the studied trees.

Among the most likely and most severe impacts of low temperature at these tree species limits are late spring frost events (Sakai & Weiser, 1973; Saxe *et al.*, 2001; Larcher, 2003). The occurrence of such extreme events *in situ* may, however, not correlate with trends in mean temperature. Both these meteorological covariables and the actual freezing resistance of these taxa are currently under study.

In conclusion, the present study has yielded clear evidence that recruitment does occur above the current adult limit in most species studied, which demonstrates the potential for an upward migration of trees in the Alps in response to ongoing climate warming. In some species, recruitment was found at the same elevation as which adults were found, but the limit of recruits was never below the adult tree limit, except for *S. aucuparia*, which is so heavily browsed that recruits have probably been eliminated from open terrain above the tree line. The results of this demographic survey are in line with the current upward shift of the upper elevational limits of broad-leaved tree species recently reported in western European mountains (Lenoir *et al.*, 2008).

ACKNOWLEDGEMENTS

We are grateful to Jens Paulsen for his guidance in the protocol of the survey and to Juliana Neumann, Jonas Thommen and Remo Wild for their assistance in the field. This work has been funded by the European Research Council (ERC) grant 233399 (project TREELIM) and the Swiss Federal Office of the Environment (BAFU) through their 'Forests and climatic change' program (project MATCHTREE). We further thank the Commune de Bex, the Commune de Lavey-Morcles and local foresters for providing support. We are grateful to three anonymous referees and to the editors for their valuable comments on a previous version of the manuscript.

REFERENCES

- Akatov, P.V. (2009) Changes in the upper limits of tree species distribution in the Western Caucasus (Belaya River basin) related to recent climate warming. *Russian Journal of Ecology*, **40**, 33–38.
- Auffret, A.G., Meineri, E., Bruun, H.H., Ejrnaes, R. & Graae, B.J. (2010) Ontogenetic niche shifts in three *Vaccinium* species on a sub-alpine mountain side. *Plant Ecology & Diversity*, **3**, 131–139.
- Austin, M.P. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling*, **157**, 101–118.
- Austin, M.P. & Gaywood, M.J. (1994) Current problems of environmental gradients and species response curves in relation to continuum theory. *Journal of Vegetation Science*, **5**, 473–482.
- Azola, C. & Harrell, F.E. (2006) *An introduction to S-Plus and the Hmisc and design libraries*. Available at: <http://biostat.mc.vanderbilt.edu/RS>.
- Batllori, E., Camarero, J.J. & Gutierrez, E. (2010) Current regeneration patterns at the tree line in the Pyrenees indicate similar recruitment processes irrespective of the past disturbance regime. *Journal of Biogeography*, **37**, 1938–1950.
- Brändli, U.-B. (2010) *Swiss National Forest Inventory. Results of the third inventory 2004–2006*. Paul Haupt, Bern.
- Cairns, D.M. & Moen, J. (2004) Herbivory influences tree lines. *Journal of Ecology*, **92**, 1019–1024.
- Clark, C.J., Poulsen, J.R., Levey, D.J. & Osenberg, C.W. (2007) Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *The American Naturalist*, **170**, 128–142.
- Cox, D.R. & Snell, E.J. (1989) *The analysis of binary data*. Chapman and Hall, London.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Franke, R. (1982) Smooth interpolation scattered data by local thin plate splines. *Computers & Mathematics with Applications*, **8**, 237–281.
- Garbarino, M., Weisberg, P.J. & Motta, R. (2009) Interacting effects of physical environment and anthropogenic disturbances on the structure of European larch (*Larix decidua* Mill.) forests. *Forest Ecology and Management*, **257**, 1794–1802.
- Gehrig-Fasel, J., Guisan, A. & Zimmermann, N.E. (2007) Tree line shifts in the Swiss Alps: climate change or land abandonment? *Journal of Vegetation Science*, **18**, 571–582.
- Giesecke, T., Miller, P.A., Sykes, M.T., Ojala, A.E.K., Seppä, H. & Bradshaw, R.H.W. (2010) The effect of past changes in inter-annual temperature variability on tree distribution limits. *Journal of Biogeography*, **37**, 1394–1405.
- Grubb, P.J. (1977) Maintenance of species-richness in plant communities: the importance of regeneration niche. *Biological Reviews of the Cambridge Philosophical Society*, **52**, 107–145.
- Harsch, M.A., Hulme, P.E., McGlone, M.S. & Duncan, R.P. (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, **12**, 1040–1049.

- Hofgaard, A., Dalen, L. & Hytteborn, H. (2009) Tree recruitment above the treeline and potential for climate-driven treeline change. *Journal of Vegetation Science*, **20**, 1133–1144.
- Jump, A.S., Hunt, J.M. & Penuelas, J. (2007) Climate relationships of growth and establishment across the altitudinal range of *Fagus sylvatica* in the Montseny Mountains, northeast Spain. *Ecoscience*, **14**, 507–518.
- Jump, A.S., Matyas, C. & Penuelas, J. (2009) The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology and Evolution*, **24**, 694–701.
- Kollas, C., Vitasse, Y., Randin, C.F., Hoch, G. & Körner, C. (2012) Unrestricted quality of seeds in European broad-leaved tree species growing at the cold boundary of their distribution. *Annals of Botany*, **109**, 473–480.
- Körner, C. (2007a) Climatic treelines: conventions, global patterns, causes. *Erdkunde*, **61**, 316–324.
- Körner, C. (2007b) Significance of temperature in plant life. *Plant growth and climate change* (ed. by J.I. Morison and M.D. Morecroft), pp. 48–69. Blackwell Publishing Ltd, Oxford.
- Körner, C. (2012) *Alpine treelines*. Springer, Basel, in press.
- Körner, C. & Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, **31**, 713–732.
- Körner, C., Ohsawa, M., Spehn, E., Berge, E., Bugmann, H., Groombridge, B., Hamilton, L., Hofer, T., Ives, J., Jodha, N., Messerli, B., Pratt, J., Price, M., Reasoner, M., Rodgers, A., Thonell, J. & Yoshino, M. (2005) Mountain systems ecosystems and human well-being. *Current state and trends: findings of the condition and trends working group*, Millennium Ecosystem Assessment, pp. 681–716. Island Press, Washington, DC.
- Kuijper, D.P., Jędrzejewska, B., Brzeziecki, B., Churski, M., Jędrzejewski, W. & Żybura, H. (2010) Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieża Primeval Forest, Poland. *Journal of Vegetation Science*, **21**, 1082–1098.
- Kullman, L. (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, **90**, 68–77.
- Larcher, W. (2003) *Physiological plant ecology: ecophysiology and stress physiology of functional groups*, 4th edn. Springer, Germany.
- Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768–1771.
- Lenoir, J., Gégout, J.C., Pierrat, J.C., Bontemps, J.D. & Dhôte, J.F. (2009) Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). *Ecography*, **32**, 765–777.
- McCullagh, P. & Nelder, J. (1989) *Generalized linear models*, 2nd edn. Chapman and Hall, London.
- Mellert, K.H., Fensterer, V., Küchenhoff, H., Reger, B., Kölling, C., Klemmt, H.J. & Ewald, J. (2011) Hypothesis-driven species distribution models for tree species in the Bavarian Alps. *Journal of Vegetation Science*, **22**, 635–646.
- Mitas, L. & Mitasova, H. (1988) General variation approach to the interpolation problem. *Computers & Mathematics with Applications*, **16**, 983–992.
- Moen, J., Cairns, D.M. & Lafon, C.W. (2008) Factors structuring the treeline ecotone in Fennoscandia. *Plant Ecology & Diversity*, **1**, 77–87.
- Morin, X., Augspurger, C. & Chuine, I. (2007) Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? *Ecology*, **88**, 2280–2291.
- Motta, R. (2003) Ungulate impact on rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* (L.) Karst.) height structure in mountain forests in the eastern Italian Alps. *Forest Ecology and Management*, **181**, 139–150.
- Nagelkerke, N.J.D. (1991) A note on a general definition of the coefficient of determination. *Biometrika*, **78**, 691–692.
- Ohsawa, M. (1995) Latitudinal comparison of altitudinal changes in forest structure, leaf-type, and species richness in humid monsoon Asia. *Vegetatio*, **121**, 3–10.
- Pither, J. (2003) Climate tolerance and interspecific variation in geographic range size. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 475–481.
- R Development Core Team (2011) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Randin, C.F., Jaccard, H., Vittoz, P., Yoccoz, N.G. & Guisan, A. (2009) Land use improves spatial predictions of mountain plant abundance but not presence-absence. *Journal of Vegetation Science*, **20**, 996–1008.
- Sakai, A. & Weiser, C.J. (1973) Freezing resistance of trees in North America with reference to tree regions. *Ecology*, **54**, 118–126.
- Saxe, H., Cannell, M.G.R., Johnsen, O., Ryan, M.G. & Vourlitis, G. (2001) Tree and forest functioning in response to global warming. *New Phytologist*, **149**, 369–400.
- Stohlgren, T.J., Bachand, R.R., Onami, Y. & Binkley, D. (1998) Species–environment relationships and vegetation patterns: effects of spatial scale and tree life-stage. *Plant Ecology*, **135**, 215–228.
- Van Houwelingen, J.C. & Le Cessie, S. (1990) Predictive value of statistical models. *Statistics in Medicine*, **9**, 1303–1325.
- Wardle, P. & Coleman, M.C. (1992) Evidence for rising upper limits of four native New Zealand forest trees. *New Zealand Journal of Botany*, **30**, 303–314.
- Woodward, F.I. (1990) The impact of low temperatures in controlling the geographical distribution of plants. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **326**, 585–593.
- Woodward, F.I. & Williams, B.G. (1987) Climate and plant-distribution at global and local scales. *Vegetatio*, **69**, 189–197.
- Zimmermann, N.E. & Kienast, F. (1999) Predictive mapping of alpine grasslands in Switzerland: species versus community approach. *Journal of Vegetation Science*, **10**, 469–482.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Performance of the generalized linear models fitted to presence/absence data.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCHES

Yann Vitasse is a post-doctoral researcher in the Department of Plant Ecology at the University of Basel (Switzerland). His scientific interests cover biogeography, evolutionary biology and phenology, and his current research focuses on the adaptation of trees at their upper elevational limits in term of physiological traits such as leaf phenology, growth and frost resistance.

All the authors are involved in the project 'TREELIM', which aims to provide a mechanistic explanation of the climatic limits of major European broad-leaved tree taxa (<http://pages.unibas.ch/botschoen/treelim/index.shtml>).

Author contributions: C. Körner conceived the ideas; C. Körner, Y.V. and G.H. conceived the field protocol; Y.V. collected the data with the support of students; Y.V, C.F.R. and A.L analysed the data; Y.V. led the writing with input from all the other authors.

Editor: Ole Vetaas

Supplementary material

S1: Performance of the generalized linear models fitted to presence/absence data on the probability of occurrence of each life stage of 10 tree species in both study regions (western and eastern Switzerland).

	West						East					
	Seedlings		Saplings		Adults		Seedlings		Saplings		Adults	
	R^2	AUC	R^2	AUC	R^2	AUC	R^2	AUC	R^2	AUC	R^2	AUC
<i>Abies alba</i>	0.16	0.63	0.12	0.60	0.20	0.66	0.20	0.67	0.19	0.67	0.24	0.70
<i>Acer pseudoplatanus</i>	0.22	0.67	0.15	0.63	0.24	0.70	0.11	0.59	0.11	0.59	0.21	0.71
<i>Corylus avellana</i>	0.28	0.75	0.28	0.75	0.27	0.74	0.16	0.64	0.14	0.62	0.20	0.67
<i>Fagus sylvatica</i>	0.29	0.77	0.34	0.78	0.43	0.83	0.19	0.65	0.19	0.64	0.30	0.70
<i>Fraxinus excelsior</i>	0.44	0.82	0.42	0.81	0.38	0.81	0.23	0.69	0.19	0.66	0.22	0.70
<i>Laburnum alpinum</i>	0.21	0.67	0.22	0.68	0.23	0.66	-	-	-	-	-	-
<i>Prunus avium</i>	0.21	0.70	0.25	0.73	0.24	0.75	0.17	0.66	0.15	0.66	0.18	0.66
<i>Quercus petraea</i>	0.33	0.78	0.34	0.78	0.34	0.78	-	-	-	-	-	-
<i>Sorbus aria</i>	0.11	0.61	0.12	0.60	0.16	0.63	0.21	0.69	0.13	0.64	0.14	0.64
<i>Sorbus aucuparia</i>	0.08	0.56	0.12	0.62	0.08	0.56	0.09	0.57	0.14	0.64	0.10	0.60

R^2 , adjusted geometric mean squared rescaled for a maximum of 1 and adjusted for both the number of observations and predictors in the model; AUC, area under the curve of a receiver operating characteristic plot based on the predictions emerging from the cross-validation (see Materials and Methods for further details).

Chapter 7

Extended summary

Extended summary

Aim

This thesis assessed factors that contribute to the explanation of the upper elevational and latitudinal limits of European broad-leaved tree species by using a set of ecological analysis, including *in situ* temperature measurements, a transplant experiment and a survey of the reproductive cycle and demography at the species limits. The following key questions were answered in five chapters:

- i Do the elevational thermal limits of broad-leaved tree species correspond to their latitudinal thermal limits?
- ii Can we use temperature data from weather stations to predict temperature at broad-leaved tree species limits?
- iii Which facet of temperature at which phenological stage explain the most the elevational and latitudinal cold limits of broad-leaved tree species?
- iv Does seed quality restrict the reproduction of species at high elevation?
- v Do the elevational limits of juvenile trees match with the respective adult tree limits or do the results offer an indication for recent species upward shift?

Studied species & study region

Ten broad-leaved tree species were selected for this thesis: *Acer pseudoplatanus* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Laburnum alpinum* (Mill.) Bercht. & J. Presl, *Prunus avium* L., *Quercus petraea* (Matt.) Liebl., *Sorbus aria* L., *Tilia platyphyllos* Scop., *Sorbus aucuparia* L. and *Ilex aquifolium* L. The choice of species was driven by the aim of drawing conclusions beyond species level and beyond the regional focus. Thus, the selected species have a wide European distributional range and a wide elevational range in common. At the same time they cover a broad spectrum of

plant families, namely Rosaceae, Fagaceae, Aceraceae, Oleaceae, Tiliaceae, Aquifoliaceae and Fabaceae.

The studies were carried out in three distinct regions: In the Western Swiss Alps near Martigny (46°6'N, 7°4'E), in the Eastern Swiss Alps near Chur (46°51'N, 9°32'E) and in the South of Sweden (from 57°42' to 59°39'N, ca. 12°E). Both regions in Switzerland were selected because most broad-leaved tree species studied here, find their elevational limit in these regions and reach their highest positions in Switzerland. Furthermore, the large and steep elevational gradients found in these regions facilitated surveys, specimen collections and common garden experiments. In southern Sweden we studied species at their latitudinal limits, allowing a large-scale comparison.

Comparisons of the elevational and latitudinal upper limits of broad-leaved tree species

Christophe F. Randin, Jens Paulsen, Yann Vitasse, Chris Kollas, Thomas Wohlgemuth, Niklaus E. Zimmermann and Christian Körner

We compared temperatures at the upper elevational and latitudinal limits of 18 deciduous tree species respectively in Switzerland and North of Europe, and hypothesized that species exhibit the same position (relative to the tree-line) along the elevational and latitudinal gradients, which can be expected if species have reached their thermal cold limit at both high latitude and high elevation. We developed a method to identify a least-biased estimate of the elevational and latitudinal cold temperature limits and for comparing relative rank positions of species. We applied an algorithm to calculate the elevation of the potential treeline for each point in the gridded landscape of Europe and Switzerland. For each occurrence of each species, elevation was extracted from digital elevation models. The vertical distance between

the elevation of the potential regional climatic treeline and the uppermost tree positions of a species was calculated and used for comparisons between elevation and latitude. We found that each species' elevational distance to the treeline was strongly correlated to their latitudinal distance to the treeline ($R^2 = 0.65$; P -value < 0.001). A first group of nine species showed very similar thermal distances to the potential treelines along both, the elevational gradient and the latitudinal gradient. A second group of seven species occupied climatic niche closer to the thermal treeline at their latitudinal range edge. Only two species (*Sorbus aria* and *Quercus pubescens*) appeared to have not filled their thermal niche latitudinally, because their elevational limits in the Alps were found to be at significantly cooler growing season temperatures than their latitudinal distribution limits. Our study thus, provides support for the common concept of the species range–environment equilibrium for most investigated species. Notably, we did not find stronger deviations in filling thermal niches at the latitudinal limits as compared to the elevational limits, although the former requires a species to expand over a greater geographical distance.

In situ temperatures at the cold limits of broad-leaved tree species and their deviation from records of weather stations

Chris Kollas, Christophe F. Randin, Yann Vitasse, Christian Körner

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 the actual climatic conditions experienced by trees. In this study I 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 positions in the forest: at understory height (50 cm), 2-m above ground, in the top of tree canopies and at 10 cm depth in the soil. I 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 of weather station data remained 1.4 ± 0.2 K (mean \pm se, 12 sites) cooler than in situ conditions during the growing season (2.0 ± 0.2 K cooler during the dormant season). At the time when 2-m air temperature reached its absolute monthly minimum, temperature in the top of the tree canopy was found 0.4 ± 0.1 K colder (mean \pm se, 12 sites) during the growing season and 0.9 ± 0.1 K during the dormant season.

The results add to the evidence that spatially and/or temporally coarse-resolution climatic data are not matching actual life conditions of plants. The 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. Thus, (1) 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. And (2), improved geographic climatic layers providing resolution refinement in space and/or time may turn out to be meaningless, unless they are corrected for microclimatic differences. These proxy data for the actual bioclimate may be significantly improved by accounting for the systematic deviations reported here.

Critical temperatures determining the elevational and latitudinal range limits of European broad-leaved trees

Chris Kollas, Christophe F. Randin, Christian Körner

In this study I aimed to test three temperature-related hypotheses of European broad-leaved tree species limits in altitude and latitude. I hypothesized that: (1) annual absolute minimum temperature at the species limit does not exceed the maximum freezing tolerance of buds (2) Late spring frost events during bud-break are regularly exceeding the freezing tolerance of unfolding leaves and flowers at the species boundary (3) Minimum requirement of warm temperature during the growing season can not be met above the current range limit (incomplete tissue and seed maturation). The study was conducted on European broad-leaved tree species elevational limits in the Swiss Alps (1165-2160 m a.s.l.) and the respective latitudinal limits in South Sweden (57°N – 59°N). I used miniature data loggers to assess *in situ* temperatures at seven broad-leaved tree species limits in the study areas. This temporal high-resolution data was then correlated with nearest weather stations to reconstruct 50 years of daily climate data and to predict weekly absolute minimum temperatures within 100 years at the species elevational and latitudinal limits.

I found that at their elevational limit most studied tree species experienced mid-winter lowest temperatures considerably warmer than their known winter frost resistance (work in progress in TREELIM work package 3, A. Lenz et al.). In contrast, the lowest temperatures that species experienced at their latitudinal limit were considerably lower than at their elevational limits in the Alps, and far below their expected winter frost resistance (LT50 gained in the Alps and Germany). Winter minima, thus, do not seem to be decisive in the Alps. Along both gradients (elevation & latitude), I found similar growing season lengths and deleterious late spring frost events to occur during and shortly after the period of bud-break at 41 to 100 years return periods. Thus, minimum temperatures during bud-break are most likely causing dam-

age to broad-leaved trees and thus, along with short growing seasons, exert a significant influence on species' low temperature elevational and latitudinal limits. Hence, process-based growth models – that depend to great extent on empirically derived thresholds for species growth and survival - will be greatly improved by incorporating these constraints during sensitive phenological stages in spring.

Further, the study showed that coupling microclimatic measurements (by data-loggers) with regional climate measurements (by weather stations) helps to overcome specific shortcomings of each method (i.e. short period of employment for data loggers and inflexibility for weather stations). The combination of both devices, thus provides an excellent tool to scale up temperature measurements.

Reproduction and Recruitment limitation at the upper elevational limits of tree species in Switzerland

Chris Kollas, Yann Vitasse, Christophe F. Randin, Günter Hoch and Christian Körner (on reproduction, Chapter 5)

and

Yann Vitasse, Günter Hoch, Christophe F. Randin, Armando Lenz, Chris Kollas and Christian Körner (on recruitment, Chapter 6)

The low-temperature range limit of tree species might be determined by their ability to produce and disperse viable seeds or by failure during the establishment of recruits. Biological processes such as flowering, pollen transfer, pollen tube growth, fertilization, embryogenesis, seed maturation, germination and seedlings growth into samplings are known to be affected by cold temperatures. The aim of the studies was to (1) assess the quality of seeds and (2) to assess current tree recruitment near the cold-temperature limit of 10 major European tree species in the Swiss Alps. We first collected seeds for each species (five seed families per location and species) from stands close to optimal growth conditions (low elevation) and from marginal

stands (highest elevation), replicated in two regions in the Swiss Alps in 2009. Further, we measured seed weight, seed size, storage tissue quality, seed viability and germination success. Second, for each species, occurrences were recorded along six elevational transects (in the western and eastern Swiss Alps) according to three size classes from seedlings to adult trees in 25-m elevation steps above and below their regional upper elevational limit, in 2010. Two methods were used to compare upper elevational limits between seedlings, saplings and adults within species. First, we focused on the uppermost occurrence observed in each life stage for a given species within each studied region; and second, we predicted their upper distribution range using polynomial models fitted to presence/absence data. We found that all species examined produced a lot of viable seeds at their current high-elevation range limit during a summer ranked 'normal' by long-term temperature records. Low- and high-elevation seed sources showed hardly any trait differences. The concentration of non-structural carbohydrates in seeds tended to be higher at high elevation. Additionally, in one species, *Sorbus aucuparia*, all measured traits showed significantly higher seed quality in high-elevation seed sources. In addition, the observed and predicted limits of tree species occurrences (each life stage) showed that all species were represented by young individuals in the vicinity of the limit of adult trees. Moreover, tree recruitment (both seedlings and saplings) was detected and predicted significantly beyond adult tree limits in most of the species. Across regions, seedlings and saplings were on average found at elevations 73 m higher than adult trees. Thus, under current conditions, neither seed quality nor seedling establishment constitutes a serious limitation of recruitment at the current upper elevational limits of major European trees in the Swiss Alps. The recruits found beyond the adult limits demonstrate the potential for an upward migration of trees in the Alps in response to ongoing climate warming.

Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species

Yann Vitasse, Günter Hoch, Christophe F. Randin, Armando Lenz, Chris Kollas, J. F. Scheepens, Christian Körner

Phenological events, such as the initiation and the end of seasonal growth, are thought to be under strong evolutionary control because of their influence on tree fitness. Although numerous studies highlighted genetic differentiation in phenology among populations from contrasting climates, it remains unclear whether local adaptation could restrict phenological plasticity in response to current warming. Seedling populations of seven deciduous tree species from high and low elevations in the Swiss Alps were investigated in eight common gardens located along two elevational gradients from 400 to 1700 m. We addressed the following questions: Are there genetic differentiations in phenology between populations from low and high elevations? Are populations from the upper elevational limit of a species' distribution able to respond to increasing temperature to the same extent as low-elevation populations? Genetic variation of leaf unfolding date between seedlings from low and high populations was detected in six out of seven tree species. Except for beech, populations from high elevations tended to flush later than populations from low elevations, emphasizing that phenology is likely to be under evolutionary pressure. Furthermore, seedlings from high elevation exhibited lower phenological plasticity to temperature than low-elevation provenances. This difference in phenological plasticity may reflect the opposing selective forces involved (i.e. a trade-off between maximising growing season length and avoiding frost damages). Nevertheless, environmental effects were much stronger than genetic effects, suggesting a high phenological plasticity to enable tree populations to track ongoing climate change, which includes the risk of tracking unusually warm springs followed by frost.

Conclusions and future perspective

Species' constraints at their elevational and latitudinal limits

The possible factors that could constrain the cold, high elevation and high latitude limits of European broad-leaved tree species were assessed. Seed quality and demography indicate that reproduction and recruitment are not constraining the studied broad-leaved tree species upper elevational limits. The data show that minimum temperatures in winter are not posing any risk at these species at high elevation. In contrast, late spring frost along with short growing seasons are more likely decisive for the natural elevational and latitudinal limits of these broad-leaved tree species.

Linking eco-physiology to biogeography

The evidences that suggest that broad-leaved tree species upper limits are most likely constrained by two main temperature-based candidates (growing season length and late spring frost) underline the necessity to go further towards new assessments for testing these assumptions. An assessment via geographical information system could first provide the spatial extent where freezing temperatures ($-3\pm 1^{\circ}\text{C}$) occurred during bud-break of dominant species such as e.g. *Fagus sylvatica*. Second, the same approach could be used to calculate the range delimited by a certain minimum growing season length (e.g. 159 days for *F. sylvatica*, Chapter 4). These two mapping data sets could then be compared with the maps of the actual distribution of *F. sylvatica*. Emergent results could be: (1) the most likely temperature based constraint of species limits and (2) regions within the distribution of the species where other abiotic factors such as land-use history may override the temperature constraints.

Annex A

Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species

Yann Vitasse, Günter Hoch, Christophe F. Randin, Armando Lenz, Chris Kollas, J. F. Scheepens, Christian Körner
Oecologia, Special Issue. in press (2012)

Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species

Yann Vitasse^{a,*}, Günter Hoch^a, Christophe F. Randin^a, Armando Lenz^a, Chris Kollas^a, J. F. Scheepens^a, Christian Körner^a

^a *Institute of Botany, University of Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland*

**Corresponding author. Tel.: +41 61 267 3506; fax: +41 61 267 2980; E-mail address: Yann.Vitasse@unibas.ch*

Abstract

Phenological events, such as the initiation and the end of seasonal growth, are thought to be under strong evolutionary control because of their influence on tree fitness. Although numerous studies highlighted genetic differentiation in phenology among populations from contrasting climates, it remains unclear whether local adaptation could restrict phenological plasticity in response to current warming. Seedling populations of seven deciduous tree species from high and low elevations in the Swiss Alps were investigated in eight common gardens located along two elevational gradients from 400 to 1700 m. We addressed the following questions: Are there genetic differentiations in phenology between populations from low and high elevations? Are populations from the upper elevational limit of a species' distribution able to respond to increasing temperature to the same extent as low-elevation populations? Genetic variation of leaf unfolding date between seedlings from low and high populations was detected in six out of seven tree species. Except for beech, populations from high elevations tended to flush later than populations from low elevations, emphasizing that phenology is likely to be under evolutionary pressure. Furthermore, seedlings from high elevation exhibited lower phenological plasticity to temperature than low-elevation provenances. This difference in phenological plasticity may reflect the opposing selective forces involved (*i.e.* a trade-off between maximising growing season length and avoiding frost damages). Nevertheless, environmental effects were much stronger than genetic effects, suggesting a high phenological plasticity to enable tree populations to track ongoing climate change, which includes the risk of tracking unusually warm springs followed by frost.

Keywords: Leaf unfolding; Budset; Common garden; Genecology; Elevational gradients

Introduction

Deciduous tree species in temperate climate need to adapt their phenology to optimize the timing of growth and reproduction according to local biotic and abiotic factors (Polgar and

Primack 2011). Genetic diversity within and among populations and phenotypic plasticity of phenological key-events, such as the emergence of leaves or flowers, play crucial roles in adaptation, and thus in species survival and their competitive abilities in the context of the rapid

ongoing climate change (Savolainen et al. 2007). In fact, tree phenology fulfills the three criteria required to be considered as adaptive, that is, being able to evolve in response to selective pressures. First, there is a high phenological variation within populations (e.g. Baliuckas et al. 2005; Alberto et al. 2011), second, phenological traits show a high level of heritability (e.g. Billington and Pelham 1991; Howe et al. 2000), and third, phenological traits are tightly related to individual performance/fitness through biotic (Tikkanen and Julkunen-Tiitto 2003; van Asch and Visser 2007; Wesolowski and Rowinski 2008) and abiotic interactions (Augsburger 2008; Chuine 2010). Temperature is assumed to be the main abiotic selective drivers leading to clinal variation of diverse adaptive traits along elevational gradients (Oleksyn et al. 1998; Premoli et al. 2007; Bresson et al. 2011), whereas in semi-arid regions, moisture availability can exert similar selective pressure (Broadhead et al. 2003). Variations of functional phenotypic traits along environmental gradients result from three major components which can be partitioned by conducting analyses of variance (Schlichting 1986). The three sources of variance include phenotypic variance due to genotypes (VG), phenotypic variance due to environments (VE), and variance due to the interaction of genotypes with the environment ($VG \times VE$). The two latter components represent the phenotypic plasticity, with VE considered as the environmental component of the plasticity, and $VG \times VE$ as the phenotypic plasticity due to genetic differences among genotypes/provenances. The $VG \times VE$ interaction reflects genetic diversity in plasticity and is, thus, assumed to represent the heritable component of phenotypic plasticity (Schlichting 1986; Thompson 1991). So, some genotypes/provenances may show more and others less phenotypic plasticity along the same environmental gradient. Over the last century, numerous experiments using common gardens have shown genetic differentiation of tree phenology among populations from different elevational or latitudinal provenances (review in Langlet 1971; Morgenstern 1996, with references therein). While these experiments were mostly established to provide information for forest management, there is now renewed interest to assess the ability of tree populations to

cope with ongoing climate change (Aitken et al. 2008; Lindner et al. 2010). One question that remains open is whether tree populations growing in contrasting climates will have the same capability to respond to environmental change such as the ongoing climatic changes (Vitasse et al. 2009b; Doi et al. 2010; Hoffmann and Sgro 2011).

At the upper elevational limit of tree species, cold conditions strongly constrain tree phenology: late frosts in spring are frequent, and bud burst timing must be optimized to minimize the danger of frost damage, while at the same time maximizing the length of the growing season to ensure growth and the production of viable seeds. Tree populations growing at their upper elevational limits may therefore undergo a strong selective abiotic pressure and could be well differentiated from those growing at lower elevations, provided there was sufficient time for genetic differentiation and sufficient genetic isolation. Leading edge populations are usually smaller and more isolated than populations inhabiting the centre of the distribution range, leading to a lower genetic diversity (Willi et al. 2007) and possibly to a weaker phenotypic plasticity to cope with new environmental conditions. On the other hand, these populations could also benefit from gene flow from populations inhabiting warmer areas, which would introduce alleles (pre)-adapted to warmer climate and thus allow leading edge populations to cope with rapid climate warming (Lindner et al. 2010; Kremer et al. 2012). Phenotypic plasticity can be directly enhanced by natural selection in heterogeneous environments (Thompson 1991; Schlichting and Pigliucci 1993) and has been proposed as a catalyst in evolutionary processes for local adaptation (Pigliucci et al. 2006). Yet, although numerous studies have reported genetic differentiation in phenology among tree populations from contrasting climates, only few studies addressed whether these populations also diverge in their phenotypic plasticity including the two components VE and $VE \times VG$ (but see Rehfeldt et al. 2002; Baliuckas and Pliura 2003; Williams et al. 2008; Vitasse et al. 2010). The reason is that most of the studies used only one common garden, and hence, a single common climate which can be more suitable for some provenances than others.

Since both genetic- and environment-related factors affect plant phenotype, interpretation of results from a single common garden (commonly established at a warm location) can give misleading results and do not allow a proper assessment of the response of the tested populations to environmental changes.

Elevational gradients provide a unique “in situ experiment” for exploring the impact of temperature on tree phenology (Körner 2000). The relative short distance between elevations with markedly different temperatures in mountain terrain enables the analyse of temperature effects on plants at otherwise similar conditions. We used common gardens established at different elevations in two main valleys in the Swiss Alps including seven tree species widely distributed in Europe to examine genetic differentiation between low- and high- elevation populations and their plastic responses in leaf unfolding and timing of budset to temperature changes. For each species, seedlings from seeds harvested at low and high elevation within each of the two studied areas were investigated. The objectives of this study were to quantify (a) whether populations of deciduous trees growing at their upper elevational limits in the Swiss Alps are genetically adapted in their phenology to face low temperature conditions; (b) the extent to which leaf phenology is influenced by genetic factors (provenance) and temperature; and (c) to compare phenological plasticity between populations from low and high elevations. We hypothesized that (i) cold temperatures have led to genetic differentiation in leaf phenology between tree populations growing at high and lower elevations, assuming that at high elevation, populations undergo a strong directional selection by freezing temperatures, favouring late flushing individuals; and that (ii) populations naturally occurring at upper elevations exhibit a lower phenological plasticity to temperature.

Materials and methods

Study species and seed sources

Seven deciduous tree species having a wide distribution range in Europe were selected. *Fraxinus excelsior* L., mainly distributed at low elevation up to about 1500 m in the Swiss Alps; *Fagus sylvatica* L. and *Prunus avium* L., occurring from low to mid elevation up to about 1700 m; *Laburnum alpinum* (Mill.) Bercht. / J. Presl. and *Acer pseudoplatanus* L., two predominantly mid-montane species found up to about 1900 m; and both *Sorbus aria* L. and *Sorbus aucuparia* L. distributed between lower montane level and elevations higher than 1900 m, in particular *S. aucuparia* which also occurs at the alpine tree-line. The precise elevation limits of these species in the two study areas are provided in Vitasse et al. (2012).

For each species, seeds were collected from June to November 2009, according to their maturation stage, at both high and low elevations in two regions of the Swiss Alps, 200 km apart: the region around St-Maurice, VS (west) and the region around Haldenstein, GR (east) (see Kollas et al. 2012 for further details). Seeds of *L. alpinum* were obtained in the western region only because this species does not occur naturally in the eastern region of the Swiss Alps. The western and eastern regions were considered as replicates to test low against high elevational provenances. Within regions and species, the elevational difference between populations from low and high elevation ranged from 660 m for *P. avium* to 1360 m for *A. pseudoplatanus* and the average distance between low and high populations was on average 15 km (Table 1). For each species and both regions, mature trees occur more or less continuously between the selected low and high populations (see Fig. 2 in Vitasse et al. 2012 for further details). For each selected population and species, seeds were collected from five randomly sampled trees which were at least 50 m apart but within an elevational band of 50 m.

Table 1: Elevation range of the four sampled provenances for the seven species included in the study (West Low, West High, East Low, East High) with the elevational difference ($\Delta_{\text{Elevation}}$) and the average distance (Δ_{Distance}) between low and high provenances within each region.

Species	West		East	
	Low-High ($\Delta_{\text{Elevation}}$)(m)	Δ_{Distance} (km)	Low-High ($\Delta_{\text{Elevation}}$)(m)	Δ_{Distance} (km)
<i>Fraxinus excelsior</i>	420–1440 (1020)	16.2	570–1230 (660)	23.4
<i>Prunus avium</i>	356–1075 (719)	27.7	575–1235 (660)	12.0
<i>Laburnum alpinum</i>	690–1770 (1080)	1.2	Species not present	
<i>Acer pseudoplatanus</i>	400–1760 (1360)	16.1	590–1430 (840)	9.6
<i>Sorbus aria</i>	570–1750 (1180)	7.4	620–1290 (670)	14.1
<i>Sorbus aucuparia</i>	950–2060 (1110)	15.5	930–1870 (930)	27.0
<i>Fagus sylvatica</i>	540–1240 (700)	5.2	610–1280 (670)	17.4

Growth conditions

Seeds were sown in an unheated open-window greenhouse at Witterswil (47°29'35"N, 7°31'14"E) after a cold treatment in spring 2010 (see Kollas et al. 2012 for further details). Immediately after germination, each seedling was replanted in a square container (14 cm wide \times 23 cm deep) containing three litres of the following substrate: 30% pumice stone, 20% bark compost, 20% quartz sand, 16% cocofibre, 10% turf and 4% clay. A fertiliser was applied in each pot in a slow release tablet form (Plantacote® Pluss 6M) containing all essential elements and the full range of trace elements needed for optimal growth (7.5 g containing 14%N, 9%P, 14%K, 2%MgO + trace elements). The alternative of using similarly reciprocal native soils or inocula was dismissed after mycorrhiza expert consultation. Such a treatment would have exerted uncontrolled bias (site \times provenance \times soil source interactions). About one week after repotting, seedlings were moved outside the greenhouse in order to acclimate them to cooler conditions. A total of 4442 containers were then brought to all common garden sites by trucks during the second week of June 2010 for the eastern region and during the fourth week of June 2010 for the western region.

Common garden sites and experimental design

Common gardens were established at 437, 1058, 1522 and 1708 m a.s.l. in the western region and at 606, 1002, 1251 and 1400 m a.s.l. in the eastern region (Table 2) within the two seed collection areas in the Swiss Alps. The western

common gardens were located near St Maurice, VS (46°12'48"N, 7°00'09"E) on a south-west facing slope, the eastern gardens were located near Haldenstein, GR (46°52'44"N, 9°31'32"E) on a south-east facing slope (Table 2). All common gardens were installed in open conditions. Each common garden was divided into three separate blocks, except the highest gardens in each of the two regions that consisted of only two blocks because fewer individuals were available (Online Resource 1). One block consisted of two plots 1.50 m \times 3 m each. Each block contained all species randomly distributed within the block with the four provenances (East Low, East High, West Low, and West High) randomly distributed within species' subplots. Within blocks, each provenance was represented by ten individuals corresponding to five mother trees sampled per population (called hereafter "family") and two replicate seedlings per family. The same systematic design was applied in each of the eight gardens. Thus, a maximum of 30 individual containers per seed provenance were grown in each common garden for all species (five families \times two replicates \times three blocks). Depending on the success of seed germination some provenances were represented by fewer individuals (see Online Resource 1). Each block was delimited by a wooden frame filled with a 10 cm sand layer separated from the underlying ground by a permeable plastic foil layer. The containers were placed on top of the sand layer with additional sand filling up the gaps between containers in order to insulate the root zones from short-term atmospheric temperature changes. A shade cloth (40-45 % reduction of incoming solar radiation) was in-

stalled in each garden at the beginning of the growing season in spring 2010 and 2011, after leaf emergence for all species in order to reduce evapotranspiration and full sun-exposure (seed beds are not commonly under full light in natural forest seedlings). A fence of 2 m height around the blocks prevented browsing of large herbivores. To avoid water limitation later in the season, plants were watered in all gardens maximally three times a week when the weather was hot and dry, by a local person assigned to each area during the growing season 2010 and 2011. Thus, we aimed to avoid any effects of limiting soil nutrient and water availability on tree phenology in order to focus on the effect of different temperatures induced by the elevational gradient. At the beginning of the second growing season, the slower-growing species *Fagus sylvatica* and *Sorbus aria* were moved to the southern side of each block to reduce shading effects from the other (taller) species. A few individuals died during the experiment (<3%) and a few were damaged by mice (<1%). Damaged or poorly growing individuals were not included in the analyses. Thus, an average of 531 individuals per common garden were included in statistical analyses (Online Resource 1). Throughout the paper, the term provenance is used to refer to individuals of a given species coming from seeds sampled at a specific elevation in a specific region (i.e. East Low, East High, West Low, and West High).

Meteorological data

Air temperature was recorded hourly in each common garden at 0.5 m above the ground using small data loggers (TidBit v2 UTBI-001, Onset computer corporation, Bourne, MA, USA) positioned under a white double-layered plastic shelter to prevent any exposure to rain or to direct sunlight. In early spring, data loggers in one common garden (Falera, 1251 m a.s.l in the eastern region) stopped working. In this common garden, early spring temperatures were thus interpolated using linear regression between hourly data of the closest common garden (Arella, 1002 m a.s.l, about 20 km distant) and data recorded in Falera during the period May-June ($R^2 > 0.92$). The temperature lapse rate in early spring (March-April) was about 0.49 K for every 100 m increase of elevation in

the western region and about 0.37 K in the eastern region (see Table 2). A late spring frost occurred at the highest gardens of both study regions in mid-April 2011 when leaves of the majority of species were unfolded (Online Resource 2). These events caused substantial frost damage only in *Fraxinus excelsior* (Online Resource 3).

Phenological observations

The timing of leaf emergence and bud set was monitored in all gardens in 2011. In spring 2011, each seedling was observed weekly by one observer assigned to each region to assess the timing of leaf unfolding. These observers were trained at the beginning of the growing season by one of the authors (YV) to minimize observer bias. The stage of the apical bud development was recorded using a categorical scale from 0 (no bud activity) to 4 (leaves out and flat). At stage 1, buds were swollen and/or elongating; at stage 2, buds were open and leaves were partially visible; at stage 3, leaves had fully emerged from the buds but were still folded, crinkled or pendant, depending on species; at stage 4, at least one leaf was fully unfolded. Species and provenance were compared using the average date when leaves of seedlings reached stage 3 which was estimated by linear interpolation when necessary (i.e. when this stage occurred in between two monitoring dates). Seedlings that suffered from severe frost damage occurring around the date of bud break were recorded. Furthermore, we examined each individual to assess the bud set, on 20th and 21st of July 2011 in the western region and on 26th and 27th of July 2011 in the eastern region. The apical bud was regarded as formed (score 1) when it was clearly visible in axils of the uppermost leaves. A score of 0 was attributed to seedlings continuing to produce new leaves or when no winter bud was visible.

Data analysis

Genetic differentiation in leaf phenology as well as its phenological plasticity to temperature between low and high provenances were tested using general linear model ANOVAs. For the date of leaf unfolding, the statistical model accounted for the following sources of variation:

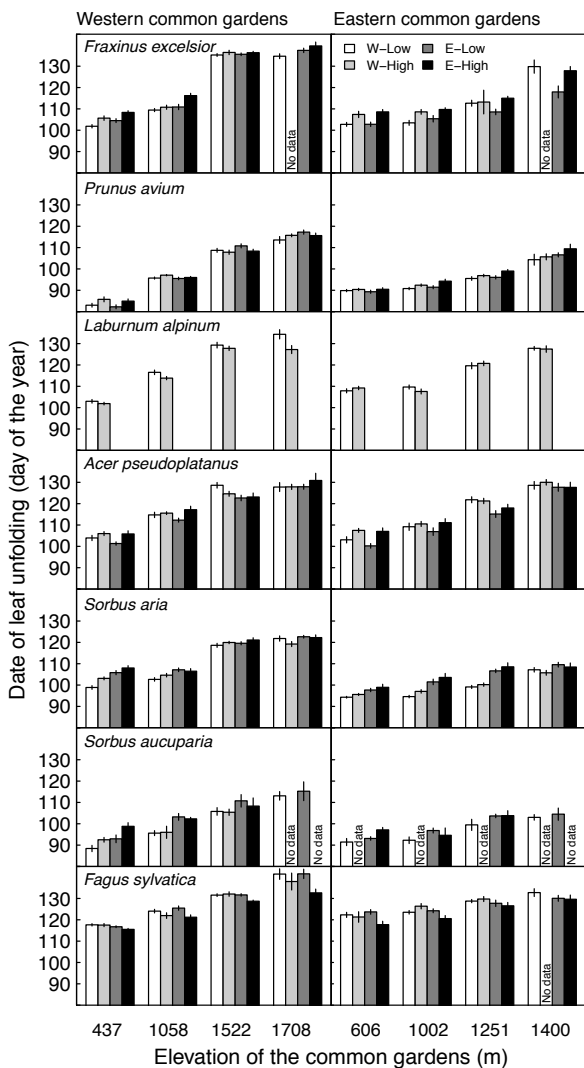


Figure 1: Average date of leaf unfolding for each provenances of the seven species examined in the eight common gardens established at different elevations. W-Low, populations from western part of Switzerland and low elevation; W-High, populations from western part of Switzerland and high elevation; E-Low, populations from eastern part of Switzerland and low elevation; E-High, populations from eastern part of Switzerland and high elevation.

the region of common gardens (West vs. East), the elevation of common gardens nested within the region of common gardens, the region of origin (West vs. East), the elevation of origin nested within the region of origin (Low vs. High), the interaction between the region of origin and the elevation of common gardens and the interaction between the elevation of origin and the elevation of common gardens. Although the region of origin could have been con-

sidered as random effect by nature, we decided to treat it as fixed effect due to the low number of factor levels (only two regions) which does not allow reliable estimation of the associated variance term when considered as random effect (Bolker et al. 2009). Additionally, the design did not allow the quantification of the seed family effect within provenance because the number of replicates per mother tree was too small and too variable among provenances and gardens to allow for a proper estimation of this effect. Because all the seedlings in each common garden shared the same soil conditions with no limitation in water availability and nutrients, we assumed that a significant main effect of the region or the elevation of common garden on phenology indicates temperature induced phenotypic plasticity (VE). Similarly, a significant interaction between the region or the elevation of origin and the elevation of the garden indicates that the magnitude of the phenological response is dependent on the origin of the population which is the result of genetically based phenotypic plasticity (VE \times VG). Here it is important to notice that we are considering plasticity at the population level, as an average across individuals from each provenance, rather than in the strict sense, i.e. at the genotype level. The budset score was analysed for each region of common gardens separately because the monitoring date was different in each region.

The data for spring phenology were examined for assumptions of homogeneity of variance and normal distribution and the binomial data (budset data) were examined for over-dispersion before carrying out the analyses and were found to conform to model requirements. Spring temperature was calculated for each species as the mean temperature from 30-day before the date of leaf unfolding of the earliest provenance to the leaf unfolding date of the latest provenance. Hence, this mean spring temperature differs among species according to their phenology. Linear regressions were used to assess the effect of spring temperature on timing of leaf unfolding for each provenance. These linear regressions represent the reaction norm of the leaf unfolding date of each provenance to temperature changes and allow to compare the phenological plasticity among provenances within species and among species.

Results

Leaf unfolding date

Phenological plasticity due to temperature (VE)

In both regions, leaf emergence was significantly delayed with increasing elevation of the common gardens for all species (Fig.1) with elevation explaining from 41% (*S. aucuparia*) to 86% (*P. avium*) of the total variance in leaf unfolding date (Table 3). Individuals located in the western gardens generally flushed later than those in the eastern gardens (Fig. 1, Table 3, P-value highly significant for all species except *F. sylvatica*). The region effect of gardens was principally due to the difference in elevation between the two highest common gardens of the two regions (290 m higher in the western region), that resulted in colder spring temperatures in the western gardens ($\Delta T=1.6$ K, calculated for T_{2-4} , see Table 2). The date of leaf unfolding occurred earlier with increasing temperatures (i.e. with decreasing elevation) and was linearly related to temperature across the eight gardens for all species (Fig. 2). However, the magnitude of the phenological plasticity (slopes of regression lines of unfolding date on temperature) dramatically differed among species. For example, *F. excelsior* and *P. avium* exhibited the highest plasticity in response to temperature changes with an average shift of -5.4 ± 0.4 days K^{-1} (slope value ± 1 SD) and -4.8 ± 0.2 days K^{-1} , whereas *F. sylvatica* showed the lowest plasticity with -2.6 ± 0.2 days K^{-1} (Table 4). The percentage of the total variance observed in leaf unfolding date due to environmental factors (both region and elevation effects) was 86% for *P. avium* and was more than 50% for all other species (Fig. 3).

Genetic differentiation among provenances (VG)

Overall, both the elevation and the region of origin had a significant effect on the timing of leaf unfolding for the majority of tree species, indicating a clear genetic differentiation between low and high provenances as well as between provenances from the western and the eastern part of the Swiss Alps (Table 3). In *A. pseudoplatanus*, *F. excelsior*, *P. avium* and *S. aria*,

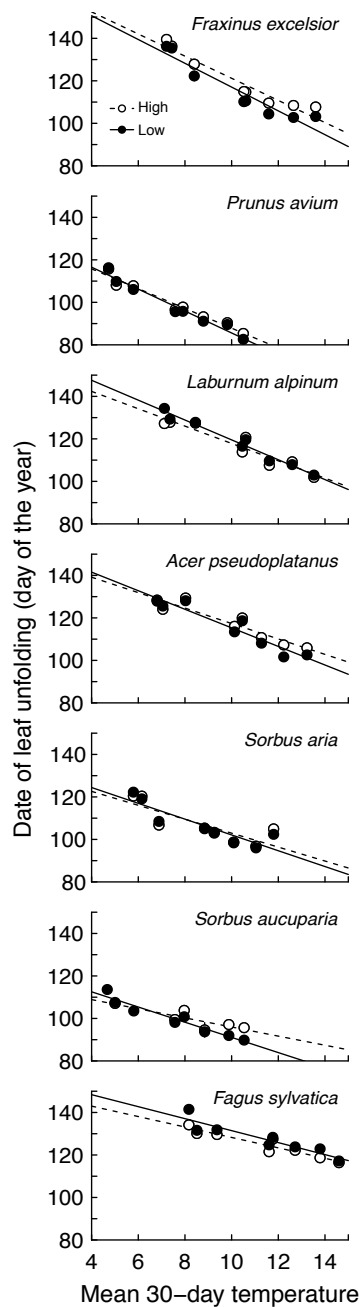


Figure 2: Relationship between mean 30-day air temperature recorded in the common gardens prior to the flushing period and leaf unfolding dates for low and high elevation provenances of the seven studied tree species. The leaf unfolding date corresponds to the mean of all individuals per common garden for low and high elevation provenances (both region of origin pooled) with standard errors and regression lines. For each species, the temperature corresponds to the mean air temperature during 30 days before the leaf unfolding date of the earliest provenance until the unfolding date of the latest provenance. Black circles and solid lines correspond to populations from low elevations; white circles and dashed lines correspond to populations from high elevations. All linear regressions were significant at the $p < 0.05$ level.

Table 2: Location, elevation, slope aspect, and temperatures that occurred before leaf flushing began for the eight common gardens.

Region (close city, exposure)	Site	Elevation (m)	Latitude	Longitude	T ₁	T ₂	T ₃	T ₄	T ₅	Spring onset
West (St-Maurice, SW)	Eslex	437	46°11'52"N	7°01'33"E	2.2	3.9	8.2	14.1	16.6	14 February
	Les Posses	1058	46°16'26"N	7°02'37"E	-0.5	2.4	5.1	11.1	13.7	5 March
	Rosseline	1522	46°12'55"N	7°02'37"E	-2.1	1.1	2.9	8.1	10.6	24 March
	Les Martinaux	1708	46°12'53"N	7°03'03"E	-1.6	0.7	2.7	7.6	10.5	25 March
East (Haldenstein, SE)	Böfel	606	46°52'18"N	9°31'06"E	1.2	2.7	7.5	13.4	15.8	21 February
	Arella	1002	46°52'25"N	9°30'31"E	0.6	2.9	6.7	12.7	14.3	25 February
	Falera	1251	46°48'14"N	9°14'23"E	-0.5	1.8	5.6	11.7	13.6	5 March
	Nesselboden	1400	46°52'09"N	9°29'24"E	-1.8	0.6	3.7	9.1	10.7	21 March

T₁, T₂, T₃, T₄, T₅, monthly mean temperature (°C) of January, February, March, April and May 2011.

¹Spring onset values were derived from linear regressions between monthly mean temperatures from January to May 2011 and time, as the date when the threshold of 5°C was reached. These values are used as a proxy for the elevational trends of the advance of spring phenology.

Table 3: ANOVA results for data of leaf unfolding for seedlings of the seven deciduous tree species planted in eight common gardens in two regions of the Swiss Alps

Source of variation	<i>Fraxinus.e.</i>		<i>Prunus.a.</i>		<i>Laburnum.a.</i>		<i>Acer.p.</i>		<i>Sorbus.ar.</i>		<i>Sorbus.au.</i>		<i>Fagus.s.</i>					
	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F				
<i>Environmental effects</i>																		
Region of gardens (R _g)	1	468.4***	1.2	1	273.2***	<0.1	1	39***	<0.1	1	955.1***	34.8	1	20.2***	<0.1	1	1.6	<0.1
Elevation of gardens (E _g)	6	376.6***	79.6	6	599.0***	86.1	6	215.1***	71.7	6	245.8***	41.4	6	38.5***	55.8	6	138.5***	61.7
Block	14	0.8	<0.1	14	1.1	<0.1	14	1.8*	0.7	14	1.3	0.2	14	0.7	<0.1	14	1.7*	1.0
<i>Genetic effects</i>																		
Region of origin (R _o)	1	10.7**	<0.1	1	3.4	<0.1	-	-	0.1	1	138.4***	5.9	1	25.5***	9.0	1	12.8***	<0.1
Elevation of origin (E _o)	2	35.1***	2.1	2	5.7**	0.3	1	11.4***	1.9	2	6.5**	0.3	2	0.1	<0.1	2	20.1***	3.5
<i>Environmental * genetic effects</i>																		
R _o x E _g	7	4.6***	1.3	7	1.6	<0.1	-	-	0.1	7	6.2***	1.6	7	0.6	<0.1	7	0.6	<0.1
E _o x E _g	12	1.9*	0.7	14	1.9*	0.5	7	2.3*	1.1	14	1.4	0.4	7	0.7	<0.1	13	1.9*	0.4
Residuals	612	-	15.8	699	-	13.6	322	-	18.4	560	-	15.9	173	-	35.2	552	-	33.7

All sources of variation were treated as fixed factors. The elevation of common garden (Eg) was treated as a factor nested in region of common gardens (Rg), elevation of origin (Eo) nested in region of origin (Ro) and block nested in common garden and region of common gardens. d.f., degree of freedom; F, F-values from Fisher test; VC, variance component. Level of significance: *** P < 0.001, ** P < 0.01, * P < 0.05, (*) P < 0.1.

populations originating from low elevations flushed significantly earlier than did populations originating from high elevations, especially in the lower common gardens. In addition, eastern provenances flushed slightly later than western provenances (Figs. 1 & 2). This region of origin effect was strongest in *S. aria*, explaining 6.2% of the total variance (Fig. 1 & Table 3). For *F. sylvatica* both the effect of elevation and region of origin were significant, but the genetic cline of differentiation was opposite to the other species, i.e. high elevation provenances or eastern provenances tended to flush earlier than those from low elevations or from the western region. In contrast, no genetic differentiation was found between low and high provenances for *S. aucuparia* and between eastern and western region of origin for *P. avium* (Table 3). The percentage of variance explained by genetic effects was smaller than the percentage of variance explained by environmental effects, accounting from 0.3 to 9% for *P. avium* and *S. aucuparia*, respectively. Interestingly, both *Sorbus* species exhibited strong phenological differentiation among provenances that accounted for more than 6% of the total variance (Fig. 3).

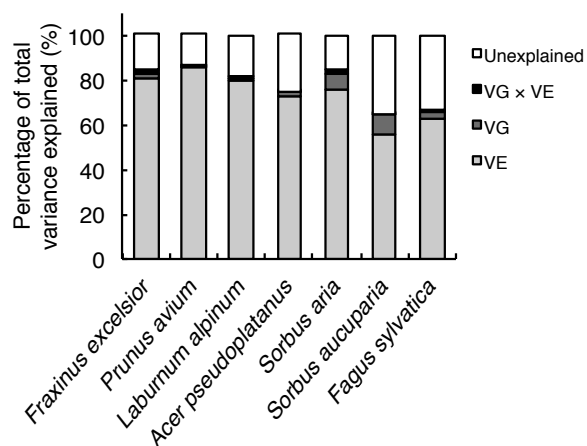


Figure 3: Contribution (expressed in percentage) of each genetic and environmental component explaining the variability of the leaf unfolding date observed across the common gardens. VE, proportion of the variance due to environmental factors; VG, proportion of the variance due to genetic effects; VE × VG, proportion of the variance due to the interaction between genetic and environmental effects. The proportions were directly extracted from the variance component analysis reported in Table 3.

Genetic differences in phenological plasticity (VG × VE)

A significant interaction in leaf unfolding date between the region of origin and the elevation of the gardens was only found for *F. excelsior* and *S. aria* (Table 3). For these two species, provenances from western Alps tended to have a greater plasticity to temperature than provenances from the eastern Alps (Fig. 1).

A significant interaction in leaf unfolding date between the elevation of provenances and the elevation of the gardens was found for four out of seven species, namely *F. sylvatica*, *F. excelsior*, *L. alpinum* and *P. avium* (Table 3). Within region of origin, populations from low elevations exhibited systematically greater plasticity of leaf unfolding date in response to temperature changes than populations from high elevations (Table 4 & Fig. 2). On average, the slope of the linear regressions between the leaf unfolding date and spring temperature was 0.59 0.10 days K⁻¹ greater for low provenances than for high provenances (paired t-test: $t = -5.73$, $P < 0.001$). However, within species no significant difference was found among provenances in their phenological shift to changing temperatures (tested by analysis of covariance: $p > 0.05$). The variance component due to interactions between environment (region or elevation of the gardens) and provenances (region or elevation of origin) was much smaller than VE and VG, reaching a maximum of only 2% for *S. aria* and *F. excelsior* (Fig. 3).

Budset timing

Plasticity due to environment (VE)

Within a region, elevation of gardens significantly affected bud formation in all species (Table 5, Fig. 4). Budset tended to occur later in gardens located at high elevation, irrespective of the provenance. This was particularly visible in the western gardens, where the two highest gardens were situated above 1500 m a.s.l (Fig. 4).

Genetic differentiation among provenances (VG)

All species except *L. alpinum* and *F. excelsior* exhibited genetic differentiation in the timing

of budset between provenances originating from low and high elevations (Table 5). Formation of apical buds tended to occur earlier for provenances originating from high elevations irrespective of the elevation of the garden (Fig. 4). This effect was quite strong for *A. pseudoplatanus* and both *Sorbus* species. No significant effect of the region of origin was detected in budset score, except for *P. avium* in the eastern gardens, where populations from the western region of origin tended to set buds earlier than populations from the eastern region of origin.

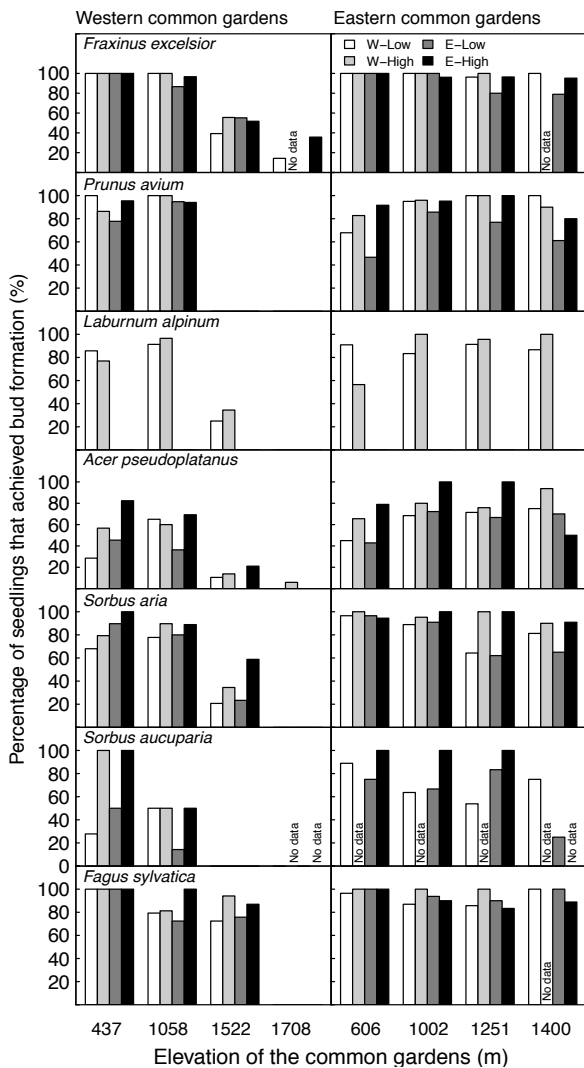


Figure 4: Contribution (expressed in percentage) of each genetic and environmental component explaining the variability of the leaf unfolding date observed across the common gardens. VE, proportion of the variance due to environmental factors; VG, proportion of the variance due to genetic effects; VE \times VG, proportion of the variance due to the interaction between genetic and environmental effects. The proportions were directly extracted from the variance component analysis reported in Table 3.

Genetic differences in phenological plasticity (VG \times VE)

Only few significant interactions between environmental and genetic effects were detected for budset score (Table 5). Interactions between elevation of origin and elevation of the gardens were detected in budset timing for *S. aucuparia* in the western gardens and for *L. alpinum* in the eastern gardens. An interaction between the region of origin and the elevation of the gardens was also detected in *S. aucuparia* in the western gardens. For all other species no significant interaction was found between environmental and genetic effects.

Discussion

The common gardens used in this study enabled the partitioning of environmental and genetic components responsible for tree seedling phenological patterns observed in situ. Furthermore, the experimental set-up allowed us to test exclusively the effect of temperature on tree seedling phenology as seedlings shared the same growth history and soils, and because they grew without water limitations and under standardized nutrient supply throughout the test period. Overall, our results showed that tree seedlings exhibited a strong phenological plasticity in their leaf unfolding date in response to temperature with substantial variation among species. Further, we demonstrated that the high elevation provenances exhibited smaller phenological plasticity, irrespective of the species and that phenological patterns along elevational gradients are, to a large extent, controlled by environmental conditions and to a much lesser extent by genetic differentiation among populations and interactions between these two drivers.

Plasticity of the leaf unfolding date (VE and VE \times VG)

This study highlighted high inter-specific variations in the degree of phenological plasticity to changing temperatures, and that climate (in essence temperature) is the main driver of phenological plasticity in tree seedlings in spring. The shifts of leaf unfolding date with elevation or spring temperature found here, were close to the ones found in situ on mature trees along

Table 3: Response of the date of leaf unfolding to mean 30-day temperature occurring before leaf unfolding for each provenance of the seven examined tree species (slope of the linear regressions, days $K^{-1} \pm 1$ SD). All slopes were significantly different from 0 ($P < 0.05$).

Provenance	W-Low	W-High	E-Low	E-High	Overall
<i>Fraxinus excelsior</i>	-6.0 ± 0.6	-5.0 ± 1.0	-5.4 ± 0.9	-5.1 ± 0.6	-5.4 ± 0.4
<i>Prunus avium</i>	-4.7 ± 0.3	-4.5 ± 0.4	-5.3 ± 0.4	-4.7 ± 0.4	-4.8 ± 0.2
<i>Laburnum alpinum</i>	-4.7 ± 0.3	-4.1 ± 0.5	-	-	-4.4 ± 0.3
<i>Acer pseudoplatanus</i>	-4.3 ± 0.6	-3.6 ± 0.6	-4.4 ± 0.6	-3.7 ± 0.5	-4.0 ± 0.3
<i>Sorbus aria</i>	-4.2 ± 0.8	-3.4 ± 0.9	-3.3 ± 0.8	-2.9 ± 0.9	-3.5 ± 0.4
<i>Sorbus aucuparia</i>	-3.6 ± 0.5	-	-3.5 ± 0.4	-2.1 ± 0.7	-3.0 ± 0.3
<i>Fagus sylvatica</i>	-2.9 ± 0.5	-2.6 ± 0.6	-2.7 ± 0.5	-2.4 ± 0.3	-2.6 ± 0.2

For each species, temperature corresponds to the mean 30-day temperature before the leaf unfolding date of the earliest provenance to the leaf unfolding date of the latest provenance. W-Low, provenance from western region and low elevation; W-High, western region and high elevation; E-Low, eastern region and low elevation; E-High, eastern region and high elevation.

temporal or spatial gradients in other mountain areas (Lebourgeois et al. 2010; Davi et al. 2011; Cufar et al. 2012). For example, Vitasse et al. (2009b) reported along elevational gradients in Pyrenees (France) a comparable shift of 1.9 days K^{-1} for *F. sylvatica*, 5.0 days K^{-1} for *A. pseudoplatanus* and 6.6 days K^{-1} for *F. excelsior* with a similar ranking among these species. Hence, our results suggest that, under continued global warming, tree species having high phenological plasticity in response to temperature (e.g. *F. excelsior* or *A. pseudoplatanus*) will likely respond to a greater extent than species with low phenological plasticity (e.g. *F. sylvatica* or *S. aucuparia*). Different responses of phenology to temperature change among species could ultimately affect their competitive abilities and elevational distributions. Species exhibiting the highest phenological plasticity might be temperature dependent only and at risk of frost damage, while species with low plasticity might have a dual control of bud burst by temperature and photoperiod and be less at risk to track unusual weather. The role of the photoperiod in modulating bud burst dates has been previously demonstrated in *F. sylvatica* growing under controlled conditions (Wareing 1953; Heide 1993; Caffarra and Donnelly 2011; Basler and Körner 2012). Accordingly, *F. sylvatica* exhibited the lowest phenological plasticity to temperature in this study, which might reflect a photoperiodically controlled delay of bud burst at the lowest elevation gardens. Interestingly and in line with our hypothesis, the genetic differentiation between low and high

provenances affects the magnitude of the plasticity, given that for all species low elevation provenances exhibited greater phenological plasticity than high elevation provenances to temperature changes induced by elevational gradients used for the experimental gardens. This pattern might have been induced either by a directional selection for reduced temperature sensitivity or a more stringent interaction with photoperiodism, which together may reduce the risk of damage by unpredictable late spring frost events after warm weather episodes. This interaction between provenance and environment has crucial implication for modelling future phenological responses of temperate tree species. Variation in responses to temperature among populations might reduce the predictive power and the transferability of phenological models when they are calibrated on genetically differentiated populations. Nevertheless, we found that the environmental component of the plasticity was far stronger than genetic effects, highlighting that phenotypic variations of leaf phenology observed in situ for tree seedlings are mainly the consequence of plasticity due to environmental variation rather than genetic effects. This is in line with the few studies that have adequately separated and quantified genetic and environmental contributions on leaf traits related to tree fitness (Kramer 1995; Baliuckas and Pliura 2003; Vitasse et al. 2010; Bresson et al. 2011). However, genetic differentiation among tree populations might be expected to be more pronounced along

Table 5: Results of ANOVAs of budset scores for seedlings of the seven deciduous tree species planted in eight common gardens in two regions of the Swiss Alps.

	<i>Fraxinus e.</i>		<i>Prunus a.</i>		<i>Laburnum a.</i>		<i>Acer p.</i>		<i>Sorbus ar.</i>		<i>Sorbus au.</i>		<i>Fagus s.</i>	
	d.f.	χ^2	d.f.	χ^2	d.f.	χ^2	d.f.	χ^2	d.f.	χ^2	d.f.	χ^2	d.f.	χ^2
Region West														
<i>Environmental effects</i>														
Elevation of gardens (E_g)	1	177.1***	1	207.8***	1	57.1***	1	47.6***	1	137.1***	1	31.0***	1	93.5***
Block	9	8.0	9	101.4***	9	47.0***	9	55.2***	9	88.4***	9	19.2*	9	84.4***
<i>Genetic effects</i>														
Region of origin (R_o)	1	<0.1	1	3.6 ^(*)	-	-	1	<0.1	1	3.8 ^(*)	1	0.1	1	0.2
Elevation of origin (E_o)	2	3.2 ^(*)	2	7.7*	1	0.3	2	16.0***	2	12.2**	2	8.9*	2	10.4**
<i>Environmental * genetic effects</i>														
$R_o \times E_g$	1	3.2	1	1.9	-	-	1	3.5 ^(*)	1	3.3 ^(*)	1	6.0*	1	0.2
$E_o \times E_g$	2	0.2	2	0.5	1	0.8	2	2.1	2	<0.1	2	7.5*	2	5.7 ^(*)
<i>Residuals</i>	312	-	269	-	159	-	283	-	351	-	99	-	316	-
Region East														
<i>Environmental effects</i>														
Elevation of gardens (E_g)	1	14.8***	1	8.5**	1	8.5**	1	9.3**	1	20.3***	1	3.1 ^(*)	1	4.1*
Block	9	5.8	9	30.7***	8	9.7	9	39.8***	9	22.9**	8	8.0	9	17.5*
<i>Genetic effects</i>														
Region of origin (R_o)	1	3.5 ^(*)	1	6.8**	-	-	1	0.5	1	2.3	1	0.8	1	<0.1
Elevation of origin (E_o)	2	5.7 ^(*)	2	19.5***	1	1.4	2	15.8***	2	21.6***	1	8.9*	2	5.3 ^(*)
<i>Environmental * genetic effects</i>														
$R_o \times E_g$	1	0.6	1	2.6	-	-	1	<0.1	1	<0.1	1	<0.1	1	1.8
$E_o \times E_g$	2	0.6	2	3.7	1	8.7**	2	0.8	2	2.7	1	<0.1	2	0.1
<i>Residuals</i>	306	-	294	-	120	-	274	-	331	-	60	-	228	-

All sources of variation were treated as fixed factors with binomial error distribution. The elevation of origin (E_o) nested in region of origin (R_o) and block nested in common garden. d.f., degree of freedom; χ^2 correspond to the difference in deviance. Level of significance: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, (*) $P < 0.1$.

latitudinal gradients than along elevational gradients, because of the greater distance between core and leading edge populations that could mitigate gene flow. Directional selection may therefore more easily lead to genetic differentiation along latitudinal gradients (Jump et al. 2009), which, on the other hand, would reduce the genetic potential of populations growing on their upper latitudinal to respond to ongoing climate warming.

Genetic differentiation in the leaf unfolding date between low and high provenances

Genetic differentiation among populations of tree seedlings can be due to differences in chilling and forcing requirement to break bud dormancy, or in their different sensitivity to photoperiod. For the majority of the species, our results showed that provenances from high elevations tended to flush later than provenances from low elevations, similarly to the phenotypic cline observed in-situ along elevational gradients (co-gradient variation). Although a genetic differentiation of the date of leaf unfolding was often found among provenances from different elevations in common garden experiments, the genetic cline can be opposite to the phenotypic cline observed along environmental gradients (counter-gradient variation). For example, seedling populations from high elevations were found to flush/sprout earlier than those from lower elevations in *Abies amabilis*, *Abies lasiocarpa*, *Pseudotsuga menziesii* and *Fagus sylvatica* (Worrall 1983; von Wuehlisch et al. 1995; Chmura and Rozkowski 2002; Acevedo-Rodriguez et al. 2006; Vitasse et al. 2009a; Gomory and Paule 2011), whereas they exhibited delayed flushing in *Prunus serotina*, *Fraxinus excelsior* and *Quercus petraea* (Barnett and Farmer 1980; Vitasse et al. 2009a; Alberto et al. 2011), or no significant difference in an array of species (Sharik and Barnes 1976; Vitasse et al. 2009a). These contrasting results demonstrate that species react differently but consistently to the evolutionary forces occurring along elevational gradients. The genetic clines occurring along environmental gradients have been generally thought as a consequence of divergent selection among populations due to either biotic or abiotic selection pressures. However, a recent

study suggested that interaction between gene flow and assortative mating occurring along strong environmental gradients may lead to such co-variation of genetic and phenotypic clines among populations, without any divergent selection (Soularue and Kremer 2012). Nevertheless, divergent selection may have shaped both co-gradient and counter-gradient variation among species co-existing along a same environmental gradient, depending on their sensitivity to a given selective pressure. In particular, along elevational gradients the balance between maximizing growth and minimizing the risk of frost damage might be a crucial evolutionary force leading to genetic differentiation in phenology between populations from low and high elevations. The short duration of the growing season at high elevations can be critical for the development of mature seeds and hardened tissues and buds for winter. Early flushing, thus, lengthens the period for growth, and subsequently increases competitive ability and the chance of producing mature seeds, while it simultaneously increases the risk of being exposed to late frosts that could damage flowers, leaves and meristem tissues. Thus, at the elevational limit of a species' range, two contrasting "strategies" might be selected for, possibly resulting in different clines among species co-existing along the same climatic gradient. In line with other studies, we found that genetic and phenotypic clines vary in opposite directions for seedlings of *F. sylvatica*, that is, seedlings from high elevations flushed earlier than those from low elevations when planted in a common garden (von Wuehlisch et al. 1995; Chmura and Rozkowski 2002; Vitasse et al. 2009a; Vitasse et al. 2010; Gomory and Paule 2011). Natural selection may have favoured individuals exhibiting earlier leaf unfolding at high elevation, suggesting that for this species developmental constraints restrict fitness more than the risk of frost damage does. However, because it was shown that significant genetic variation within populations can be preserved in traits under strong selective pressure (Howe et al. 2003), further investigations are needed to assess the genetic variation of phenological traits existing within populations along elevational gradients.

Environmental control of budset timing and genetic differentiation between low and high elevation provenances

Maturation of winter buds in late summer and rising frost hardiness in autumn must be initiated before occurrence of frosts and are therefore assumed to play a key role in tree fitness (Hurme et al. 1997; Charrier and Ameglio 2011). Until recently, photoperiod (detected by the phytochrome receptor) was thought to be the only environmental control that determines budset timing of the majority of temperate tree species (Tanino et al. 2010). Yet, recent experimental studies demonstrated that, under a same photoperiod, temperature has a modulating role on the endogenous program of summer/autumn phenology, with low temperatures advancing the onset of growth cessation in several deciduous tree species (Molmann et al. 2005; Tanino et al. 2010; Heide 2011; Rohde et al. 2011). Although the date of monitoring budset in this study was too late to detect and disentangle both environmental and genetic effects unambiguously, we found that, within the region of the gardens, the elevation of the gardens significantly affected bud formation in all species. Further, bud formation occurred later in the two highest elevation gardens, irrespective of provenances. Except for *L. alpinum* and *F. excelsior*, a genetic differentiation between low and high elevation provenances was found, with low elevation provenances tending to achieve bud set later than high elevation provenances. Among the few common garden experiments which investigated the time of growth cessation or budset with respect to the elevation of provenances, the same trend was reported for *F. sylvatica* (Chmura and Rozkowski 2002) and for two *Betula* species (Sharik and Barnes 1976). Genetic differentiation between low and high elevation provenances is likely the result of directional selection favouring individuals having earlier bud set and leaf senescence at high elevation, and thus, higher freezing tolerance in early autumn (Charrier and Ameglio 2011).

Conclusions

The ability of populations to thrive under contrasting climates depends on their genetic differentiation across climatic gradients and the ge-

netic variation within populations (Aitken et al. 2008; Wang et al. 2010). In agreement with our first hypothesis, this study demonstrated that seedlings from tree populations growing at their upper elevational limits exhibit genetic adaptation in leaf phenology. Directional selection seems to operate in spite of the short distance among populations along elevational gradients and a presumably abundant gene flow across such gradients (Alberto et al. 2010). Our results also underlined that seedlings of tree populations in the Alps have high phenological plasticity in response to temperature changes, with substantial inter-specific differences. Interestingly, seedlings from high elevation provenances exhibited a lower phenological plasticity to temperature than those from low elevation provenances. Due to the large environmental effect and the small genetic effect on leaf unfolding date, our results suggest that seedlings of both populations of deciduous tree species growing at the upper elevation margin and lower elevation-populations have a high phenological plasticity to track ongoing climate change. Seedlings are known to exhibit more opportunistic phenology than adult trees, given that their success is not only constrained by a short thermal season, but also by canopy closure, and thus light limitation (Augspurger 2008). Hence the dominance of phenotypic over genotypic responses (in the sense of tracking concurrent temperatures) might be seedling specific. We thus expect genotypic responses to be more pronounced in the adult life stage.

Acknowledgements

We are grateful to Serge Ricciardelli and Roger Frei for their assistance in the field for monitoring spring phenology. We wish to thank Fernando Koostella, Snorri Örn Rafnsson, Lea Steinle, Pascale Flury, Martin Trischler and José Monteiro for their help in the construction and maintenance of the common gardens. We are also grateful to the Swiss Army for logistic help to move the containers to all common gardens, as well as the municipality of Bex, Lavey-Morcles and Haldenstein and the local foresters for their great support. The research leading to these results has been funded by the European Research Council (ERC) grant 233399 (project

TREELIM). We are grateful to two anonymous reviewers for their valuable comments improving a previous version of the manuscript.

References

- Acevedo-Rodriguez R, Vargas-Hernandez JJ, Lopez-Upton J, Mendoza JV (2006) Effect of geographic origin and nutrition on shoot phenology of Mexican Douglas-Fir (*Pseudotsuga* sp.) seedlings. *Agrociencia* 40:125-137
- Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1:95-111 doi: 10.1111/J.1752-4571.2007.00013.X
- Alberto F, Bouffier L, Louvet JM, Lamy JB, Delzon S, Kremer A (2011) Adaptive responses for seed and leaf phenology in natural populations of sessile oak along an altitudinal gradient. *Journal of Evolutionary Biology* 24:1442-1454 doi: 10.1111/j.1420-9101.2011.02277.x
- Alberto F, Niort J, Derory J, Lepais O, Vitalis R, Galop D, Kremer A (2010) Population differentiation of sessile oak at the altitudinal front of migration in the French Pyrenees. *Molecular Ecology* 19:2626-2639 doi: 10.1111/j.1365-294X.2010.04631.x
- Augsburger CK (2008) Early spring leaf out enhances growth and survival of saplings in a temperate deciduous forest. *Oecologia* 156:281-286 doi: 10.1007/s00442-008-1000-7
- Baliuckas V, Lagerstrom T, Norell L, Ersson G (2005) Genetic variation among and within Populations in Swedish species of *Sorbus aucuparia* L. and *Prunus padus* L. assessed in a nursery trial. *Silvae Genetica* 54:1-8
- Baliuckas V, Pliura A (2003) Genetic variation and phenotypic plasticity of *Quercus robur* populations and open-pollinated families in Lithuania. *Scandinavian Journal of Forest Research* 18:305-319 doi: 10.1080/02827580310005153
- Barnett PE, Farmer RE, Jr. (1980) Altitudinal variation in juvenile characteristics of southern Appalachian black cherry (*Prunus serotina* Ehrh.). *Silvae Genetica* 29:157-160
- Basler D, Körner C (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology*, in press doi: 10.1016/j.agrformet.2012.06.001
- Billington HL, Pelham J (1991) genetic-variation in the date of budburst in scottish birch populations - implications for climate change. *Functional Ecology* 5:403-409
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127-135 doi: 10.1016/j.tree.2008.10.008
- Bresson CC, Vitasse Y, Kremer A, Delzon S (2011) To what extent is altitudinal variation of functional traits driven by genetic adaptation in European oak and beech? *Tree Physiology* 31:1164-1174 doi: 10.1093/treephys/tpr084
- Broadhead JS, Ong CK, Black CR (2003) Tree phenology and water availability in semi-arid agroforestry systems. *Forest Ecology and Management* 180:61-73 doi 10.1016/S0378-1127(02)00602-3
- Caffarra A, Donnelly A (2011) The ecological significance of phenology in four different tree species: effects of light and temperature on bud burst. *International Journal of Biometeorology* 55:711-721 doi: 10.1007/s00484-010-0386-1
- Charrier G, Ameglio T (2011) The timing of leaf fall affects cold acclimation by interactions with air temperature through water and carbohydrate contents. *Environmental and Experimental Botany* 72:351-357 doi: 10.1016/j.envexpbot.2010.12.019
- Chmura DJ, Rozkowski R (2002) Variability of beech provenances in spring and autumn phenology. *Silvae Genetica* 51:123-127
- Chuine I (2010) Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B-Biological Sciences* 365:3149-3160 doi: 10.1098/rstb.2010.0142
- Cufar K, De Luis M, Saz MA, Crepinsek Z, Kajfez-Bogataj L (2012) Temporal shifts in leaf phenology of beech (*Fagus sylvatica*) depend on elevation. *Trees-Struct Funct* doi: 10.1007/s00468-012-0686-7
- Davi H, Gillmann T, Cailleret M, Bontemps A, Fady B, Lefèvre F (2011) Diversity of leaf unfolding dynamics among tree species: New insights from a study along an altitudinal gradient. *Agricultural and Forest Meteorology* 151:1504-1513 doi: 10.1016/J.Agrformet.2011.06.008
- Doi H, Takahashi M, Katano I (2010) Genetic diversity increases regional variation in phenological dates in response to climate change. *Global Change Biology* 16:373-379 doi: 10.1111/j.1365-2486.2009.01993.x
- Gomory D, Paule L (2011) Trade-off between height growth and spring flushing in common beech (*Fagus sylvatica* L.). *Annals of Forest Science* 68:975-984 doi: 10.1007/s13595-011-0103-1
- Heide OM (1993) Dormancy Release in Beech Buds (*Fagus-Sylvatica*) Requires Both Chilling and Long Days. *Physiologia Plantarum* 89:187-191
- Heide OM (2011) Temperature rather than photoperiod controls growth cessation and dormancy in *Sorbus* species. *Journal of Experimental Botany* doi: 10.1093/jxb/err213
- Hoffmann AA, Sgro CM (2011) Climate change and evolutionary adaptation. *Nature* 470:479-485 doi: 10.1038/nature09670
- Howe GT, Aitken SN, Neale DB, Jermstad KD, Wheeler NC, Chen THH (2003) From genotype to phenotype: unraveling the complexities of cold

- adaptation in forest trees. *Canadian Journal of Botany-Revue Canadienne De Botanique* 81:1247-1266 doi: 10.1139/B03-141
- Howe GT, Saruul P, Davis J, Chen THH (2000) Quantitative genetics of bud phenology, frost damage, and winter survival in an F-2 family of hybrid poplars. *Theoretical and Applied Genetics* 101:632-642
- Hurme P, Repo T, Savolainen O, Paakkonen T (1997) Climatic adaptation of bud set and frost hardiness in Scots pine (*Pinus sylvestris*). *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 27:716-723
- Jump AS, Matyas C, Penuelas J (2009) The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology & Evolution* 24:694-701 doi: 10.1016/j.tree.2009.06.007
- Kollas C, Vitasse Y, Randin CF, Hoch G, Körner C (2012) Unrestricted quality of seeds in European broad-leaved tree species growing at the cold boundary of their distribution. *Annals of Botany* 109:473-480 doi: 10.1093/aob/mcr299
- Körner C (2000) Why are there global gradients in species richness? Mountains might hold the answer. *Trends in Ecology & Evolution* 15:513-514 doi: 10.1016/s0169-5347(00)02004-8
- Kramer K (1995) Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warming. *Plant, Cell and Environment* 18:93-104
- Kremer A, Ronce O, Robledo-Arnuncio JJ, Guillaume F, Bohrer G, Nathan R, Bridle JR, Gomulkiewicz R, Klein EK, Ritland K, Kuparinen A, Gerber S, Schueler S (2012) Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology Letters* 15:378-392 doi: 10.1111/j.1461-0248.2012.01746.x
- Langlet O (1971) Two hundred years genecology. *Taxon* 20:653-722
- Lebourgeois F, Pierrat JC, Perez V, Piedallu C, Cecchini S, Ulrich E (2010) Simulating phenological shifts in French temperate forests under two climatic change scenarios and four driving global circulation models. *International Journal of Biometeorology* 54:563-581 doi: 10.1007/s00484-010-0305-5
- Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolstrom M, Lexer MJ, Marchetti M (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management* 259:698-709 doi: 10.1016/j.foreco.2009.09.023
- Molmann JA, Asante DKA, Jensen JB, Krane MN, Ernstsens A, Junttila O, Olsen JE (2005) Low night temperature and inhibition of gibberellin biosynthesis override phytochrome action and induce bud set and cold acclimation, but not dormancy in PHYA overexpressors and wild-type of hybrid aspen. *Plant Cell and Environment* 28:1579-1588 doi: 10.1111/j.1365-3040.2005.01395.x
- Morgenstern EK (1996) Geographic Variation in Forest Trees: Genetic Basis and Application of Knowledge in Silviculture. UBC Press, Vancouver
- Oleksyn J, Modrzyński J, Tjoelker MG, Zytkowski R, Reich PB, Karolewski P (1998) Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. *Functional Ecology* 12:573-590
- Pigliucci M, Murren CJ, Schlichting CD (2006) Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology* 209:2362-2367 doi: 10.1242/jeb.02070
- Polgar CA, Primack RB (2011) Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist* 191:926-941 doi: 10.1111/j.1469-8137.2011.03803.x
- Premoli AC, Raffaele E, Mathiasen P (2007) Morphological and phenological differences in *Nothofagus pumilio* from contrasting elevations: Evidence from a common garden. *Austral Ecology* 32:515-523 doi: 10.1111/j.1442-9993.2007.01720.x
- Rehfeldt GE, Tchebakova NM, Parfenova YI, Wykoff WR, Kuzmina NA, Milyutin LI (2002) Intraspecific responses to climate in *Pinus sylvestris*. *Global Change Biology* 8:912-929
- Rohde A, Bastien C, Boerjan W (2011) Temperature signals contribute to the timing of photoperiodic growth cessation and bud set in poplar. *Tree Physiology* 31:472-482 doi: 10.1093/treephys/tpr038
- Savolainen O, Pyhajarvi T, Knurr T (2007) Gene flow and local adaptation in trees. *Annual Review of Ecology Evolution and Systematics* 38:595-619 doi: 10.1146/annurev.ecolsys.38.091206.095646
- Schlichting CD (1986) The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics* 17:667-693 doi: 10.1146/annurev.ecolsys.17.1.667
- Schlichting CD, Pigliucci M (1993) Control of phenotypic plasticity via regulatory genes. *American Naturalist* 142:366-370
- Sharik TL, Barnes BV (1976) Phenology of shoot growth among diverse populations of yellow birch (*Betula alleghaniensis*) and sweet birch (*B. lenta*). *Canadian Journal of Botany* 54:2122-2129
- Soularie J-P, Kremer A (2012) Assortative mating and gene flow generate clinal phenological variation in trees. *BMC Evolutionary Biology* 12:79 doi: 10.1186/1471-2148-12-79
- Tanino KK, Kalcsits L, Silim S, Kendall E, Gray GR (2010) Temperature-driven plasticity in growth cessation and dormancy development in deciduous woody plants: a working hypothesis suggesting how molecular and cellular function is affected by temperature during dormancy induction. *Plant Molecular Biology* 73:49-65 doi: 10.1007/s11103-010-9610-y

- Thompson JD (1991) Phenotypic plasticity as a component of evolutionary change. *Trends in Ecology & Evolution* 6:246-249 doi: 10.1016/0169-5347(91)90070-e
- Tikkanen OP, Julkunen-Tiitto R (2003) Phenological variation as protection against defoliating insects: the case of *Quercus robur* and *Operophtera brumata*. *Oecologia* 136:244-251 doi: 10.1007/S00442-003-1267-7
- van Asch M, Visser ME (2007) Phenology of forest caterpillars and their host trees: The importance of synchrony. *Annual Review of Entomology* 52:37-55 doi: 10.1146/annurev.ento.52.110405.091418
- Vitasse Y, Bresson CC, Kremer A, Michalet R, Delzon S (2010) Quantifying phenological plasticity to temperature in two temperate tree species. *Functional Ecology* 24:1211-1218 doi: 10.1111/j.1365-2435.2010.01748.x
- Vitasse Y, Delzon S, Bresson CC, Michalet R, Kremer A (2009a) Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière* 39:1259-1269 doi: 10.1139/X09-054
- Vitasse Y, Delzon S, Dufrene E, Pontailier JY, Louvet JM, Kremer A, Michalet R (2009b) Leaf phenology sensitivity to temperature in European trees: do within-species populations exhibit similar responses? *Agricultural and Forest Meteorology* 149:735-744 doi: 10.1016/j.agrformet.2008.10.019
- Vitasse, Y., Hoch, G., Randin, C.F., Lenz, A., Kollas, C., Körner, C. (2012) Tree recruitment of European tree species at their current upper elevational limits in the Swiss Alps. *Journal of Biogeography* doi: 10.1111/j.1365-2699.2012.02697.x.
- vonWuehlisch G, Krusche D, Muhs HJ (1995) Variation in temperature sum requirement for flushing of beech provenances. *Silvae Genetica* 44:343-346
- Wang TL, O'Neill GA, Aitken SN (2010) Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecological Applications* 20:153-163 doi: 10.1890/08-2257.1
- Wareing PF (1953) Growth studies in woody species. V. Photoperiodism in dormant buds of *Fagus sylvatica*. *Physiologia Plantarum* 6:692-706
- Wesolowski T, Rowinski P (2008) Late leaf development in pedunculate oak (*Quercus robur*): An antiherbivore defence? *Scandinavian Journal of Forest Research* 23:386-394 doi: 10.1080/02827580802419026
- Willi Y, Van Buskirk J, Schmid B, Fischer M (2007) Genetic isolation of fragmented populations is exacerbated by drift and selection. *Journal of Evolutionary Biology* 20:534-542 doi: 10.1111/j.1420-9101.2006.01263.x
- Williams JL, Auge H, Maron JL (2008) Different gardens, different results: native and introduced populations exhibit contrasting phenotypes across common gardens. *Oecologia* 157:239-248 doi: 10.1007/s00442-008-1075-1
- Worrall J (1983) Temperature - bud-burst relationships in amabilis and subalpine fir provenance tests replicated at different elevations. *Silvae Genetica* 32:203-209

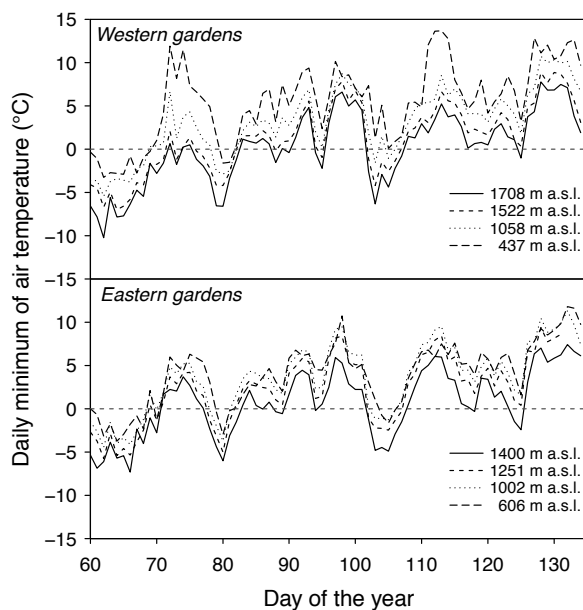
Supplementary material

S1: Numbers of individuals per provenance and common garden used for analysis of phenology.

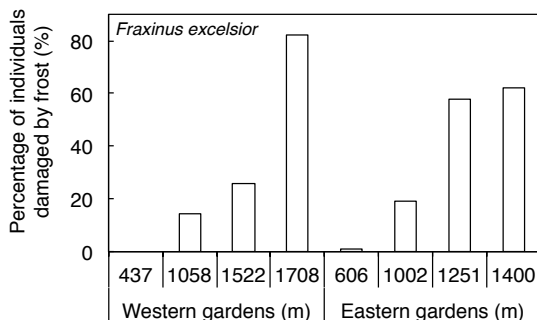
Elevation (m)	<i>Acer pseudoplatanus</i>				<i>Fagus sylvatica</i>				<i>Fraxinus excelsior</i>				<i>Laburnum alpinum</i>		<i>Prunus avium</i>				<i>Sorbus aria</i>				<i>Sorbus aucuparia</i>							
	WL	WH	EL	EH	WL	WH	EL	EH	WL	WH	EL	EH	WL	WH	WL	WH	EL	EH	WL	WH	EL	EH	WL	WH	EL	EH	WL	WH	EL	EH
Region West																														
437	21	30	22	17	30	18	30	24	28	9	29	28	24	26	28	28	29	24	29	30	30	18	18	5	8	5				
1058	20	30	22	13	30	17	29	23	27	9	30	30	24	30	25	26	22	18	27	30	30	18	18	5	9	4				
1522	21	30	22	19	29	17	33	24	28	9	29	30	24	29	27	28	30	23	29	30	30	18	18	5	10	7				
1708	8	20	11	4	20	11	15	17	16	-	20	20	16	20	8	19	20	20	16	20	20	12	12	-	4	-				
Region East																														
606	21	29	21	19	29	8	21	22	28	5	30	29	24	24	28	30	30	24	29	30	30	18	13	-	6	5				
1002	20	27	18	16	23	8	17	20	26	5	26	26	24	23	28	30	30	23	18	25	22	7	13	-	6	5				
1251	21	29	19	18	28	8	21	21	28	5	30	29	24	24	27	27	27	20	29	30	30	18	13	-	6	5				
1400	8	16	10	6	12	-	6	10	15	-	20	23	16	12	6	12	20	16	16	20	20	12	8	-	4	-				

WL, populations from western part of Switzerland and low elevation; WH, populations from western part of Switzerland and high elevation; EL, populations from eastern part of Switzerland and low elevation; EH, populations from eastern part of Switzerland and high elevation.

S2: Daily minimum temperature recorded at seedlings height in spring at the four common gardens in each region. Note that a late frost event occurred in mid April in both regions.



S3: Percentage of individuals of *Fraxinus excelsior* damaged by the late frost event occurring in mid April (see Online Resource 2) for every common garden (represented by their elevation). All individuals were pooled in each garden irrespective of provenances, as no difference was found among provenances.



Curriculum Vitae

Name: Chris Kollas

Date and place of birth: 13. July 1979, Berlin, Germany

Nationality: German

Contact details: Section of Plant Ecology, Institute of Botany, University of Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland; Email: Chris.Kollas@unibas.ch; Phone: +41 (0)612673506; Cell phone: +41 (0)774123793; Fax: +41 (0)612673504

Education

1986–1991 Primary schools in Berlin, Augsburg and Eisenhüttenstadt, Germany

1992–1999 Secondary school, Albert-Schweitzer Gymnasium Eisenhüttenstadt, Germany

1999–2000 Military service & Alternative civilian service, Osterode & Eisenhüttenstadt, Germany

2000–2007 Magister Artium in Geography & Computer Science, Berlin, Germany

2004–2005 Studies in Geography, Mendoza, Argentine

Magister Artium thesis:

«Klimafolgenforschung in Brandenburgs Forst - Regionalstudie zu angepassten Waldbausystemen im Forstrevier Schönholz» (Climate Impact Research in the forest of Brandenburg - regional study on adapted scenarios of forest management) Supervision: Prof. W. Cramer and Prof. W. Endlicher

since 2009 PhD candidate at the Botanical Institute, University of Basel, Switzerland.

Title of the ERC-funded Project: «TREELIM - A functional explanation of low temperature tree species limits» Doctoral supervisor: Prof. Dr. Christian Körner

Publications included in the thesis

Kollas C, Randin C, Körner Ch: Critical temperatures determining the elevational and latitudinal range limits of European broad-leaved trees. *in prep. for Journal of Biogeography*

Kollas C, Randin C, Vitasse Y, Körner Ch: How accurate can weather stations predict temperatures at tree species limits? *submitted to Agricultural and Forest Meteorology*

Randin C, Paulsen J, Vitasse Y, **Kollas C**, Wohlgemuth T, Zimmermann N, Körner Ch: Do elevational limits of deciduous tree species match with their thermal latitudinal limits? *Global Ecology and Biogeography, in press*

Kollas C, Vitasse Y, Randin C, Hoch G, Körner Ch 2012: Unrestricted quality of seeds in European broad-leaved tree species growing at the cold boundary of their distribution. *Annals of Botany* 109: 473-480

Vitasse Y, Hoch G, Randin CF, Lenz A, **Kollas C**, Körner Ch 2012: Tree recruitment of European tree species at their current elevational limits in the Alps. *Journal of Biogeography* 39:1439-1449

Publications not included in the thesis

Kollas C, Lasch P, Suckow F, Rock J 2009: Bioenergy potential in Germany – assessing spatial pattern of biomass production with aspen short-rotation coppice. *International Agrophysics* 23:343-352

Lasch P, **Kollas C**, Rock J, Suckow F 2009: Potentials and Impacts of Short Rotation Coppice Plantation with Aspen in Eastern Germany under Climate Change. *Regional Climate Change* 10:83-94

Rock J, Lasch P, **Kollas C** 2009: Auswirkungen von absehbarem Klimawandel auf Kurzumtriebsplantagen. In: *Anbau und Nutzulandwirtschaftlichen Flächen*. Wiley 2009.

Teaching experience

2005-2007 Teacher for the formation of young adults *German language and Mathematics*, weekly, Internationaler Bund, Berlin, Germany

2008 Teacher for first-year undergraduate course *Tree growth modelling*, 1 day, Fachhochschule Eberswalde, Germany

2011 Assistent for Blockkurs *Ökologie – Teil Pflanzenökologie, Dendrology*, 1 week, Ch. Körner i.a., Botanical Institute, University of Basel, Switzerland, Field location: Rueun, Switzerland

2011 Assistent for lecture in statistics *Introduction to statistical software R*, 1 week, S. Leuzinger, Eidgenössische Technische Hochschule (ETH), Zürich, Switzerland

2012 Assistent for Blockkurs *Ökologie – Teil Pflanzenökologie, Plant water relations and Infrared Thermometry*, 1 week, Ch. Körner i.a., Botanical Institute, University of Basel, Switzerland, Field location: Torgon, Switzerland

2012 Two-hour lecture *Functional explanations of low temperature tree species limit* with Y. Vitasse and A. Lenz, Botanical Institute, University of Basel, Switzerland

Conferences attended during the thesis

(with authors and title of contribution)

GMBA-DIVERSITAS meeting, Chandolin, Switzerland, July 2010. Without contribution.

EXTREMES 2010: International Workshop in Recent Achievements on the Study of Extreme Events, Potsdam, Germany, September 2010. Without contribution.

12th Congress of the European Ecological Federation, Avila, Spain, September 2011.

Kollas C, Vitasse Y, Randin CF, Hoch G., Körner CH. *Seed quality of European broad-leaved tree species does not decrease towards their upper elevational distribution limits*. Poster.

GfÖ Jahrestagung, Lüneburg, Germany, September 2012.

Kollas C, Randin CF, Vitasse Y, Körner Ch. *How accurate can weather stations predict temperatures at tree species limits?* Poster.